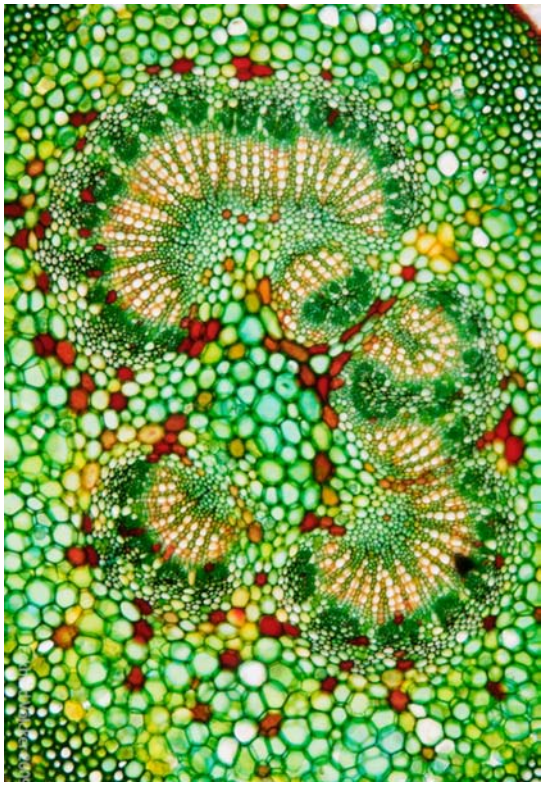
Chapter 3

The Plant Cell and the Cell Cycle



KEY CONCEPTS

1. Every plant is constructed from small compartments called cells. Each cell is a living individual, possessing the basic characteristics of life, including movement, metabolism, and the ability to reproduce. Some cells in a plant develop specialized capabilities that contribute to the life of the whole organism.

2. Plant cells contain organelles with specialized functions. The nucleus, ribosomes, and endomembrane system participate in the synthesis of proteins; the plastids and mitochondria capture and convert energy into useful forms; the cytoskeleton directs the movement of other components around the cell. Learning the anatomy of a cell helps one understand its activities.

3. Cells reproduce by dividing. Cell division is the most complicated process that any cell can undergo. Specific genes and proteins cooperate to regulate the timing of the events in cell division.

3.1 CELLS AND MICROSCOPY

Cells Are the Basic Units of Plant Structure and Function

In the late 1600s, an English experimentalist named Robert Hooke used his improved version of a microscope to look at shavings of cork tissue (the dead outer bark of an oak tree). He described "little boxes or cells distinct from one another…that perfectly enclosed air." Later, Nehemiah Grew, an English clergyman, recognized that leaves were formed from collections of cells filled not with air, but with fluid and green inclusions (Fig. 3.1). It took many years for the ubiquity of cells to be realized, but in 1838 the Belgian botanist Matthias Schleiden and zoologist Theodor Schwann proposed that all plants and animals are composed of cells. Later, in 1858, Rudolf Virchow suggested that cells possess a characteristic of life ascribed by

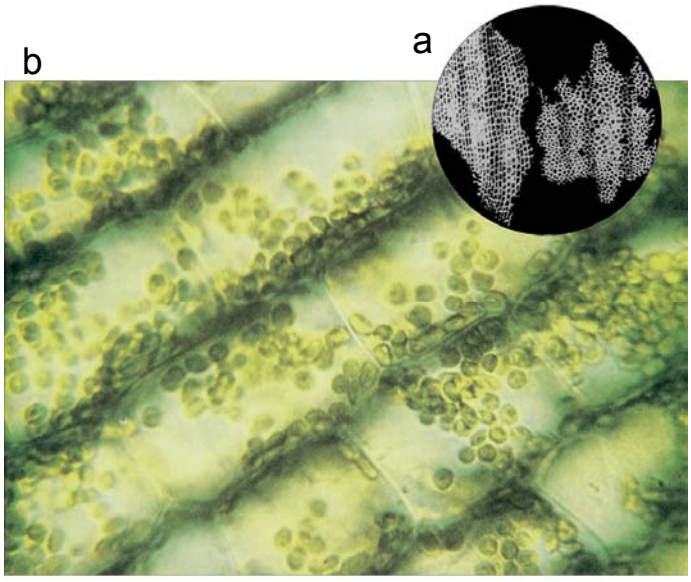


Figure 3.1. Plant cells through the microscope. (**a**) A drawing of cell walls from the cork tissue of an oak (*Quercus* sp.) tree, published in 1665 by Robert Hook in his *Micrographia*. (**b**) A light micrograph of leaf tissue from the aquatic plant *Elodea*, showing how the tissue is divided into cells.

earlier observers only to organisms--that is, cells reproduce themselves, and all cells arise by reproduction from previous cells. This set of propositions, now known as the cell theory, is one of the key principles of biology.

Almost all cells have certain similarities in structure, because they share the same activities and the same problems. Most cells grow--that is, they get larger, and they divide to form new cells. In mature plants, many cells stop growing, but even these continue to synthesize new components. All these cells must accumulate chemicals that they need for the synthesis of new components. They must find sources of energy that promote the chemical reactions needed for synthesis. They must store and interpret the genetic instructions that direct the synthesis of these components at the right times and places. They must get rid of worn-out components and exclude toxins from sensitive reactions. Cells must control their own size, which means controlling the amount of water that moves into or out of them. All these functions are important to all cells, those of Archaea, Bacteria, animals, and protests, as well as plants. But these various types of organisms do differ somewhat in their cell structures. Archaea and bacteria (prokaryotes), for instance, have cells that appear simpler than those of animals, fungi, protests, and plants (eukaryotes). Prokaryotes are important in the evolution and ecology of plants, and their cells are described in Chapter 19. This chapter focuses on plant cells, their structures, and their methods of carrying out essential functions.

With few exceptions, each cell in the plant body plays a role in the health and activities of the whole plant. To be effective, some cells have specialized structures or chemicals. Certain cells are specialized for rapid growth and cell division. Other cells hcave a protective function. Cells on the outer layer of a stem, for instance, secrete water-impermeable chemicals, such as waxes; these keep water vapor from diffusing out of the plant, thus keeping the interior moist. Still other cells have a structural role, such as stiffening large organs so that they can support their own weight. Some cells are responsible for the transport of compounds from one part of the plant to another. Certain cells play key roles in sexual reproduction. In each case, the cell forms specialized structures that allow it to accomplish its mission in the life of the plant.

The specialized structures within cells are called organelles ("little organs," by analogy with the organs contained in the body of a multicellular organism). These are associated with some of the general and specialized functions that the cells must perform. The next section explains one of the most effective methods for studying organelles.

Microscopes Allow One to See Small, Otherwise Invisible Objects

Plant cells have been studied with a light microscope ever since Robert Hooke looked at cork. In fact, the development of the microscope was the technical breakthrough that led to the discovery of cells, and improvements in microscopy continue to contribute to our understanding of cell structure and function. Light microscopes use lenses, which bend light rays so that the object looks larger (Fig. 3.2). With a good compound microscope (one that has many lenses arranged in series), you can easily see cells that are 20 to 200 micrometers (μm) in diameter, and you should be able to see components as small as 1 μm in diameter (1 μm is 10^{-6} meter or one millionth of a meter or about four hundred thousandths of an inch)(Fig. 3.2c)

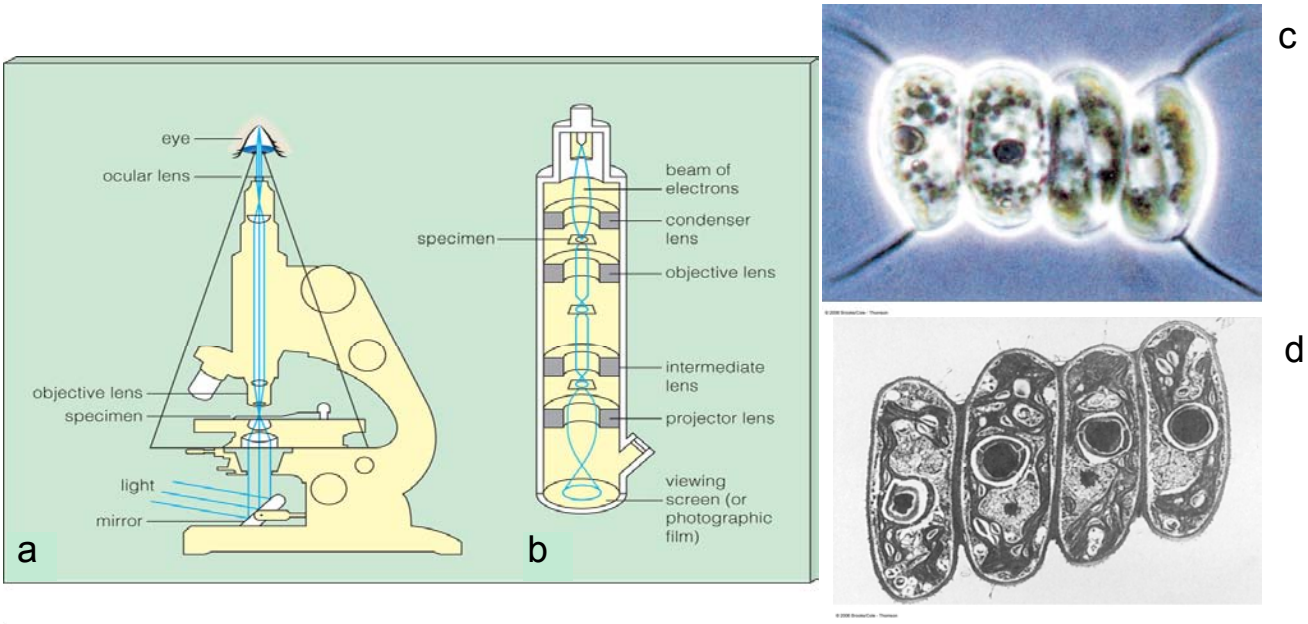


Figure 3.2. A comparison of the light microscope (**a**), the transmission electron microscope (**b**), and the images they produce, (**c**) and (**d**), respectively. A light or electron beam is focused on the sample with glass or magnetic lenses, respectively. From each part of the sample the beam radiates toward the objective lens, forming a larger image on the other side. A series of lenses remagnifies this image, which eventually is focused on the eye (light microscope) or a photographic film (electron microscope). Both micrographs show the same organism--the green alga *Scenedesmus*--at the same size. Notice that the electron micrograph (**d**) has the better resolution, but is black and white; only light micrographs (**c**) can show natural color. Some electron micrographs have color added later to highlight important elements of the picture.

A light microscope has the advantage of being usable with live specimens, but it also has limitations. One involves *contrast*. Many of the organelles of a cell do not absorb light well; therefore, light rays coming from them look the same as rays from adjacent parts of the cell. This means that you cannot tell that the organelle is there. Microscopists partially solve this problem by staining the cells. Certain stains color particular organelles, thus increasing their contrast. However, even in stained samples the scattering of light from other parts of the sample tends to wash out the image, reducing the contrast. The thicker the slice of tissue, the more serious the scattering problem. One solution to this problem is to cut a thin slice of the sample, but the soft substance of a living cell cannot withstand the chemical treatments needed for making very thin slices; therefore, this treatment kills the specimen.

