Chapter

1 Plant Cells

THE TERM *CELL* IS DERIVED from the Latin *cella,* meaning storeroom or chamber. It was first used in biology in 1665 by the English botanist Robert Hooke to describe the individual units of the honeycomb-like structure he observed in cork under a compound microscope. The "cells" Hooke observed were actually the empty lumens of dead cells surrounded by cell walls, but the term is an apt one because cells are the basic building blocks that define plant structure.

This book will emphasize the physiological and biochemical functions of plants, but it is important to recognize that these functions depend on structures, whether the process is gas exchange in the leaf, water conduction in the xylem, photosynthesis in the chloroplast, or ion transport across the plasma membrane. At every level, structure and function represent different frames of reference of a biological unity.

This chapter provides an overview of the basic anatomy of plants, from the organ level down to the ultrastructure of cellular organelles. In subsequent chapters we will treat these structures in greater detail from the perspective of their physiological functions in the plant life cycle.

PLANT LIFE: UNIFYING PRINCIPLES

The spectacular diversity of plant size and form is familiar to everyone. Plants range in size from less than 1 cm tall to greater than 100 m. Plant morphology, or shape, is also surprisingly diverse. At first glance, the tiny plant duckweed (*Lemna*) seems to have little in common with a giant saguaro cactus or a redwood tree. Yet regardless of their specific adaptations, all plants carry out fundamentally similar processes and are based on the same architectural plan. We can summarize the major design elements of plants as follows:

- As Earth's primary producers, green plants are the ultimate solar collectors. They harvest the energy of sunlight by converting light energy to chemical energy, which they store in bonds formed when they synthesize carbohydrates from carbon dioxide and water.

- Other than certain reproductive cells, plants are nonmotile. As a substitute for motility, they have evolved the ability to grow toward essential resources, such as light, water, and mineral nutrients, throughout their life span.
- Terrestrial plants are structurally reinforced to support their mass as they grow toward sunlight against the pull of gravity.
- Terrestrial plants lose water continuously by evaporation and have evolved mechanisms for avoiding desiccation.
- Terrestrial plants have mechanisms for moving water and minerals from the soil to the sites of photosynthesis and growth, as well as mechanisms for moving the products of photosynthesis to nonphotosynthetic organs and tissues.

OVERVIEW OF PLANT STRUCTURE

Despite their apparent diversity, all seed plants (see **Web Topic 1.1**) have the same basic body plan (Figure 1.1). The vegetative body is composed of three organs: **leaf**, **stem**, and **root**. The primary function of a leaf is photosynthesis, that of the stem is support, and that of the root is anchorage and absorption of water and minerals. Leaves are attached to the stem at **nodes**, and the region of the stem between two nodes is termed the **internode**. The stem together with its leaves is commonly referred to as the **shoot**.

There are two categories of seed plants: gymnosperms (from the Greek for "naked seed") and angiosperms (based on the Greek for "vessel seed," or seeds contained in a vessel). **Gymnosperms** are the less advanced type; about 700 species are known. The largest group of gymnosperms is the conifers ("cone-bearers"), which include such commercially important forest trees as pine, fir, spruce, and redwood.

Angiosperms, the more advanced type of seed plant, first became abundant during the Cretaceous period, about 100 million years ago. Today, they dominate the landscape, easily outcompeting the gymnosperms. About 250,000 species are known, but many more remain to be characterized. The major innovation of the angiosperms is the flower; hence they are referred to as *flowering plants* (see **Web Topic 1.2**).

Plant Cells Are Surrounded by Rigid Cell Walls

A fundamental difference between plants and animals is that each plant cell is surrounded by a rigid **cell wall**. In animals, embryonic cells can migrate from one location to another, resulting in the development of tissues and organs containing cells that originated in different parts of the organism.

In plants, such cell migrations are prevented because each walled cell and its neighbor are cemented together by a **middle lamella**. As a consequence, plant development, unlike animal development, depends solely on patterns of cell division and cell enlargement.

FIGURE 1.1 Schematic representation of the body of a typical dicot. Cross sections of (A) the leaf, (B) the stem, and (C) the root are also shown. Inserts show longitudinal sections of a shoot tip and a root tip from flax (*Linum usitatissimum*), showing the apical meristems. (Photos © J. Robert Waaland / Biological Photo Service.)

Plant cells have two types of walls: primary and secondary (Figure 1.2). **Primary cell walls** are typically thin (less than 1 μm) and are characteristic of young, growing cells. **Secondary cell walls** are thicker and stronger than primary walls and are deposited when most cell enlargement has ended. Secondary cell walls owe their strength and toughness to **lignin**, a brittle, gluelike material (see Chapter 13).

The evolution of lignified secondary cell walls provided plants with the structural reinforcement necessary to grow vertically above the soil and to colonize the land. Bryophytes, which lack lignified cell walls, are unable to grow more than a few centimeters above the ground.

New Cells Are Produced by Dividing Tissues Called Meristems

Plant growth is concentrated in localized regions of cell division called **meristems**. Nearly all nuclear divisions (mitosis) and cell divisions (cytokinesis) occur in these meristematic regions. In a young plant, the most active meristems are called **apical meristems**; they are located at the tips of the stem and the root (see Figure 1.1). At the nodes, **axillary buds** contain the apical meristems for branch shoots. Lateral roots arise from the **pericycle**, an internal meristematic tissue (see Figure 1.1C). Proximal to (i.e., next to) and overlapping the meristematic regions are zones of cell elongation in which cells increase dramatically in length and width. Cells usually differentiate into specialized types after they elongate.