Even if the contrast of a sample in a light microscope is good, the microscope's resolution--its ability to distinguish separate objects--is limited by several factors. Because different colors of light are affected differently by lenses, it is impossible to focus an image perfectly when it is illuminated with white light, which contains rays of all colors. Furthermore, the resolving power of a microscope is limited to one half of the wavelength of the light being used. Because the shortest wavelength seen by the human eye is about 0.4 μm, the smallest object that can be resolved in a light microscope is about 0.2 μm in diameter.

New techniques of microscope have minimized many of these limitations. Contrast can be dramatically increased by **confocal microscopy**. In this system, the illumination (a laser) and the detecting lens are both focused on one point in the sample at a time, scanning across the sample to assemble a whole picture. Because only one point is illuminated, there is not reduction in contrast from light scattered from other parts of the sample. Even in a relatively thick sample, the focal point of illumination can be very exact, which means that the light can be focused on different levels. Separate pictures of a sample taken at different levels can be assembled to form a three-dimensional picture of a cell.

Resolution can be improved by using **transmission electron microscopy** (Fig. 3.2d). Instead of light, electron microscopes use beams of electrons. Quantum theory tells us that electrons, although normally thought of as particles, also behave like light waves, with wavelengths about 1 million times shorter than those of visible light. Electron beams, having a negative charge, are bent by magnets; in a transmission electron microscope, magnets serve as lenses. Because the human eye cannot see electrons, the final image is made visible by using the electrons to excite a fluorescent plate or to expose photographic film. These electron microscopes have limitations as well. Electron beams cannot pass through air or through a whole cell. Therefore, the sample must be sliced ultrathin and examined in a vacuum. This technique clearly cannot be used while the samples are alive. Nevertheless, transmission electron microscopy has been responsible for the discovery of most of the smaller organelles in the cell.

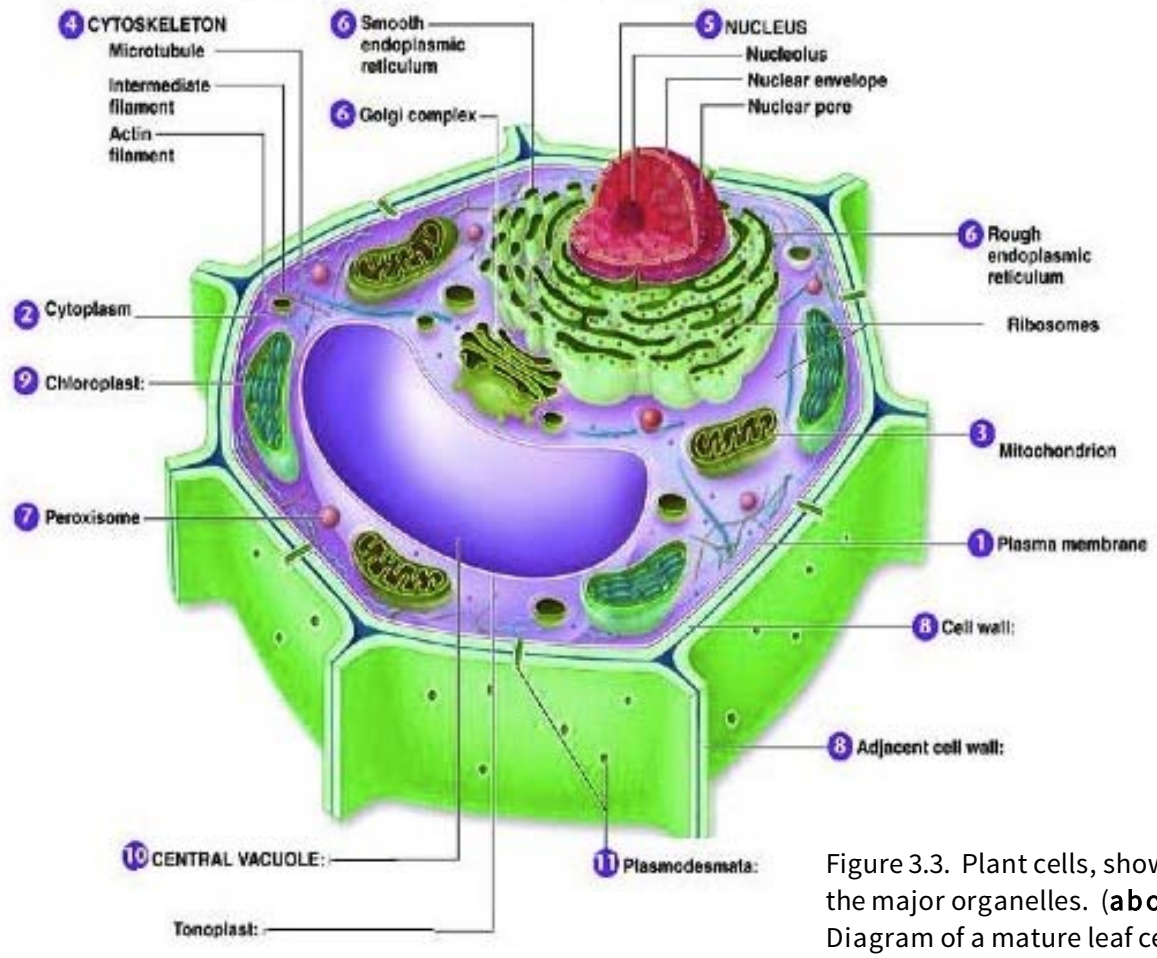
3.2 THE PLANT CELL

Living cells are found throughout the plant body. They make up the internal, photosynthetic cells of the leaf that convert light energy to chemical energy. They make up the pith and cortex of the stem and the cortex of the root. They make up the bulk of fleshy fruits. These cells all have similar organelles (Fig. 3.3), those needed for general growth and maintenance of cell function. Some also have specialized organelles for specific functions. The next section describes the components found in a generalized living plant cell.

3.3 THE BOUNDARY BETWEEN INSIDE AND OUTSIDE

The Plasma Membrane Controls Movement of Material into and out of the Cell

A thin membrane, the plasma membrane, surrounds each cell. Membranes are composed of approximately half phospholipid and half protein, with a small amount of sterols, another form of lipid (Fig. 3.4). The phospholipids and sterols provide a flexible, continuous, hydrophobic (water-excluding) sheet two molecules thick, called the **phospholipid bilayer**. This separates the aqueous solution inside the cell (called the **cytoplasm**) from that outside the cell. The phospholipid bilayer prevents ions, amino acids, proteins, carbohydrates, nucleic acids, and other water-soluble compounds inside the cell from leaking out and also prevents those outside the cell from diffusing in. This means that for one of these compounds to move in or out, there must be a special pathway or carrier. These pathways are provided by special proteins in the bilayer.



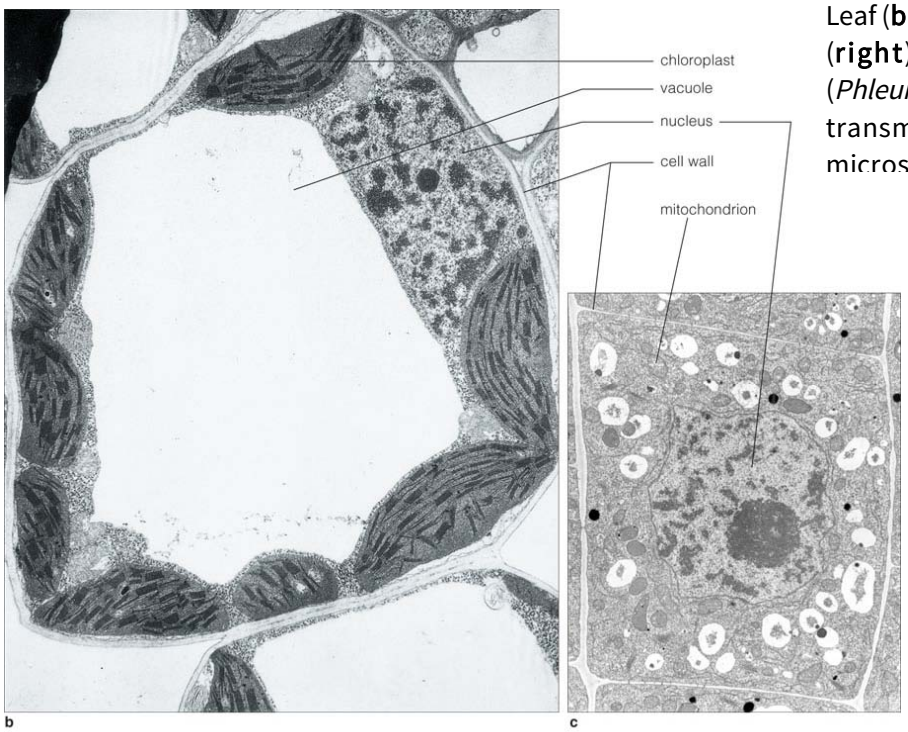


Figure 3.3. Plant cells, showing the major organelles. (**above**) Diagram of a mature leaf cell. Leaf (**below**, **left**) and root (**right**) cells of timothy grass (*Phleum pratense*) as seen in a transmission electron microscope.

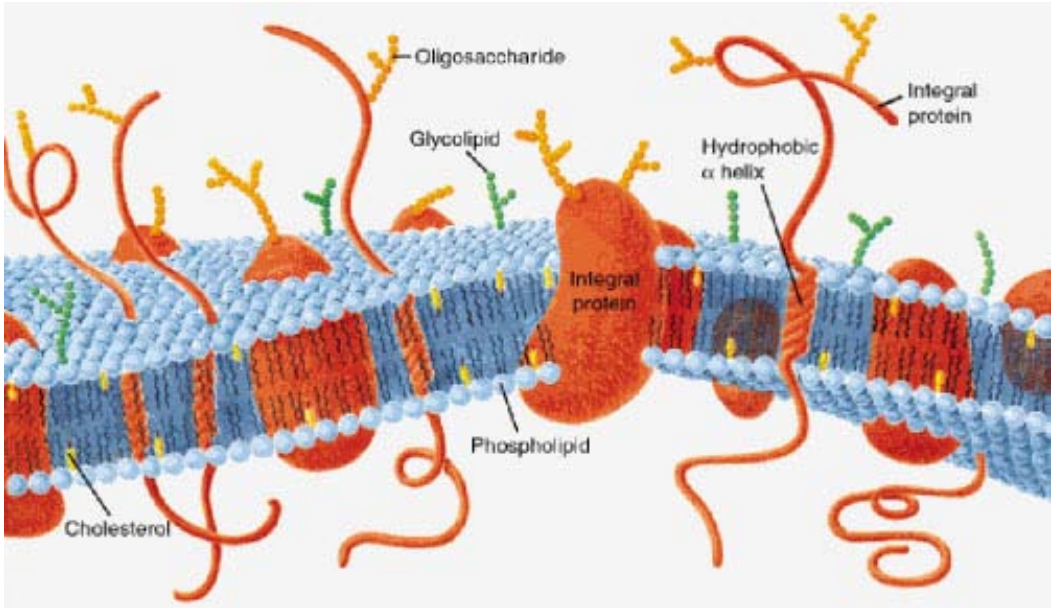


Figure 3.4. A model of the plasma membrane, showing the phospholipids bilayer, sterols, and various types of proteins floating in the bilayer.

Each type of protein in a membrane performs a different function. Some types provide the special pathways by which compounds can move into or out of a cell in a highly regulated manner. For instance, some proteins function as **ion pumps**; one important type (the **proton pump**) pumps H^+ ions from the inside to the outside of the cell (see Chapter 11 for more details). Another pumps Ca^{2+} ions to the outside of the cell. The characteristic of a pump is that it can move ions from lower to higher concentrations by using cellular energy in the form of adenosine triphosphate (ATP). Some proteins form **channels** for substances (such as K^+ ions, sucrose, or even water) to diffuse passively across the membrane, either alone or in combination with another substance, such as H^+. The combination of phospholipids, which form a relatively impermeable sheet, and proteins, which pass specific materials through the sheet, allows the plasma membrane to control transport into and out of the cytoplasm. It is thus a *selectively permeable* membrane.

An unusual property of plant cells is the existence of connections, the plasmodesmata (singular, phasmodesma)(Fig. 3.5) between the plasma membranes of adjacent cells. At a plasmodesma, the plasma membrane on one cell extends outward through the cell wall (see the next section), forming a tube and then connecting to the plasma membrane of the next cell. The continuous cytoplasm in a set of cells connected by plasmodesmata is sometimes called the symplast. A plasmodesma forms a passageway that may allow material to move from the cytoplasm of one cell to the next. It is a striking idea that plant cells are so interconnected by plasmodesmata that a plant might be considered a single super-large cell, partially divided into the compartments we call cells. However, a plasmadesma is not simply an open tube. Inside it are proteins and another membrane tube that control the transport of materials through the plasmodesma. Small molecules such as sugars and amino acids seem to pass easily. Larger molecules such as proteins and organelles generally cannot pass, although it has been discovered that some plant viruses can open plasmodesmata so that the virus particles can spread their infection from cell to cell.

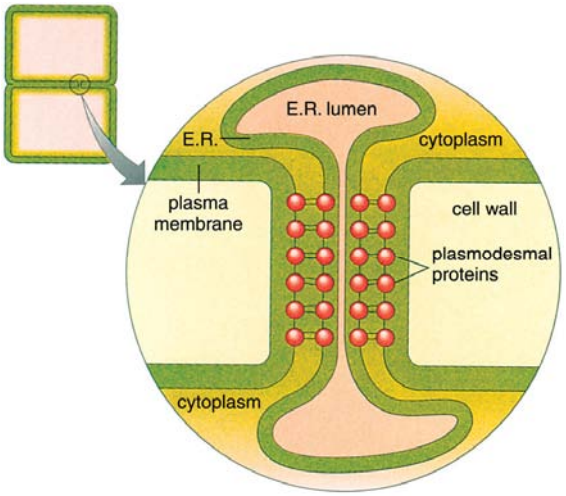


Figure 3.5. Model of a plasmodesma, showing the endoplasmic reticulum and proteins that are thought to control the flow of materials through the channel.

Does the plasma membrane define the limits of the cell? Many traditional cell biologists consider the plasma membrane to be the outer limit of the cell. According to this view, everything outside the plasma membrane is extracellular--that is, something that may have come from the cell but is not really part of it. Others point to recent research that shows there is considerable metabolic activity outside the plasma membrane. They consider the space outside the cell, next to the plasma membrane and within the fibrils of the cell wall, to be part of the cell. In either case, there is a continuity of the space around adjacent cells. This space is celled the **apoplast**. It is clear that the apoplast is an important space in a plant, but it is an open question whether it is part of the plant's cells.

The Cell Wall Limits Cell Expansion

A plant cell that is surrounded only by a plasma membrane and placed in pure water will expand until it bursts. This is because a cell contains a relative high concentration of solutes, held in by the plasma membrane. The solutes decrease the effective concentration of the water inside the cell. Water, like other chemicals, tends to move from a region of high concentration to one of low concentration. The plasma membrane prevents solutes from moving out, but it does allow water to move in. The flow of water from a relatively dilute solution to a more concentrated solution across a selectively permeable membrane is called **osmosis**. Although the inflow of water dilutes the solution inside the cell, that solution never becomes as dilute as pure water. Thus the inflow continues until the plasma membrane, which is not infinitely expandable, ruptures.

For plant cells, this problem of rupturing in a dilute solution, such as rainwater, is solved by a cell wall (Fig. 3.6). The cell wall is a relatively rigid structure that surrounds the cell just outside the plasma membrane. It is made of microfibrils formed from a polysaccharide, **cellulose**. Cellulose is a linear, unbranched chain of glucose molecules (see Fig. 2.10). Two of these chains can line up side by side, connected by hydrogen bonds. About 40 of these chains form a microfibril, which is flexible but strong, like a cable. Among the microfibrils are other, less highly organized polysaccharides (hemicelluloses and pectins) and proteins.

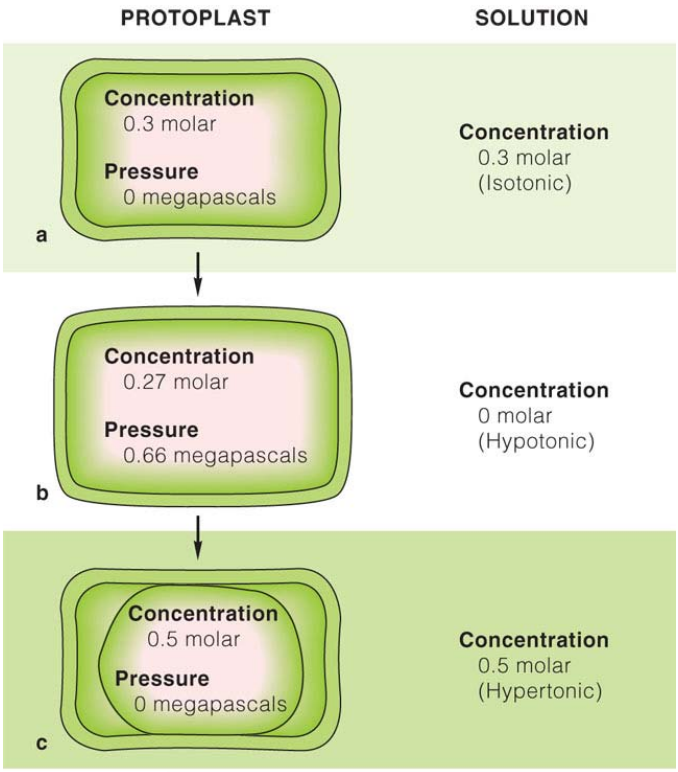
Figure 3.6. A small section of cell wall, as seen in a transmission electron microscope. The filaments are cellulose.

The microfibrils and other components form a porous network, so that water and solutes easily penetrate to the plasma membrane. If, however, an inflow of water expands the cell, it forces the plasma membrane against the cell wall; therefore, the pressure from the water tends to expand the cell. The cell wall is tough but elastic; the more it expands, the more it resists further expansion. At some point the resistance of the cell wall exactly balances the pressure of osmosis, stopping the inflow of water. This keeps the plasma membrane from expanding and rupturing (Fig. 3.7b).

When the cell stops expanding, the osmotic forces pulling water into the cell do not disappear. They are simply balanced by the pressure exerted by the cell wall. The internal hydrostatic pressure in a cell can be very high. Typical cell walls maintain pressures of 0.75 megapascal (7.5 times atmospheric pressure at sea level). Cells with such internal pressure (**turgor** pressure) become stiff and incompressible. This means that they can hold heavy weights. Even plant cells with a thin cell wall can form and support large plant organs, so long as the solution in the apoplast is sufficiently dilute that a large turgor pressure is generated. When the supply of water is cut off, a leaf wilts. This occurs because water is lost from the cell and turgor pressure decreases. Thus, in addition to preventing the cell from bursting when it is surrounded by a dilute solution, the cell wall is responsible for maintaining the high turgor pressure that gives a plant organ much of its strength.

Osmosis works in both directions. If the concentration of solutes outside the cell is greater than that inside--such as is found in salt flats--then water will flow out of the cytoplasm. The volume of the **protoplast** (the space inside the plasma membrane) will shrink, and the plasma membrane will pull away from the cell wall (Fig. 3.7c). This effect is called **plasmolysis**. A plasmolyzed cell has no turgor pressure. Thus, an accumulation of salt in the soil can cause a plant to wilt.

The cell wall that forms while the cell is growing is the *primary cell wall*. After cells stop growing, some deposit an additional cell wall layer between the primary cell wall and the plasma membrane--a *secondary cell wall* (see Fig. 4.9).



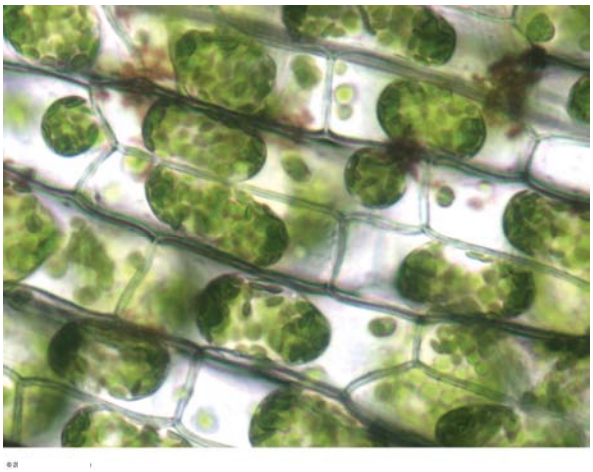


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Figure 3.7. The effect of osmosis on cell size. (**a**) The cell is assumed to have an internal concentration of solutes the same as that in the external solution. The cell protoplast is exactly the same size as the cell wall in its unstretched state. (**b**) The cell is transferred to pure water. Water enters the cell by osmosis, and the protoplast expands, pushing against the cell wall. The wall expands but pushes back, limiting the further influx of water. Water stops entering the cell when the pressure exerted by the cell wall equals the osmotic pressure forcing water into the cell. (**c**) The cell is transferred to a solution of 0.5 molar. Water moves out of the protoplast by osmosis, and the protoplast shrinks until the concentration of solutes equals 0.5 molar. The plasma membrane pulls away from the cell wall. This effect is called *plasmolysis*. (**d**) Plasmolyzed *Elodea* cells. Compare these cells to the ones in Fig. 3.1b.

The secondary cell wall generally contains cellulose microfibrils and a strong, water-impermeable substance called **lignin**. Lignin is formed from subunits derived from an amino acid. The subunits are crosslinked with many covalent bonds, forming a three-dimensional network. The crosslinks make these cell walls especially rigid and much more able to resist stretching or compression. Secondary cell walls provide much of the strength of wood (see Chapter 5). Other specialized types of cell walls have **cutin** covering them or **suberin** embedded in them. Cutin and suberin are waxy compounds made of modified fatty acids that are especially impermeable to water. Cutinized cell walls are found on the surface of leaves and other organs that are exposed to the air. They retard the evaporation of water from the cells. They also form a barrier to potential pathogens such as bacteria and fungi. The adaptations of specialized cell walls often involve chemical changes to their cell walls.

3.4 THE ORGANELLES OF PROTEIN SYNTHESIS AND TRANSPORT

Much of the cell is made of protein, and most cell activities depend on specialized proteins. Plant cells have specialized organelles that are responsible for producing proteins and for making sure that each is placed in its proper position in the cell.