The phase of plant development that gives rise to new organs and to the basic plant form is called **primary growth**. Primary growth results from the activity of apical meristems, in which cell division is followed by progressive cell enlargement, typically elongation. After elongation in a given region is complete, **secondary growth** may occur. Secondary growth involves two lateral meristems: the **vascular cambium** (plural *cambia*) and the **cork cambium.** The vascular cambium gives rise to secondary xylem (wood) and secondary phloem. The cork cambium produces the periderm, consisting mainly of cork cells.

Three Major Tissue Systems Make Up the Plant Body

Three major tissue systems are found in all plant organs: dermal tissue, ground tissue, and vascular tissue. These tis-

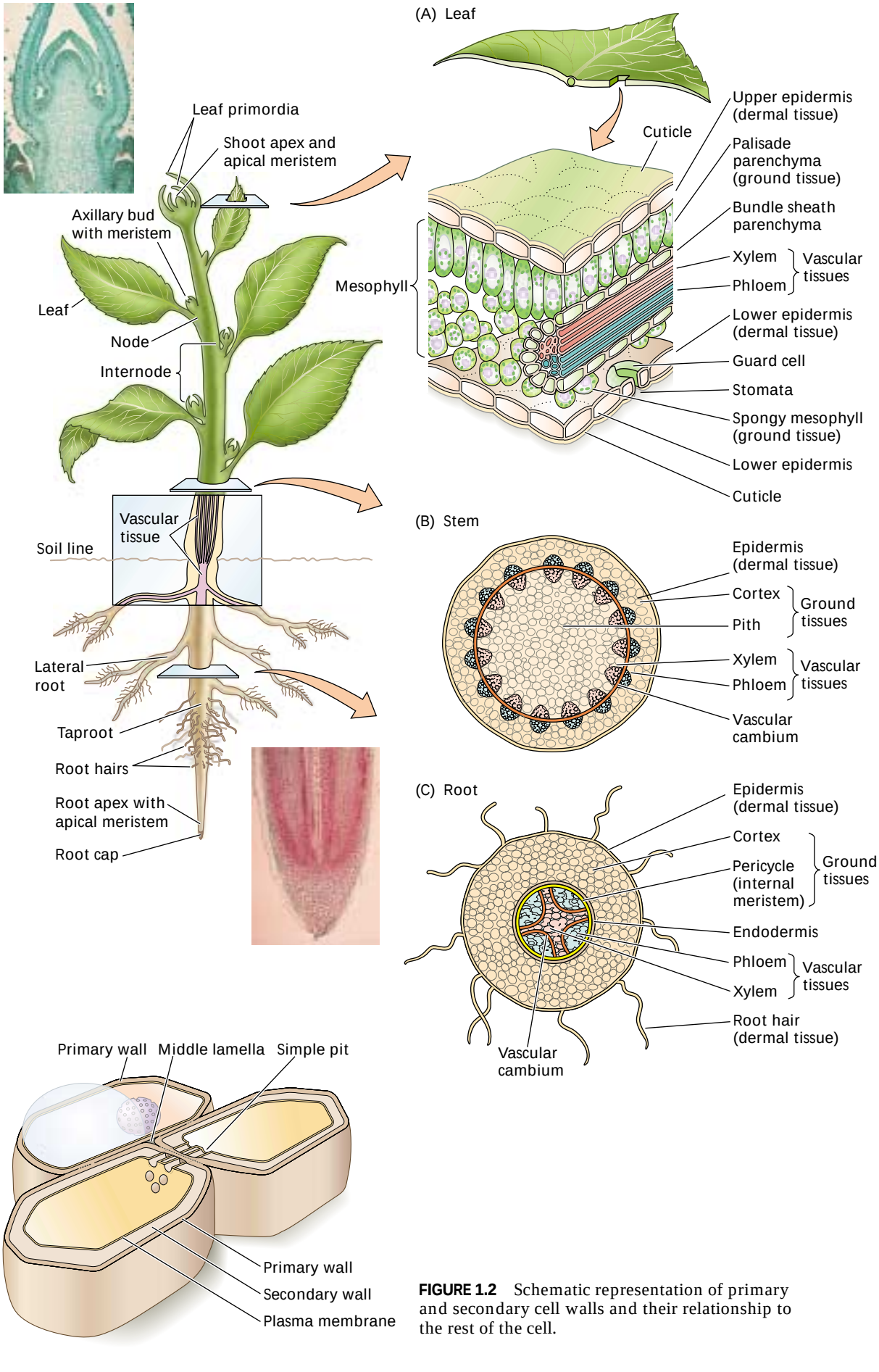
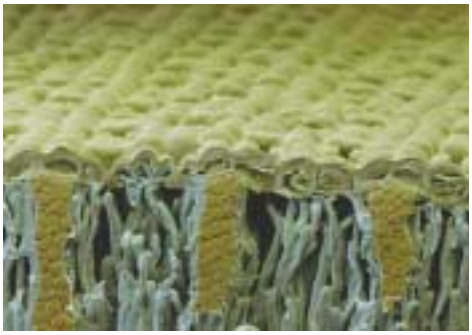
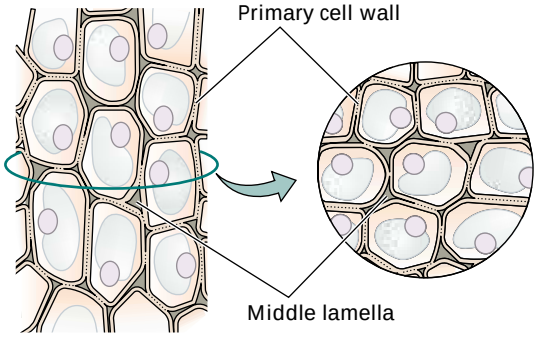


FIGURE 1.2 Schematic representation of primary and secondary cell walls and their relationship to the rest of the cell.