The Nucleus Stores and Expresses Genetic Information

One of the larger and more prominent organelles is the **nucleus**. It is ovoid or irregular in shape and up to 25 μm in diameter. It stains densely with many of the stains used for light or electron microscopy. It is surrounded by a double membrane: the **nuclear envelope**. Filaments of a protein called lamin line the inner surface of the envelope and stabilize its structure. The inner and outer membranes of the nuclear envelope connect to form pores, through which molecules may pass (Fig. 3.8). In the nucleoplasm (the portion inside the nuclear envelope) are found the **chromosomes**, which contain DNA and protein. In each chromosome, one long, double-helical molecule of DNA is wound around special proteins (*histones*) to form a chain of nucleosomes. Other proteins form scaffolds, which hold loops and helices of the chain of nucleosomes in place (Fig. 3.9).

The DNA molecules in the chromosome store genetic information in their sequences of nucleotides. This information is used to direct the synthesis of proteins. The first step in the process is transcription--the DNA is used as a template to direct the synthesis of RNA (see Chapter 15 for a detailed explanation). Much of this RNA, for unknown reasons, stays in the nucleus or is rapidly broken down. However, a small fraction of the RNA, messenger RNA (mRNA), carries the genetic information of its DNA template out of the nucleus and into the cytoplasm.

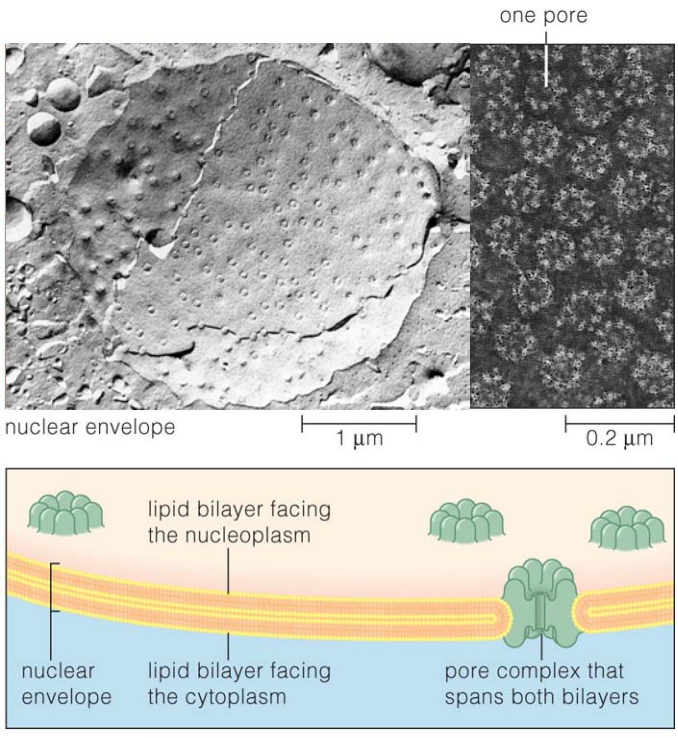


Figure 3.8. Surface view by scanning electron microscopy and sketch of the nucleus, showing the nucleolus and the nuclear envelope with pores.

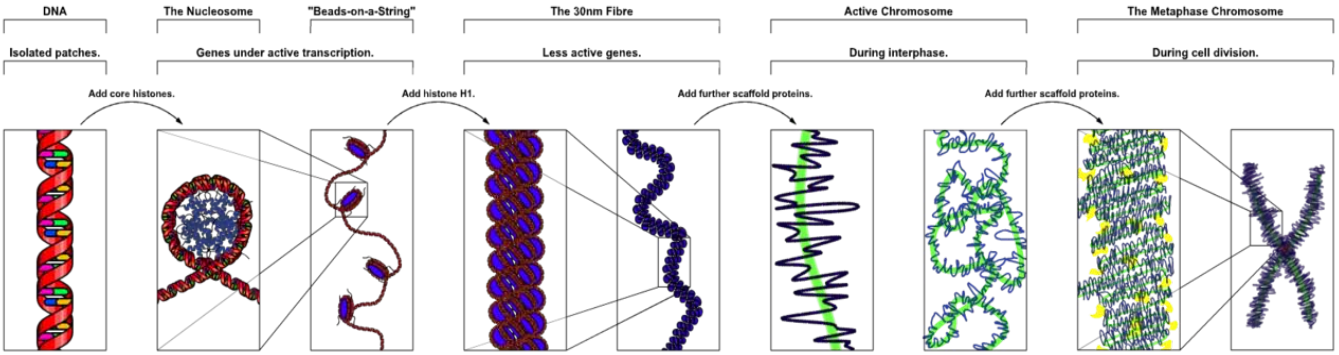


Figure 3.9. Organization of DNA in nucleoplasm.

Also in the nucleoplasm are **nucleoli** (singular, *nucleolus*), seen in the light or electron microscope as densely staining regions. These are accumulations of RNA-protein complexes. The RNA-protein complexes are ribosomes (see the next section), and nucleoli are the sites where the ribosomes are being assembled. At the centers of the nucleoli are DNA templates that guide the synthesis of ribosomal RNA.

Ribosomes and Associated Components Synthesize Proteins

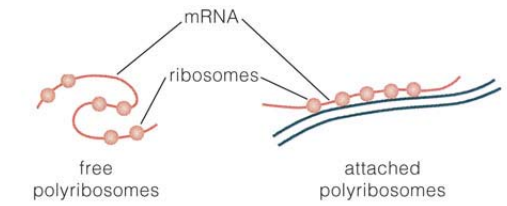
In the cytoplasm are the **ribosomes**, which are small dense bodies formed from ribosomal RNA and special proteins. In combination with other molecules, ribosomes synthesize proteins. The active ribosomes are found clustered together in **polyribosomes** (Fig. 3.10). The ribosomes in a polyribosome are held together because each is attached to the same mRNA. Because the mRNA carries information for the particular type of protein to be synthesized, all ribosomes in one polyribosome are making the same type of protein.

Although a polyribosome looks like a fixed object in an electron micrograph or a diagram, in a living cell, the ribosomes move rapidly along the mRNA, reading its base sequence and adding amino acids to a growing protein chain. At the end of the mRNA, the ribosomes fall off, releasing the completed protein into the cytoplasm.

The Endoplasmic Reticulum Packages Proteins

In a plant cell, the **endoplasmic reticulum (ER)** is generally a branched tubular membrane, often near the periphery of the cell. In three dimensions, it is a closed structure (or several closed structures); therefore, solute molecules cannot move from the cytoplasm into the inside (the lumen) expect by passing through the membrane.

There are many places in the cell in addition to the cytoplasm that need new proteins, including the membranes (plasma membrane, nuclear envelope, and other membranes to be described), certain membrane-surrounded spaces (vacuoles, vesicles), and the apoplast. One of the functions of the ER is to serve as the site where proteins are synthesized and packaged for transport to these locations. Ribosomes in a polyribosome attach to the surface of the ER. In an electron micrograph, this forms a structure known as **rough ER** (Fig. 3.10), as opposed to the **smooth ER**, which does not have ribosomes attached. As the ribosomes synthesize a



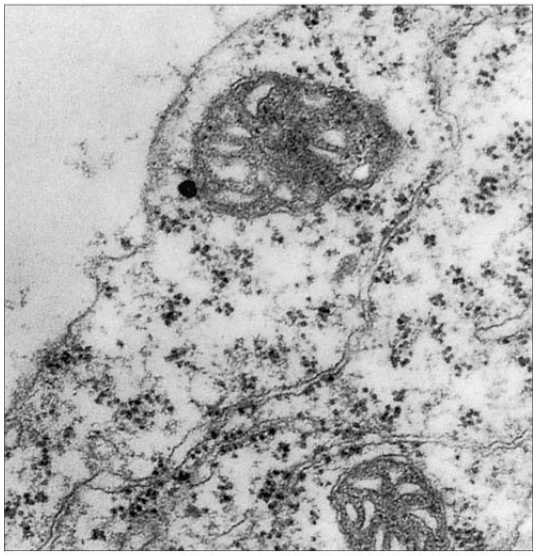


Figure 3.10. Polyribosomes as observed by transmission electron microscopy. Some of the polyribosomes in this cell from a wheat root tip were free in the cytoplasm and some were attached to the endoplasmic reticulum, forming rough ER.

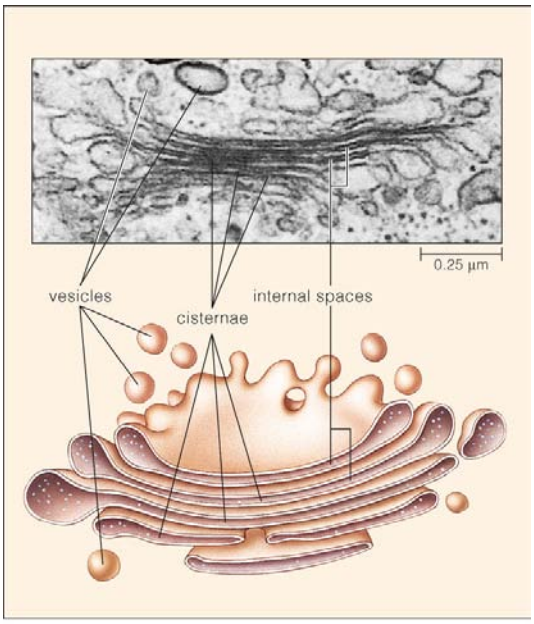


Figure 3.11. The Golgi apparatus and how it moves substances through a cell. (**a**) Transmission electron micrograph. Note the cisternae and associated vesicles. (**b**) A model of a Golgi apparatus.

protein, the protein is injected through the membrane into the lumen. Carbohydrates often are attached to proteins in the ER. This helps protect the proteins from breakdown by destructive enzymes. The proteins in the lumen may be considered to be packaged--that is, separated from the cytoplasm by a membrane. A small sphere of membrane-containing proteins (called a *vesicle*) may bud off from the ER and can carry the proteins to other locations in the cell.

The Golgi Apparatus Guides the Movement of Proteins to Certain Compartments

The **Golgi apparatus** (sometimes called a **dictyosome**) looks like a stack of membranous, flattened bladders, called **cisternae**, which often are swollen toward the edges. Although it is difficult to see in an electron micrograph, there is direction to the organelle, with the cisternae on one side different from those on the other.

The Golgi apparatus directs the flow of proteins and other substances from the ER to their destinations in the cell. For example, cell wall proteins, hemicellulose, and pectin in the ER packages pass through the cisternae of a Golgi apparatus and then move to the plasma membrane inside a small membranous sphere. When the sphere joins the plasma membrane, its membrane becomes part

of the plasma membrane. Its protein, hemicellulose, and pectin contents are then released to the outside of the cell (Fig. 3.11).

The trafficking between the Golgi apparatus, the ER and other organelles of the cell is rapid and continuous. Even though the organelles usually appear to be separate in electron micrographs and can be isolated from one another by biochemical techniques, they can be considered parts of a complex network called the **endomembrane system**.

3.5 THE ORGANELLES OF ENERGY METABOLISM

The synthesis, packaging, and transport of proteins--and many other functions--require free energy. Plant cells have two specialized organelles that provide this energy: plastids and mitochondria.

Plastids Convert Light Energy to Chemical Energy

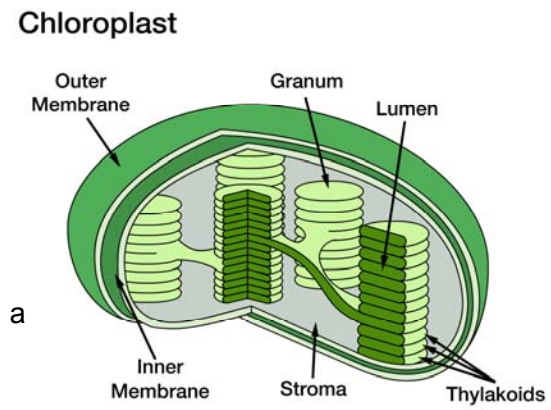
Plastids are complex organelles found in every living plant cell. One cell may have 20 to 50 plastids, each 2 to 10 μm in diameter. Characteristically, they are surrounded by a double membrane. They contain DNA and ribosomes--a full protein-synthesizing system similar but not identical to the one in the nucleus and cytoplasm. Some of the proteins of the plastid are made by this system; other are made in the cytoplasm and are transported into the plastid across its outer membranes.

Dividing plant cells always contain some small plastids, called **proplastids** (Fig 3.12c). These have a few short internal membranes and some crystalline associations of membranous material, called *prolamellar bodies*. As cells mature, their plastids develop and acquire special characteristics. In this process the components of prolamellar bodies apparently are reorganized and combined with new lipids and proteins to form more extensive internal membranes.

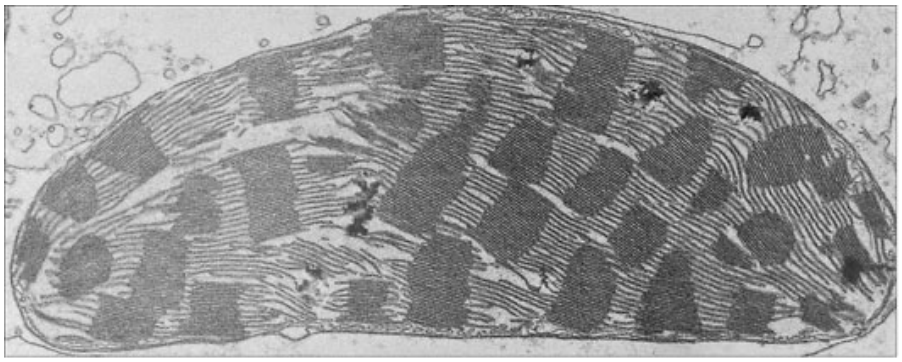
Many cells in leaves contain plastids called **chloroplasts** (Fig. 3.12a-b; *chloro-* is derived from a Greek word for a yellow-green color). Chloroplasts contain an elaborate array of membranes, the **thylakoids**. Incorporated in the thylakoid membranes are proteins that bind the green compound **chlorophyll**. It is this compound that gives green plant tissues their color. Surrounding the thylakoids is a thick solution of enzymes, the **stroma**. Together, the proteins in the thylakoids and the stromal enzymes perform photosynthesis (see Chapter 10), during which light energy is converted to chemical energy. These plastids can also store carbohydrates, the products of photosynthesis, in the form of starch grains.

In roots and some nongreen tissues in stems, the plastids are **leukoplasts** (Fig. 3.12d; *leuko-* is derived from the Greek word for "white"). In these plastids, the thylakoids are missing, although there may be some less organized membranes. These plastids also are able to store carbohydrates (imported from photosynthetic tissue) in the form of starch, because they have the enzymes for starch synthesis. Under a light microscope, one often sees white, refractile, shiny particles: starch grains. When leukoplasts contain large granules of starch, they often are called **amyloplasts** (Fig. 3.12e; *amylo-* is derived from the Greek word for "starch").

In certain colored tissues (for instance, tomato fruits and carrot roots), the plastids accumulate high concentration of specialized lipids--carotenes and



a



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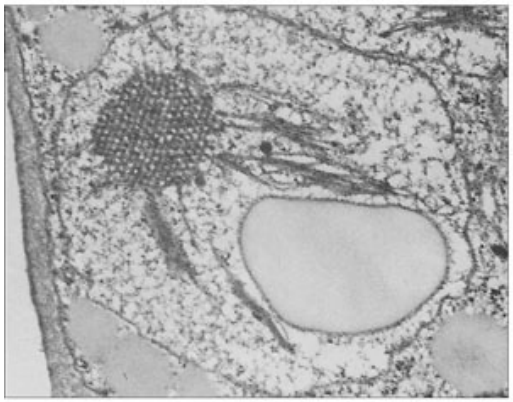

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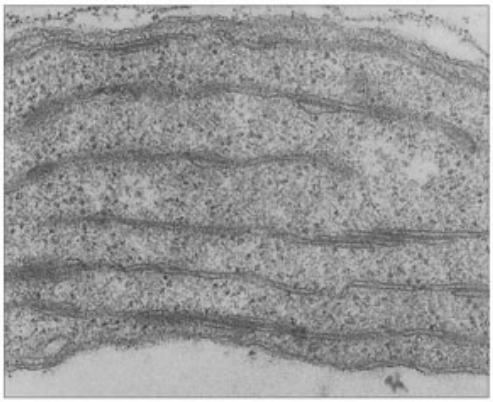

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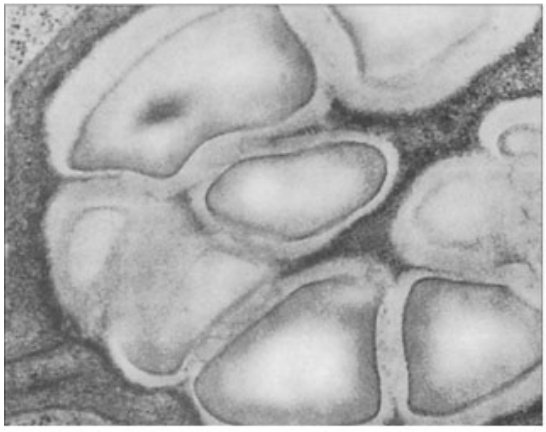

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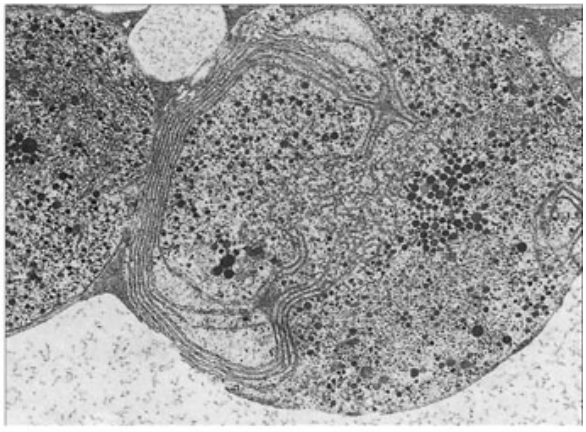

f

Figure 3.12. Plastids. (**a**) Model of a chloroplast. (**b**) A maize (*Zea mays*) leaf chloroplast, showing dense thylakoid membranes. (**c**) A maize proplastid, with only a few internal (prolamellar) membranes. (**d**) A small leucoplast from an inner white leaf of endive (*Cichorium endiva*). (**e**) An amyloplast from a bean (*Phaseolus vulgaris*) seedling, showing large starch grains. (f) A chromoplast from a mature red pepper (*Capsicum* sp.). The dark circles are globules of red and orange xanthophylls.

xanthophylls. The orange-to-red color of these lipids give the plastids their name, **chromoplasts** (Fig. 3.12f; *chromo-* means "color").

Mitochondria Make Useful Forms of Chemical Energy

In plant cells, as in the cells of all eukaryotes, there are **mitochondria** (Fig. 3.13). Mitochondria are made of two membrane sacs, one within the other. The inner membrane forms folds or fingerlike projections called **cristae**. These folds increase the surface area available for chemical reactions taking place on the membrane. In the center of the organelle, inside the inner membrane, is a viscous solution of enzymes, the **matrix**. Like plastids, mitochondria contain DNA and ribosomes, and they are able to synthesize some types of proteins.

Mitochondria are best known as the sites of oxidative respiration, the places where organic molecules are broken down into CO_2 and H_2O (see Chapter 9). During this process, some of the energy that is released is used to synthesize the energy-rich molecule ATP. ATP powers many of the important chemical reactions in the cell. Mitochondria are the source of most of the ATP in any cell that is not actively photosynthesizing.

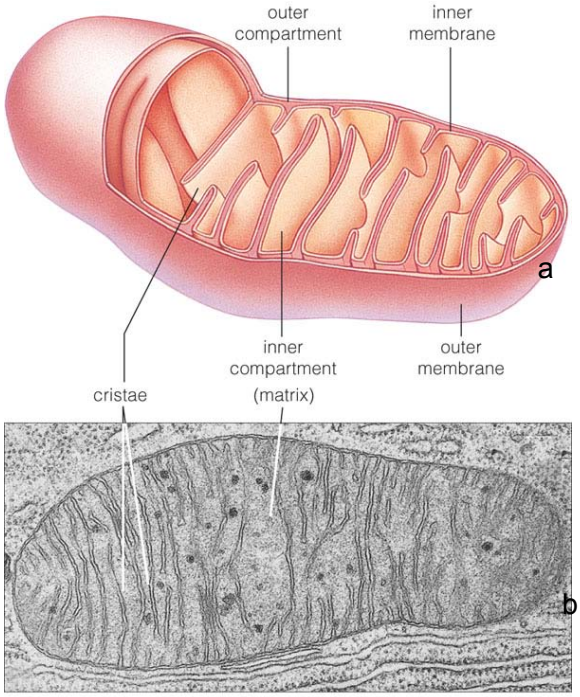

Figure 3.13. Mitochondria. (**a**) Model of a typical mitochondrion. (**b**) Transmission electron micrograph of a mitochondrion from the young leaf of a sunflower (*Carthamus tintorius*) seedling.

3.6 OTHER CELLULAR STRUCTURES

Cells have several types of organelles in addition to those already described in this chapter. Some of these organelles seem rather passive, serving mainly as storage compartments. Others are hard to see (even by microscopy), but they are very active, moving many of the other organelles around the inside of the cell in a continuous dance.

Vacuoles Store Substances

In each mature plant cell, a large compartment, bounded by a single membrane, makes up a large fraction of the cell volume (Fig. 3.3). This is the **vacuole**. The membrane surrounding it is called the tonoplast. Like the plasma membrane, the

tonoplast has a number of embedded protein pumps and channels that control the flow of ions and organic molecules into and out of the vacuole.

Depending on the cell, the vacuole may have any of several functions. It may accumulate ions (or other substances), increasing the osmotic pull of water into the cell and increasing the turgor pressure inside the cell. It may store nutrients such as sucrose (common sugar). (Our commercial sugar comes from extracting sucrose from the vacuoles of sugarcane stem or sugar beet root storage cells. Other nutritious chemicals may be stored in vacuoles. See "PLANTS, PEOPLE, AND THE ENVIRONMENT: Foods and Health" sidebar at the end of this chapter.) The vacuole may also accumulate compounds that are toxic to herbivores. Finally, it may serve as a dump for wastes that the cell cannot keep and cannot excrete. Sometimes substances accumulate in the vacuole to such a high concentration that they form crystals.