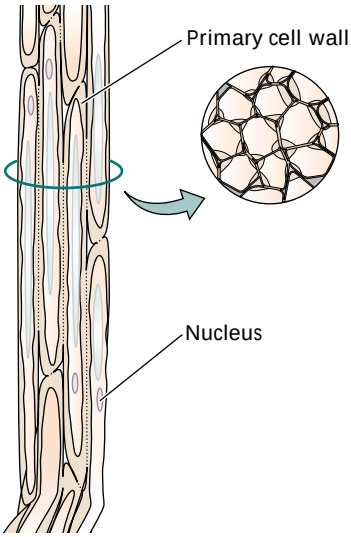
(A) Dermal tissue: epidermal cells



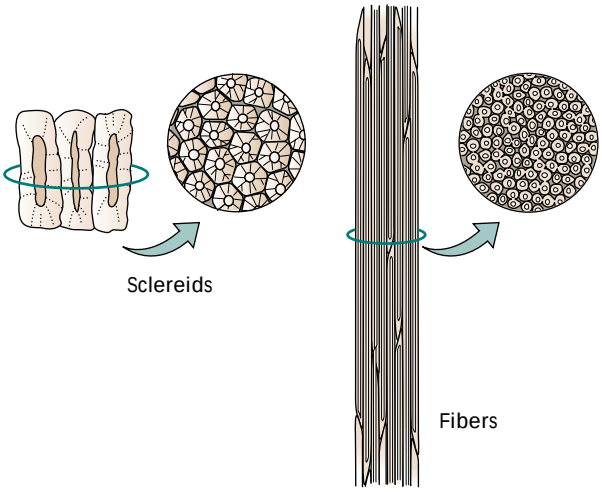
(B) Ground tissue: parenchyma cells



(C) Ground tissue: collenchyma cells



(D) Ground tissue: sclerenchyma cells



(E) Vascular tisssue: xylem and phloem

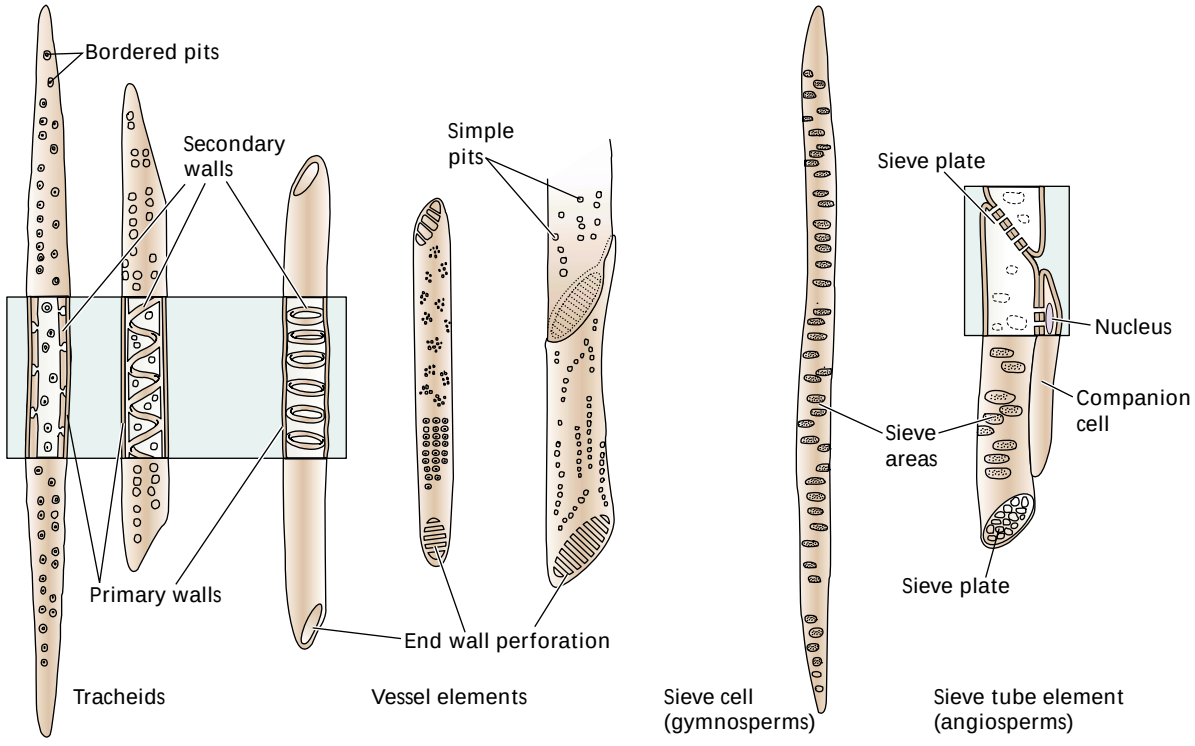


FIGURE 1.3 (A) The outer epidermis (dermal tissue) of a leaf of *welwischia mirabilis* (120×). Diagrammatic representations of three types of ground tissue: (B) parenchyma, (C) collenchyma, (D) sclerenchyma cells, and (E) conducting cells of the xylem and phloem. (A © Meckes / Ottawa / Photo Researchers, Inc.)

sues are illustrated and briefly chacterized in Figure 1.3. For further details and characterizations of these plant tissues, see **Web Topic 1.3**.

THE PLANT CELL

Plants are multicellular organisms composed of millions of cells with specialized functions. At maturity, such specialized cells may differ greatly from one another in their structures. However, all plant cells have the same basic eukaryotic organization: They contain a nucleus, a cytoplasm, and subcellular organelles, and they are enclosed in a membrane that defines their boundaries (Figure 1.4). Certain structures, including the nucleus, can be lost during cell maturation, but all plant cells *begin* with a similar complement of organelles.