Other Organelles Transport and Store Substances and Compartmentalize Reactions

The cytoplasm has many types of small, round bodies surrounded by a single membrane (Fig. 3.3), as is the vacuole. These include **vesicles**--both the small spheres of membrane that bud off the ER and carry proteins (ER vesicles) and those that travel from the Golgi apparatus to the plasma membrane (Golgi vesicles). There are also similar but more permanent organelles in the cell. In some specialized cells, protein bodies and lipid bodies store proteins or lipids. **Peroxisomes** and **glyoxysomes** serve as compartments for enzymatic reactions that need to be separated from the cytoplasm (because some products of those reactions would be toxic to enzymes in the cytoplasm). **Lysosomes** contain enzymes that break down proteins, carbohydrates, and nucleic acids. The lysosomes may have some function in removing wasters within a living cell. In addition, when they break, they release their enzymes, which dissolve the cell. In the development of a plant, there are several times when it is important to get rid of certain cells; the lysosomes accomplish this.

The Cytoskeleton Controls Form and Movement within the Cell

In high-resolution electron micrographs, a collection of long, filamentous structures within the cytoplasm can sometimes be seen. These are evidence of a higher order of organization of the organelles within the cell. They form the **cytoskeleton**, which sometimes keeps the organelles in particular places and sometimes directs their movement around the cell (the movement is called **cyclosis** or cytoplasmic streaming.)

There are several different types of structures in the cytoskeleton. One type is relatively thick (0.024 μm in diameter): the **microtubule** (Fig. 3.14a). It is assembled from protein subunits called *tubulin*. Tubulin subunits assemble in a helical manner to form a hollow cylinder. Once assembled, microtubules are fairly rigid, although they can lengthen by the addition of tubulin molecules to one end (or shorten by the loss of tubulins from the same end); therefore the length of a microtubule can change rapidly.

Certain *motor proteins* can move along microtubules. These proteins--one type called kinesins, another dyneins--move by stepping along the microtubule strand, making and breaking connections with adjacent tubulin subunits. The motor proteins may be attached to other organelles, such as vesicles. In this way, microtubules guide the movement of organelles around the cytoplasm. The power generated by motor proteins comes from the breakdown of the high-energy molecule ATP.

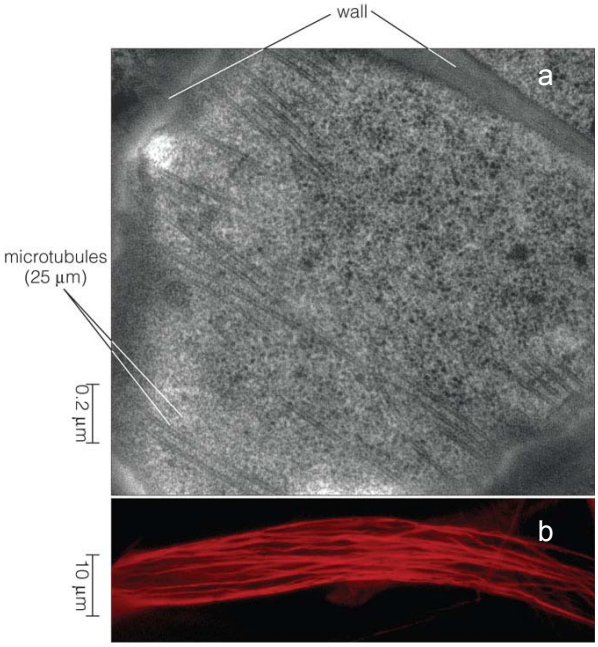

Figure 3.14. (**a**) Microtubules in a root cell of mouse-ear cress (*Arabidopsis thaliana*). (**b**) Bundles of microfilaments in a pollen tube of *Tradescantia virginiana*. Thse have been complexed with an anti-actin antibody attached to a fluorescent compound that glows red when irradiated with ultraviolet light.

Microtubules are key organelles in cell division (see next section). They also form the basis of *cilia* and *flagella,* motile organs that move cells by beating back and forth. Cilia and flagella are never found in the cells of flowering plants, but they are important to some algae and to male gametes of lower plants.

Another type of structure in the cytoskeleton is the **microfilament** (Fig. 3.14b). The microfilament, thinner (about 0.007 µm in diameter) and more flexible than the microtubule, is made of protein subunits called *actin* that fit together in a long, helical strand. Microfilaments often are found in bundles. Like microtubules, they can serve as guides for the movement of organelles. However, myosin, rather than kinesin or dynein, is the motor protein that moves along a microfilament. The energy for this movement comes from the breakdown of ATP.

Many types of specialized proteins connect microtubules and microfilaments to other organelles. These connections are thought to coordinate many of the processes of the cells. For instance, they might direct vesicles to move to the plasma membrane and deposit new wall material when triggered by the presence of hormones. This coordination is most important, and most spectacular, during the complex process of cell reproduction. As you read the next section, notice how microtubules appear to direct several of the events of cell division.

3.7 THE CELL CYCLE

What Are the Phases of the Cell Cycle?

In higher plants, cells form aggregates--tissues and organs--that have specific structures and functions. The production of new cells allows the plant body to grow by forming new organs and by increasing the number of cells in an existing tissue or organ. The following section examines the beginning of the tissue- and organ-forming process, describing how cells divide and when mechanisms control the process.

The process of cell division occurs in special regions of the plant called **meristems**. Meristems are found at the tips of roots and shoots and in some other regions of a plant. When cells divide, they must progress through a series of steps called the cell cycle. One cell cycle is the interval of time between the formation of a cell and its division to form two new cells.

The cell cycle has four phases: G1 ("gap 1"), S ("synthesis" of DNA), G2, and M ("mitosis")(Fig. 3.15). Traditionally, the G1, S, and G2 phases of the cycle are grouped together and called **interphase**. The remaining M phase is actually composed of two parts: **karyokinesis** (nuclear division) and **cytokinesis** (cytoplasmic division).

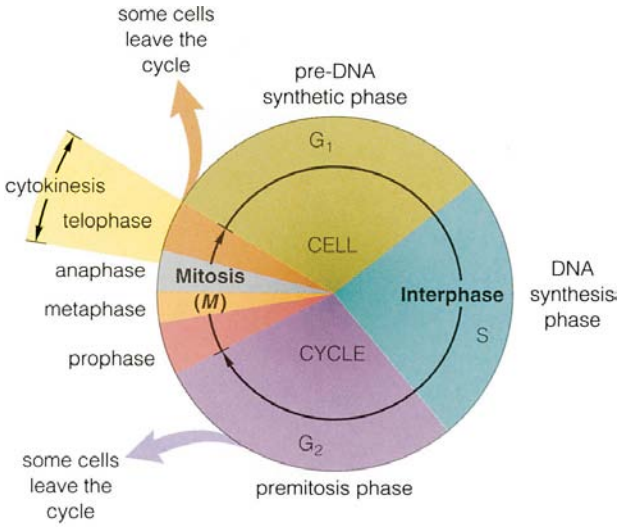

Figure 3.15. The cell cycle, consisting of the G1, S, G2, and M phases. Approximately 50% of new daughter cells leave the cycle at either G1 or G2 and begin to differentiate; the remaining cells cycle again

Specific Metabolic Events Occur in Each Cell Cycle Phase

Cells in each phase of the cell cycle are unique in structure and molecular composition. During G1, the cell prepares itself metabolically for DNA synthesis. These preparations include both the accumulation and synthesis of specific enzymes to control DNA synthesis and production of the DNA subunits so that a supply is on hand when synthesis begins.

The second phase of the cell cycle is the S phase. During this portion of the cycle, the cell duplicates its DNA molecules (see Chapter 2). The time needed for a cell to progress through the phases of the cell cycle depends on the amount of DNA per nucleus. Plants with move DNA in their nuclei have longer cell cycle times than plant with less DNA. The time for a complete cycle ranges from a few hours to days.

Unless cells are metabolically active, they cannot progress through the phases of the cell cycle. Cells must be able to synthesize enzymes and other proteins

needed for specific cell cycle events. DNA polymerase, a key protein in the synthesis of new DNA, is an example of a cell cycle-specific protein. The amounts of this protein and of histones--proteins that form the nucleosomes around which DNA winds--increase at the end of the G1 phase and during the S phase.

3.8 REGULATION OF THE CELL CYCLE

The Principal Control Point Hypothesis Identifies the Control Points in the Cell Cycle

The high-energy molecule ATP is essential for the synthesis of DNA and protein and for other processes. Cycling cells in meristems require a constant supply of carbohydrates to make ATP. If root tips are removed from seedlings and placed into sterile culture, their cells will progress through the cell cycle only if carbohydrate (sucrose) is added to the culture medium. Without sucrose, the cells stop cycling, but only at specific places in the cell cycle. Jack Van't Hof and his collaborators at Brookhaven National Laboratory on Long Island observed that such cells became arrested in G1 and G2 phases. The ratio of cells arrested in G1 and G2 varied among different species. For example, in peas (*Pisum sativum*) 50% of cells stopped in G1 and 50% in G2, whereas in sunflowers (*Helianthus annuus*) 90% stopped in G1 and 10% in G2. Cell cycle progression resumed after sucrose was added back to the culture medium.

These experiments led Van't Hof to develop the Principal Control Point Hypothesis, which proposes that control points exist in the G1 and G2 phases of the plant cell cycle (Fig. 3.16). If a cell progresses past the G1 or G2 control point, it then automatically progresses through DNA synthesis (S phase) or cell division (M phase), respectively. Metabolically, this means that sometime during the G1 phase a cell synthesizes certain proteins in preparation for DNA synthesis in the S phase. If the cell forms these critical macromolecules, it progresses through the S phase; but if it does not, the cell is arrested in G1. The same interpretation would apply to the G2 control point, except that at that time a dividing cell would need proteins that act during the M phase.

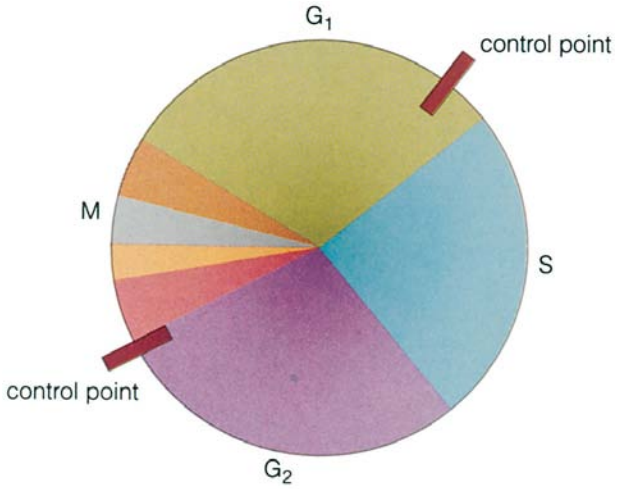

Figure 3.16. Cell cycle control points. Two control points located in G1 and G2 regulate the cell cycle in plant cells and other eukaryotes. The G1 control point is regulated by the activity of a gene called *cdc2*.

Microtubules Set the Plane of Cell Division

Microtubules are intimately involved in many aspects of the cell cycle, from the regulation of cell wall formation and cell shape to the movement of chromosomes

and control of the plane of cell division (Fig. 3.17). During G1 and S of the cell cycle, the microtubules are located around the periphery of the cell, next to the plasma membrane and cell wall. These microtubules are involved in the deposition of cellulose in the cell wall. The cell will elongate at right angles to the axis of the microtubules and cellulose, a process described in more detail in Chapter 15.

During G2 the microtubules move into a new location and form a band surrounding the nucleus, but pressed close to the cell wall (Figs. 3.17a-c and 3.18). This organization is called the preprophase band (PPB) of microtubules. Its formation precedes mitosis by hours. The orientation of the PPB somehow marks the position of the new cell wall that will form at the end of mitosis. The new cell wall defines the *plane of cell division*.