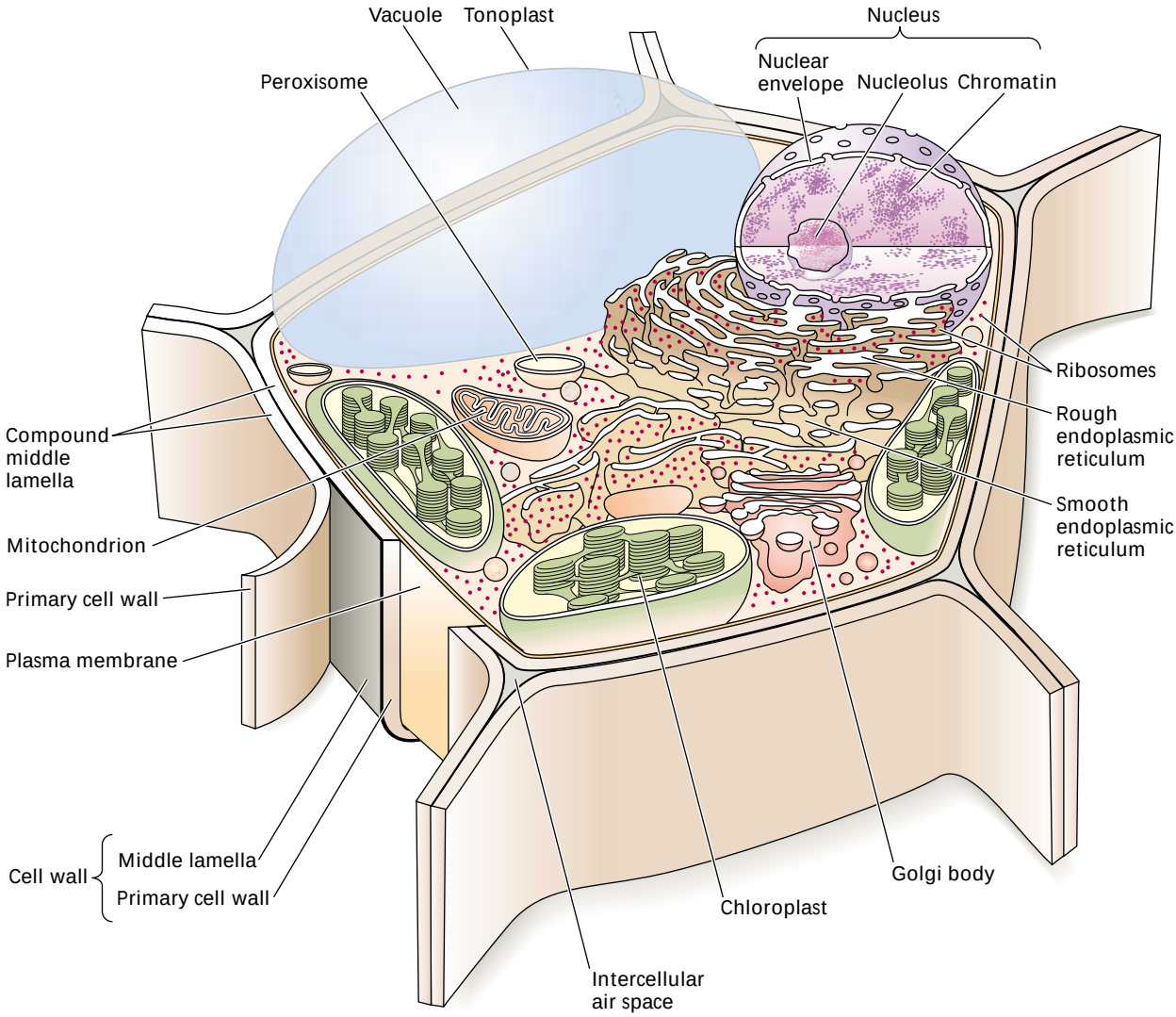


FIGURE 1.4 Diagrammatic representation of a plant cell. Various intracellular compartments are defined by their respective membranes, such as the tonoplast, the nuclear envelope, and the membranes of the other organelles. The two adjacent primary walls, along with the middle lamella, form a composite structure called the compound middle lamella.

An additional characteristic feature of plant cells is that they are surrounded by a cellulosic cell wall. The following sections provide an overview of the membranes and organelles of plant cells. The structure and function of the cell wall will be treated in detail in Chapter 15.

Biological Membranes Are Phospholipid Bilayers That Contain Proteins

All cells are enclosed in a membrane that serves as their outer boundary, separating the cytoplasm from the external environment. This **plasma membrane** (also called **plasmalemma**) allows the cell to take up and retain certain substances while excluding others. Various transport proteins embedded in the plasma membrane are responsible for this selective traffic of solutes across the membrane. The accumulation of ions or molecules in the cytosol through the action of transport proteins consumes metabolic energy. Membranes also delimit the boundaries of the specialized internal organelles of the cell and regulate the fluxes of ions and metabolites into and out of these compartments.

According to the **fluid-mosaic model**, all biological membranes have the same basic molecular organization. They consist of a double layer (*bilayer*) of either phospholipids or, in the case of chloroplasts, glycosylglycerides, in which proteins are embedded (Figure 1.5A and B). In most membranes, proteins make up about half of the membrane's mass. However, the composition of the lipid components and the properties of the proteins vary from membrane to membrane, conferring on each membrane its unique functional characteristics.

Phospholipids. Phospholipids are a class of lipids in which two fatty acids are covalently linked to glycerol, which is covalently linked to a phosphate group. Also attached to this phosphate group is a variable component, called the *head group*, such as serine, choline, glycerol, or inositol (Figure 1.5C). In contrast to the fatty acids, the head groups are highly polar; consequently, phospholipid molecules display both hydrophilic and hydrophobic properties (i.e., they are *amphipathic*). The nonpolar hydrocarbon chains of the fatty acids form a region that is exclusively hydrophobic—that is, that excludes water.

Plastid membranes are unique in that their lipid component consists almost entirely of **glycosylglycerides** rather than phospholipids. In glycosylglycerides, the polar head group consists of galactose, digalactose, or sulfated galactose, without a phosphate group (see **Web Topic 1.4**).

The fatty acid chains of phospholipids and glycosylglycerides are variable in length, but they usually consist of 14 to 24 carbons. One of the fatty acids is typically *saturated* (i.e., it contains no double bonds); the other fatty acid chain usually has one or more *cis* double bonds (i.e., it is *unsaturated*).

The presence of *cis* double bonds creates a kink in the chain that prevents tight packing of the phospholipids in the bilayer. As a result, the fluidity of the membrane is increased. The fluidity of the membrane, in turn, plays a critical role in many membrane functions. Membrane fluidity is also strongly influenced by temperature. Because plants generally cannot regulate their body temperatures, they are often faced with the problem of maintaining membrane fluidity under conditions of low temperature, which tends to decrease membrane fluidity. Thus, plant phospholipids have a high percentage of unsaturated fatty acids, such as oleic acid (one double bond), linoleic acid (two double bonds) and α-linolenic acid (three double bonds), which increase the fluidity of their membranes.

Proteins. The proteins associated with the lipid bilayer are of three types: integral, peripheral, and anchored. **Integral proteins** are embedded in the lipid bilayer. Most integral proteins span the entire width of the phospholipid bilayer, so one part of the protein interacts with the outside of the cell, another part interacts with the hydrophobic core of the membrane, and a third part interacts with the interior of the cell, the cytosol. Proteins that serve as ion channels (see Chapter 6) are always integral membrane proteins, as are certain receptors that participate in signal transduction pathways (see Chapter 14). Some receptor-like proteins on the outer surface of the plasma membrane recognize and bind tightly to cell wall consituents, effectively cross-linking the membrane to the cell wall.

Peripheral proteins are bound to the membrane surface by noncovalent bonds, such as ionic bonds or hydrogen bonds, and can be dissociated from the membrane with high salt solutions or chaotropic agents, which break ionic and hydrogen bonds, respectively. Peripheral proteins serve a variety of functions in the cell. For example, some are involved in interactions between the plasma membrane and components of the cytoskeleton, such as microtubules and actin microfilaments, which are discussed later in this chapter.

Anchored proteins are bound to the membrane surface via lipid molecules, to which they are covalently attached. These lipids include fatty acids (myristic acid and palmitic acid), prenyl groups derived from the isoprenoid pathway (farnesyl and geranylgeranyl groups), and glycosylphosphatidylinositol (GPI)-anchored proteins (Figure 1.6) (Buchanan et al. 2000).

The Nucleus Contains Most of the Genetic Material of the Cell

The **nucleus** (plural *nuclei*) is the organelle that contains the genetic information primarily responsible for regulating the metabolism, growth, and differentiation of the cell. Collectively, these genes and their intervening sequences are referred to as the **nuclear genome**. The size of the nuclear genome in plants is highly variable, ranging from about 1.2×10^8 base pairs for the diminutive dicot *Arabidopsis thaliana* to 1×10^{11} base pairs for the lily *Fritillaria assyriaca*. The