Several factors may influence the position of the PPB. Within tissues, gradients of chemicals such as plant hormones regulate the start of differentiation events such as mitosis. The hormone gradients may induce the movement of the microtubules to the PPB as a first step in the overall induction of cell division.

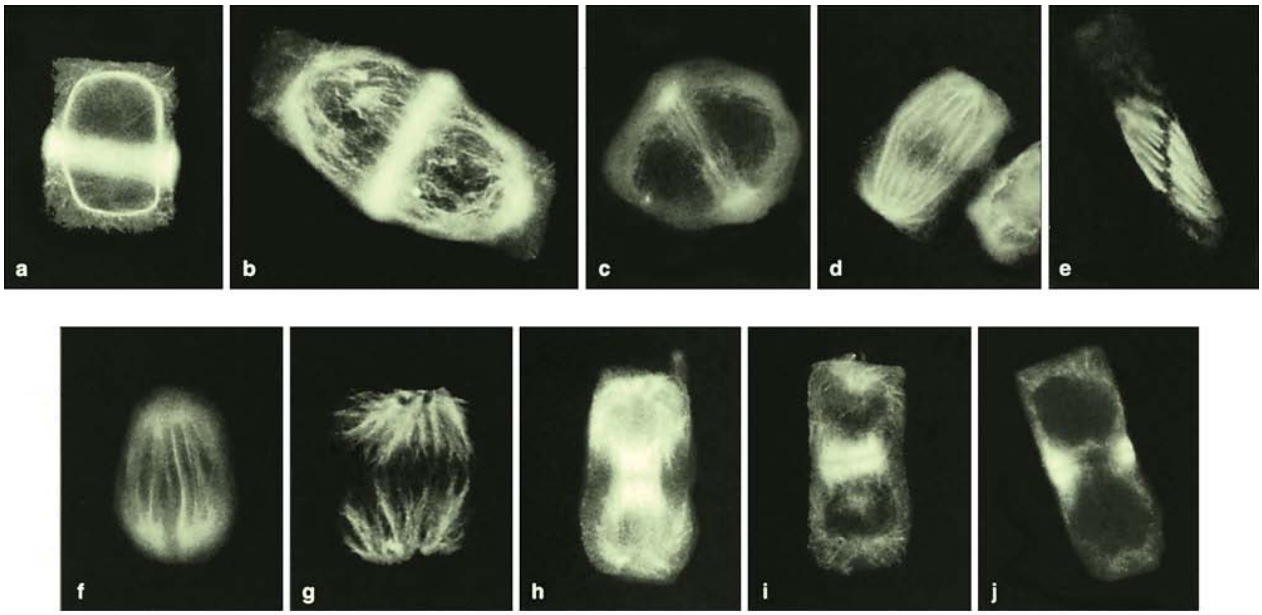

Figure 3.17. The role of microtubules in mitosis. Onion (*Allium cepa*) root tip cells were treated with tubulin antibodies tagged with a fluorescent dye and photographed by fluorescent microscopy. Thus, the photographs show only the microtubules. (**a-c**) Early prophase showing the preprophase band of microtubules plus some microtubules along the outside of the cell just inside the cell wall. (**d,e**) The spindle apparatus in early metaphase. (**f**) Metaphase chromosomes are located in the center of the cells. (**g**) Anaphase chromosomes migrate back toward the poles, and the spindle apparatus microtubules will disperse. (**h,i**) The dense accumulation of microtubules in the center of the cell shows the early formation of the cell plate. (**j**) Late telophase showing microtubules only at the periphery of the cell plate. Used by permission of S. Wick, *J. Cell Biol.* 89:685-690 (1981). Copyright The Rockefeller University Press, NY.

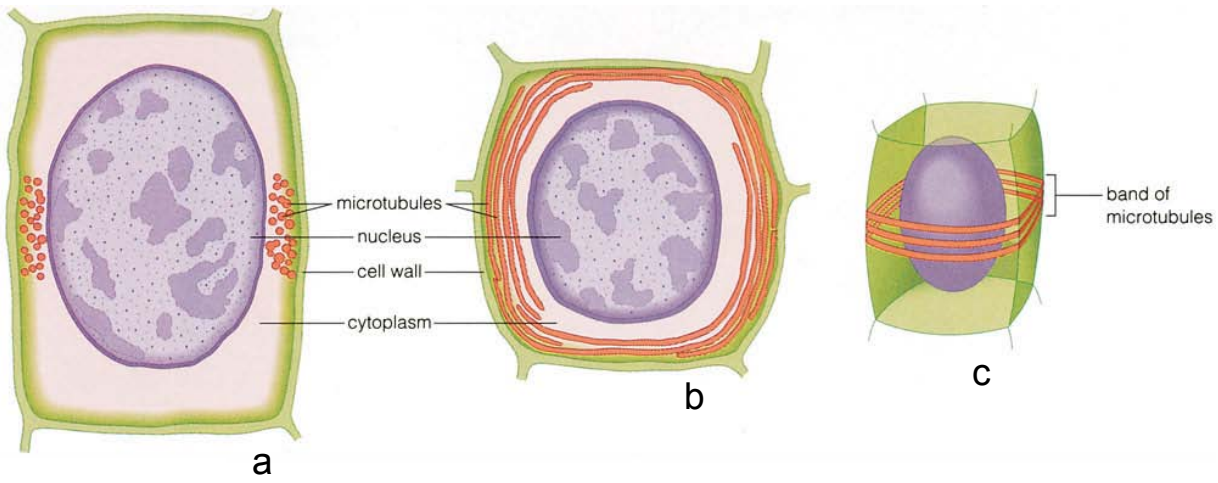

Figure 3.18. Formation of the preprophase band of microtubules in meristematic cells. (**a**) Section at right angles to the plane of future cell plate shows a cross-section of microtubules. (**b**) Section in the plane of the future cell plate shows microtubules encircling the nucleus. (c) Three-dimensional drawing of **a** and **b**. Redrawn after K. Esau and J. Cronshaw, Protoplasma 65:1. Copyright 1966 by Springer-Verlag. Reprinted by permission of the publisher.

Mitosis Occurs in Stages and Is Followed by Cytokinesis

The purpose of mitosis is to separate the DNA, which was doubled in amount during the S phase, in such a way as to produce two complete sets of genetic information. The process of mitosis is generally divided into four phases to make it easier to understand.

PROPHASE. During G1, S, and G2 phases (interphase), the DNA molecules are long and apparently tangled in the nucleus. At the start of **prophase**, the DNA molecules thicken by coiling on themselves several times to form dense chromosomes (Figs. 3.9d and 3.19ab). The nucleolus gradually disappears.

It becomes apparent during late prophase that each chromosome is composed of two intertwined DNA molecules connected by a constricted region called a **centromere** (Fig. 3.19bc). The nuclear membrane breaks down during late prophase, but the nucleoplasm does not mix with the general cytoplasm; there is a clear zone between them, devoid of organelles.

METAPHASE. In metaphase, the chromosomes arrange themselves on the equatorial plane of the cell, usually with their centromeres aligned (Fig. 3.19c). This position may be in the middle of the cell, or it may be off center, resulting in an unequal cell division. The spindle fibers, composed of bundles of microtubules, can now be seen. The spindle extends from the poles near the ends of the cell to their attachment point on each chromosome, the **kinetochore**, where motor proteins connect the centromere to the microtubules. All of the spindle fibers collectively are called the *spindle apparatus*.

The chromosomes are now distinct bodies of two closely associated halves, each half known as a **chromatid**. In plants such as corn (*Zea mays*), which have been intensively studied, each chromosome can be recognized and numbered.

There are 20 chromosomes in corn, but only 10 different types that can be distinguished by their size and form. The 10 chromosomes of corn may be arranged in 10 pairs. Geneticists have mapped corn chromosomes, showing the relative positions of many genes along their length. Because each gene is replicated, when the chromosomes split longitudinally, each chromatid contains a full set of genes.

ANAPHASE. The chromosomes do not remain long at the equatorial plane. The individual chromatids of each pair soon separate from each other and move to opposite poles of the cell (Fig. 3.19d). This period is called **anaphase**.

The mechanism of chromosome movement and the functional role of the spindle fiber microtubules are not fully understood. There are two major mechanisms to explain chromosome movement. The *assembly-disassembly mechanism* contends that microtubules move chromosomes by losing tubulin molecules from one end of the spindle. The removal of tubulin subunits from both poles of the spindle would shorten the spindle and pull the chromosomes apart. The *motor protein mechanism* contends that the chromosomes slide over microtubules of the spindle. Motor proteins at the kinetochore provide the sliding force.

TELOPHASE. When the divided chromosomes have reached the opposite poles of the cell, **telophase** begins. The chromosomes aggregate and begin to uncoil (Fig. 3.19e) into long, thin chromatin strands. The nuclear envelope and the nucleolus re-form, and the cells return once again to G1 phase of the cell cycle.

CYTOKINESIS. Cytokinesis begins before telophase is finished. A new cell wall, called the **cell plate**, starts to form between the separated nuclei (Fig. 3.19e). This process involves the **phragmoplast** (Fig. 3.17i), which consists of a band of microtubules that re-forms perpendicular to the cell plate and of many small membrane-bound vesicles. The small vesicles contain cell wall material, which is deposited first in the center of the cell and then outward until the new wall attaches to the side walls. The point of attachment, you will recall, was previously "marked" by the PPB (Fig. 3.18). Some of the new cells that are formed by mitosis and cytokinesis will divide again in plant meristems, and others will begin to differentiate to form specialized cells.