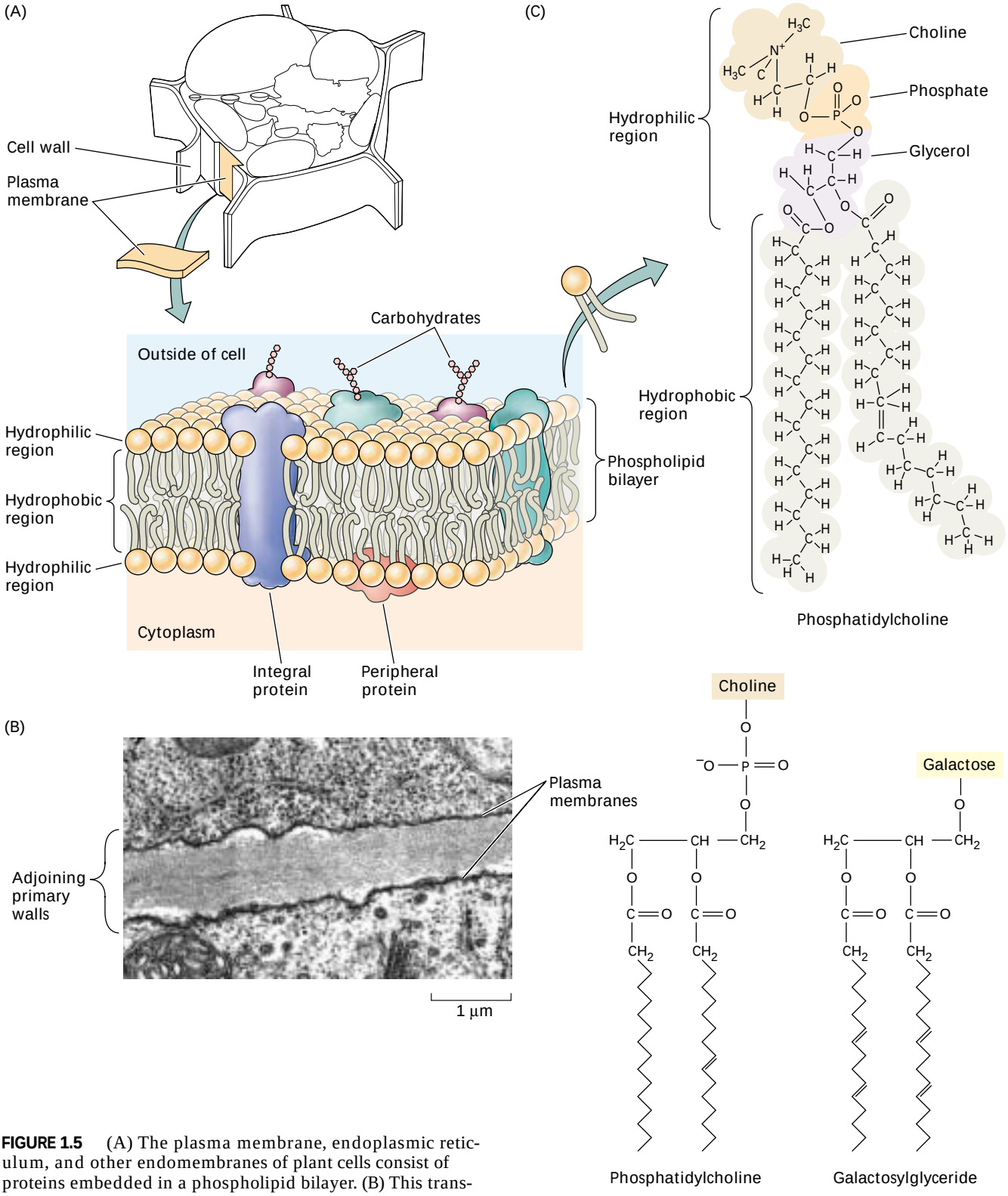


FIGURE 1.5 (A) The plasma membrane, endoplasmic reticulum, and other endomembranes of plant cells consist of proteins embedded in a phospholipid bilayer. (B) This transmission electron micrograph shows plasma membranes in cells from the meristematic region of a root tip of cress (*Lepidium sativum*). The overall thickness of the plasma membrane, viewed as two dense lines and an intervening space, is 8 nm. (C) Chemical structures and space-filling models of typical phospholipids: phosphatidylcholine and galactosylglyceride. (B from Gunning and Steer 1996.)

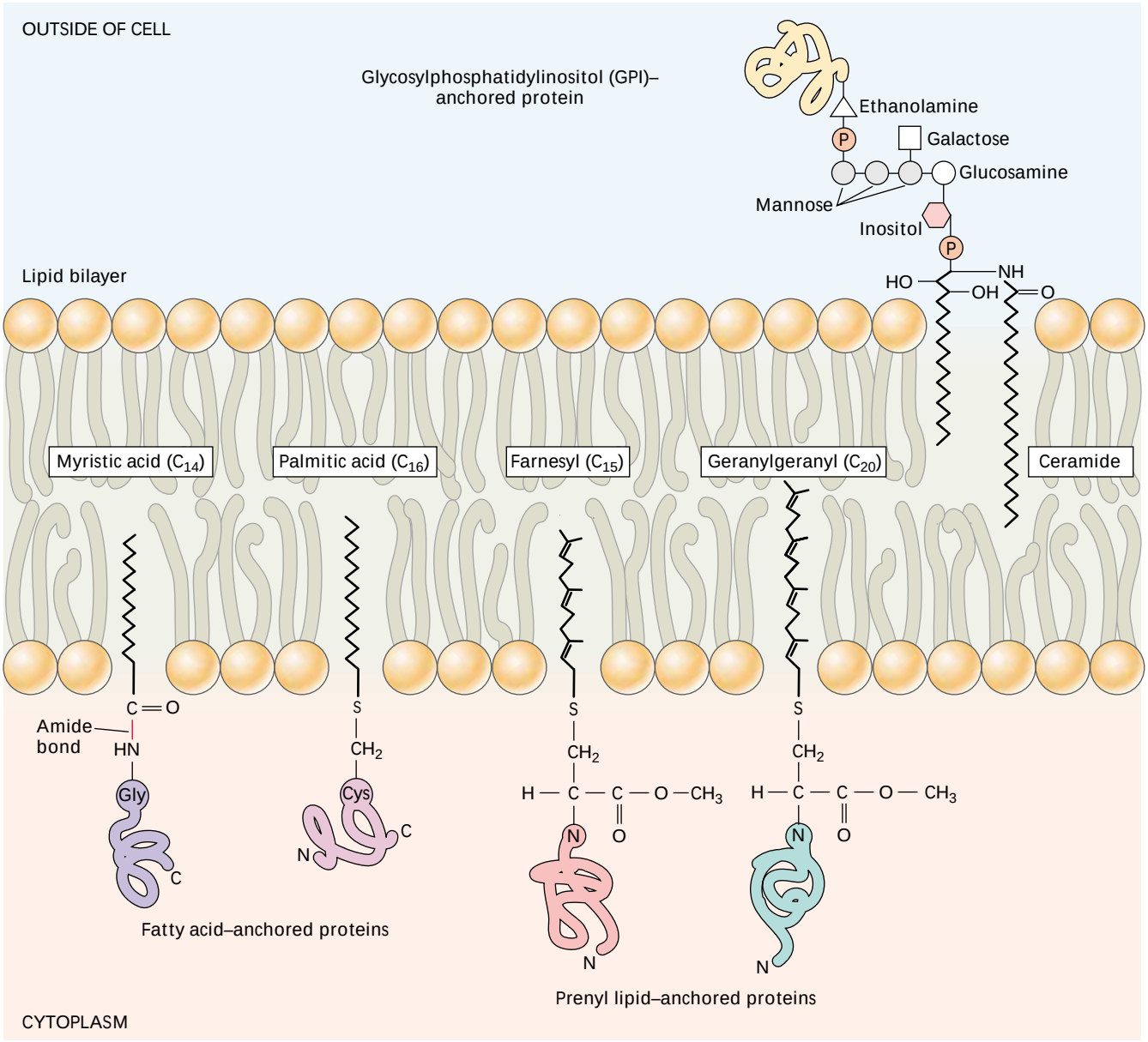


FIGURE 1.6 Different types of anchored membrane proteins that are attached to the membrane via fatty acids, prenyl groups, or phosphatidylinositol. (From Buchanan et al. 2000.)

remainder of the genetic information of the cell is contained in the two semiautonomous organelles—the chloroplasts and mitochondria—which we will discuss a little later in this chapter.

The nucleus is surrounded by a double membrane called the **nuclear envelope** (Figure 1.7A). The space between the two membranes of the nuclear envelope is called the **perinuclear space**, and the two membranes of the nuclear envelope join at sites called **nuclear pores** (Figure 1.7B). The nuclear "pore" is actually an elaborate structure composed of more than a hundred different proteins arranged octagonally to form a **nuclear pore complex** (Figure 1.8). There can be very few to many thousands of nuclear pore complexes on an individual nuclear envelope. The central "plug" of the complex acts as an active (ATP-driven) transporter that facilitates the movement of macromolecules and ribosomal subunits both into and out of the nucleus. (Active transport will be discussed in detail in Chapter 6.) A specific amino acid sequence called the **nuclear localization signal** is required for a protein to gain entry into the nucleus.

The nucleus is the site of storage and replication of the **chromosomes**, composed of DNA and its associated proteins. Collectively, this DNA–protein complex is known as

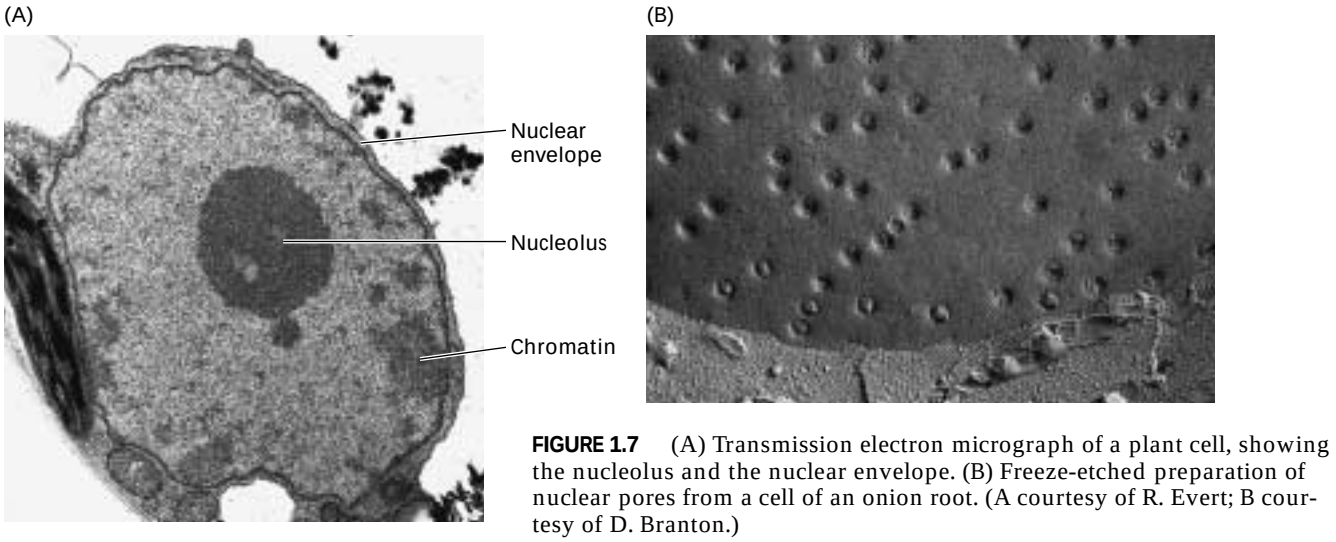


FIGURE 1.7 (A) Transmission electron micrograph of a plant cell, showing the nucleolus and the nuclear envelope. (B) Freeze-etched preparation of nuclear pores from a cell of an onion root. (A courtesy of R. Evert; B courtesy of D. Branton.)

chromatin. The linear length of all the DNA within any plant genome is usually millions of times greater than the diameter of the nucleus in which it is found. To solve the problem of packaging this chromosomal DNA within the nucleus, segments of the linear double helix of DNA are coiled twice around a solid cylinder of eight **histone** protein molecules, forming a **nucleosome**. Nucleosomes are arranged like beads on a string along the length of each chromosome.

During mitosis, the chromatin condenses, first by coiling tightly into a **30 nm chromatin fiber**, with six nucleosomes per turn, followed by further folding and packing processes that depend on interactions between proteins and nucleic acids (Figure 1.9). At interphase, two types of chromatin are visible: heterochromatin and euchromatin. About 10% of the DNA consists of **heterochromatin**, a highly compact and transcriptionally inactive form of chromatin. The rest of the DNA consists of **euchromatin**, the dispersed, transcriptionally active form. Only about 10% of the euchromatin is transcriptionally active at any given time. The remainder exists in an intermediate state of condensation, between heterochromatin and transcriptionally active euchromatin.

Nuclei contain a densely granular region, called the **nucleolus** (plural *nucleoli*), that is the site of ribosome synthesis (see Figure 1.7A). The nucleolus includes portions of one or more chromosomes where ribosomal RNA (rRNA) genes are clustered to form a structure called the **nucleolar organizer**. Typical cells have one or more nucleoli per nucleus. Each 80S ribosome is made of a large and a small subunit, and each subunit is a complex aggregate of rRNA and specific proteins. The two subunits exit the nucleus separately, through the nuclear pore, and then unite in the cytoplasm to form a complete ribosome (Figure 1.10A). **Ribosomes** are the sites of protein synthesis.