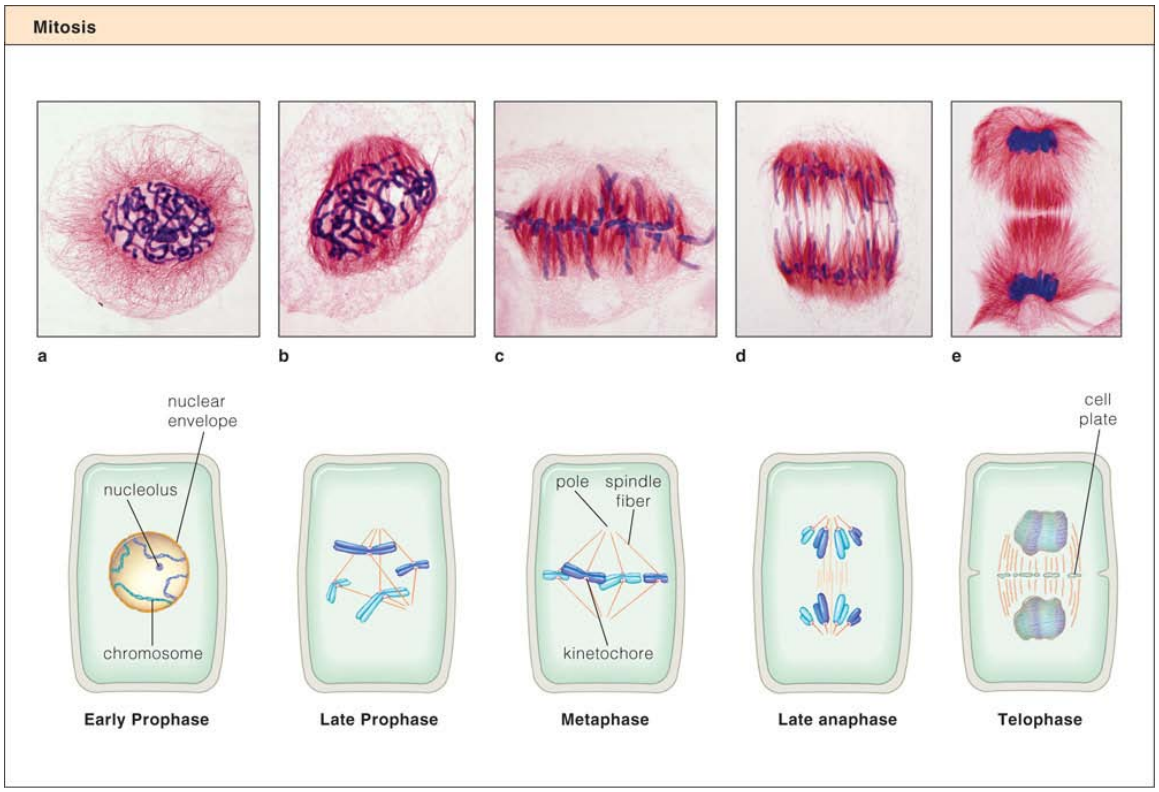

Figure 3.19. The stages of mitosis, shown in light micrographs of cells from the endosperm of the blood lily (*Haemanthus katherinae*); proteins (including microtubules) are red, and chromosomes are blue. These cells are unusual in that they do not have cell walls. The bottom row diagrams mitosis in the more typical meristem cell with a cell wall. Cells from G2 phase, with duplicated chromosomes, form the starting material for mitosis. (**a**) Early prophase: the chromosomes start to become thicker and shorter by coiling tightly. The nuclear envelope is still present. (**b**) Late prophase: the nuclear envelope and nucleolus have disappeared. On each chromosome a kinetochore becomes visible. Spindle fibers are starting to appear. (**c**) Metaphase: the coiled chromosomes are distinct. The spindle is organized, and the kinetochores line up in the middle of the spindle. (**d**) Late anaphase: the chromatids have moved to opposite poles of the cell. (**e**) Telophase: chromatids have aggregated at the opposite poles of the cell. The nuclear envelopes have not yet formed. A cell plate has formed.

KEY TERMS

amyloplasts
anaphase
apoplast
cell cycle
cell plate
cell theory
cellulose
cell wall
centromere
channels
chlorophyll
chloroplasts
chromatid
chromoplasts
chromosomes
cisternae
confocal microscopy
cristae
cutin
cyclosis
cytokinesis
cytoplasm
cytoskeleton
dictyosome
endoplasmic reticulum (ER)
glyoxysomes
Golgi apparatus
interphase
ion pumps
kinetochore
leukoplasts
lignin
lysosomes
matrix
meristems
metaphase
microfibrils
microfilament
microtubules
mitochondria
nuclear envelope
nucleoli
nucleus
organelles
osmosis
peroxisomes
phospholipid bilayer
phragmoplast
plasma membrane
plasmodesmata
plasmolysis
plastids
polyribosomes
preprophase band (PPB)
proplastids
prophase
proton pumps
protoplast
ribosomes
scanning electron microscopy
stroma
suberin
symplast
telophase
thylakoids
transmission electron microscopy
turgor
vacuole
vesicles

SUMMARY

1. All organisms are formed from one or more cells. All cells demonstrate the basic functions of life, including controlling their size, accumulating nutrients, extracting energy from the environment, reproducing, and withstanding or tolerating environmental stresses. Cells are produced only by reproduction from previously existing cells.

2. Because cells are very small, an essential tool for their study is microscopy. Light microscopes can be used to visualize live samples, but contrast and resolution are major problems in light microscopy. These limitations can be minimized or circumvented by confocal microscopy, transmission electron microscopy and scanning electron microscopy.

3. The plasma membrane surrounds the cytoplasm of the cell. It is formed from a lipid bilayer and proteins. The lipid bilayer prevents the diffusion of water-soluble molecules into or out of the cell. Proteins in the plasma membrane control the passage of molecules through the plasma membrane, among other functions.

4. The cell wall, formed from carbohydrates and proteins, prevents excess water from entering the cell through osmosis and provides the turgor pressure that gives most plant organs a firm structure.

5. The nucleus contains chromosomes made of DNA and protein. DNA serves as a template for mRNA synthesis; mRNA directs protein synthesis. The nucleolus (or plural, nucleoli) inside the nucleus is responsible for the synthesis of ribosomal RNA. Ribosomal RNA plus specific proteins form ribosomes, which together with mRNA leave the nucleus and form polyribosomes in the cytoplasm, where proteins are synthesized.

6. The endoplasmic reticulum (ER) is a tubular compartment extending around the periphery of the cell. Polyribosomes that are synthesizing proteins destined for export from the cell or for import into vesicles attach to the surface of the ER and inject their protein products into its lumen. Proteins leave the ER inside vesicles. The Golgi apparatus directs the flow of proteins and other substances in vesicles from the ER to their destinations in the cell.

7. Plastids are bounded by a double membrane and have their own DNA- and protein-synthesizing systems. There are several types of plastids, including chloroplasts, which enclose thylakoid membranes and catalyze the reactions of photosynthesis; amyloplasts, which store starch; and chromoplasts, which contain high concentrations of colored carotenoids and xanthophylls.

8. Mitochondria also are bounded by a double membrane and have their own DNA- and protein-synthesizing systems. They catalyze the oxidation of organic compounds to CO_2 and H_2O and use a portion of the energy released to synthesize ATP.

9. Among the specialized compartments bounded by a single membrane are the vacuole and some specialized vesicles. Vacuoles store salts, sugars, defensive compounds toxic to predators, and wastes. Some vesicles store energy-rich lipids or proteins (liposomes, protein bodies); some compartmentalize enzymatic reactions (glyoxysomes, peroxysomes); and some control the release of destructive enzymes (lysosomes).

10. The cytoskeleton, which is formed from protein filaments, directs the organization and movement of organelles with the cell. Motor proteins (dynein, kinesin, myosin) move along filaments, dragging other organelles with them.

11. Cells reproduce by passing through a series of events called the cell cycle. The four phases of the cell cycle are: G1, the pre-DNA synthesis phase; S, the DNA synthesis phase; G2, the premitotic phase; and M, the cell division phase.

12. Higher plant cells and fission yeast have control points at G1 and G2 phases. If critical metabolic events do not occur at these points, DNA synthesis and mitosis will not occur.

13. Microtubules have several roles in plant cell division, including control of cell plate location and regulation of chromosome movement. The PPB of microtubules forms in the G2 phase and marks the plane of cell division.

14. The stages of mitosis are prophase, metaphase, anaphase, and telophase.

Mitotic Stage	*Summary of Events*
Prophase	Chromosomes coil; the nuclear envelope and the nucleolus break down.
Metaphase	Chromosomes move to the equatorial plane; the spindle apparatus forms and attaches to the chromosomes at the kinetochores.
Anaphase	Chromosomes move to the poles by some mechanism involving the spindle fibers.
Telophase	Chromosomes uncoil; the nuclear envelope and the nucleolus re-form.

15. During cytokinesis, the cell plate, containing cell wall materials, forms first in the middle of the cell and then moves to the periphery, dividing the cytoplasm in two.

Questions

1. Explain why it is necessary to use a microscope to see a cell. Describe the difference between the image of a cell seen at high magnification with low resolution and one seen at the same magnification but with high resolution.

2. Assume a cell is a cube with 10-μm sides. What is the volume of the cell in cubic micrometers? What is the volume in cubic meters? How many of these cells would fill a teaspoon (approximately 5 cm^3)?

3. List the organelles that are needed to synthesize a protein and move it to the outside of a cell.

4. Which of the following organelles is (are) absolutely essential for the synthesis of a protein? Which will be needed for the treatment of the protein after it is made?

Nuclear envelope
Ribosome
Microtubules
Endoplasmic reticulum
Golgi apparatus

5. Almost every living plant cell has mitochondria. Explain why the presence of mitochondria is essential for a cell's well-being.

6. In what organ(s) of the plant would you find the most chloroplasts?

7. Assume that a cell must reproduce itself exactly. List the events that must occur in G1, S, G2, and M phases for the reproduction to be successful.

8. List the phases of mitosis and describe what happens in each. If you add a chemical that blocks the formation of microtubules to a cell that is starting mitosis, mitosis eventually stops. In what phase will it stop?

PLANTS, PEOPLE, AND THE ENVIRONMENT: *Foods and Health*

Food is one of life's great delights. Food nourishes, comforts, educates, protects, and provides pleasure every day of our lives. The chemicals in foods play a major role in determining how healthy we are. Plants are a major source of chemicals for energy, synthesis of body tissue, and control of environmental toxins.

Modern science and technology have provided unparalleled values to consumers in the breadth of choices in delicious, safe, and nutritious foods. These values have been driven by scientific knowledge at all levels of the agricultural enterprise, from genetic improvements in production agriculture to mathematic control of food process engineering, from molecular understanding of food safety to statistical precision in the analysis of consumer sensation. One of science's great achievements of the 20th century was building the quantitative knowledge of the nutritional requirements for humans and animals and practically eliminating primary nutrient deficiencies in the developed world.

The successes in health that were achieved by defining the essential nutrients have generated new challenges, both with respect to a better understanding of mechanisms important to chronic disease processes and the expansion in food choices. At a time when the opportunities to produce a wide variety of foods to improve health would seem unprecedented, more and more individuals lacking sufficient knowledge of themselves, or their foods, are choosing diets that increase their risk for metabolic imbalances and disease rather than making optimal choices. The prevalence of diet-related diseases such as obesity, type-2 diabetes, food allergies and intolerances, and cardiovascular disease is increasing throughout the world, highlighting our discouraging lack of scientific knowledge of the precise molecular and mechanistic links between food and health.

During the last decade, there has been a paradigm shift in how food and diet are viewed with respect to human health and wellbeing. As an example, the Food and Nutrition Board of the Institute of Medicine (IOM), working in cooperation with scientists from Canada, recently developed Dietary Reference Intakes (DRIs) for the essential nutrients. In marked contrast to the previous Recommended Dietary Allowances (RDAs), the new DRI values for nutrients are defined as targets for the "individual," rather than the general population. The philosophy underlying the development of the DRI values is to identify the amount of essential nutrients that an individual needs to consume to reduce his or her risk for chronic disease. Notably, for several nutrients, the new DRI values for certain essential nutrients have been set at levels that cannot be easily met from non-fortified foods.

The recent surge of interest by the U.S. Department of Agriculture in chemical constituents of plants (phytochemicals) illustrates the growing awareness of the potential health benefits associated with consuming certain phytochemicals. Importantly, the phytochemical profile, and content, of foods can be markedly influenced by agricultural practices, as well as by food processing. Public health officials are increasingly looking to diet as a means to reduce many common chronic diseases. This interest in dietary solutions is occurring in part as a consequence of recent steep increases in the cost of conventional medicine, and in part because of an increasing awareness that through diet one can significantly reduce the risk for

many common diseases. Thus at the national and international level, the line between food and medicine is becoming increasing blurred, and the need for research on nutrition is becoming ever more important.

Adapted from "Foods for Health" by Bruce German, Bruce Hammock, Carl Keen and Janet King, University of California, Davis.

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