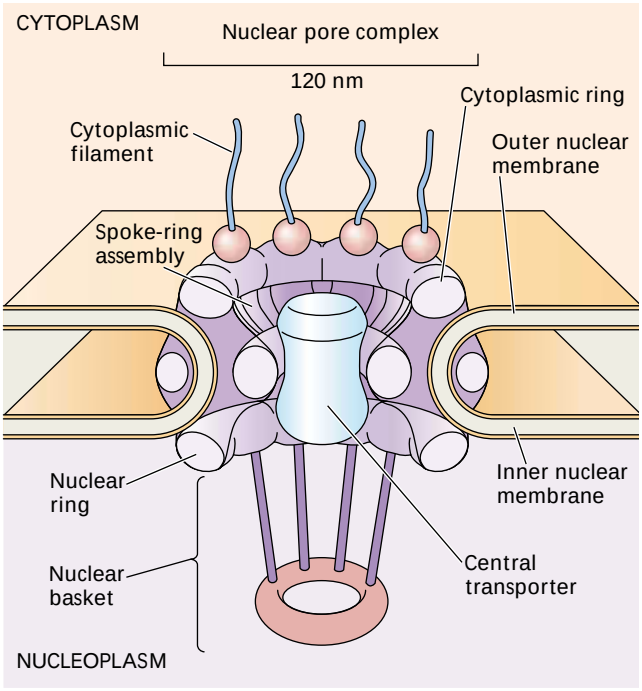


FIGURE 1.8 Schematic model of the structure of the nuclear pore complex. Parallel rings composed of eight subunits each are arranged octagonally near the inner and outer membranes of the nuclear envelope. Various proteins form the other structures, such as the nuclear ring, the spoke-ring assembly, the central transporter, the cytoplasmic filaments, and the nuclear basket.

Protein Synthesis Involves Transcription and Translation

The complex process of protein synthesis starts with **transcription**—the synthesis of an RNA polymer bearing a base

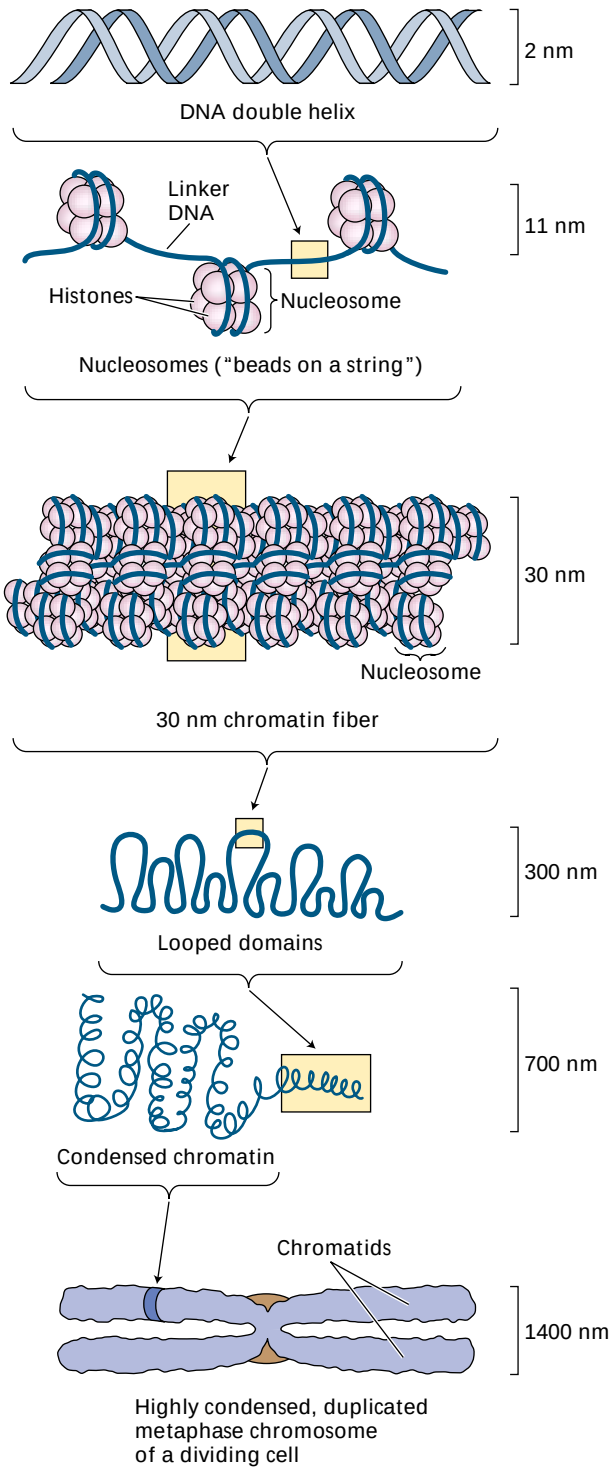


FIGURE 1.9 Packaging of DNA in a metaphase chromosome. The DNA is first aggregated into nucleosomes and then wound to form the 30 nm chromatin fibers. Further coiling leads to the condensed metaphase chromosome. (After Alberts et al. 2002.)

sequence that is complementary to a specific gene. The RNA transcript is processed to become messenger RNA (mRNA), which moves from the nucleus to the cytoplasm. The mRNA in the cytoplasm attaches first to the small ribosomal subunit and then to the large subunit to initiate translation.

Translation is the process whereby a specific protein is synthesized from amino acids, according to the sequence information encoded by the mRNA. The ribosome travels the entire length of the mRNA and serves as the site for the sequential bonding of amino acids as specified by the base sequence of the mRNA (Figure 1.10B).

The Endoplasmic Reticulum Is a Network of Internal Membranes

Cells have an elaborate network of internal membranes called the **endoplasmic reticulum** (**ER**). The membranes of the ER are typical lipid bilayers with interspersed integral and peripheral proteins. These membranes form flattened or tubular sacs known as **cisternae** (singular *cisterna*).

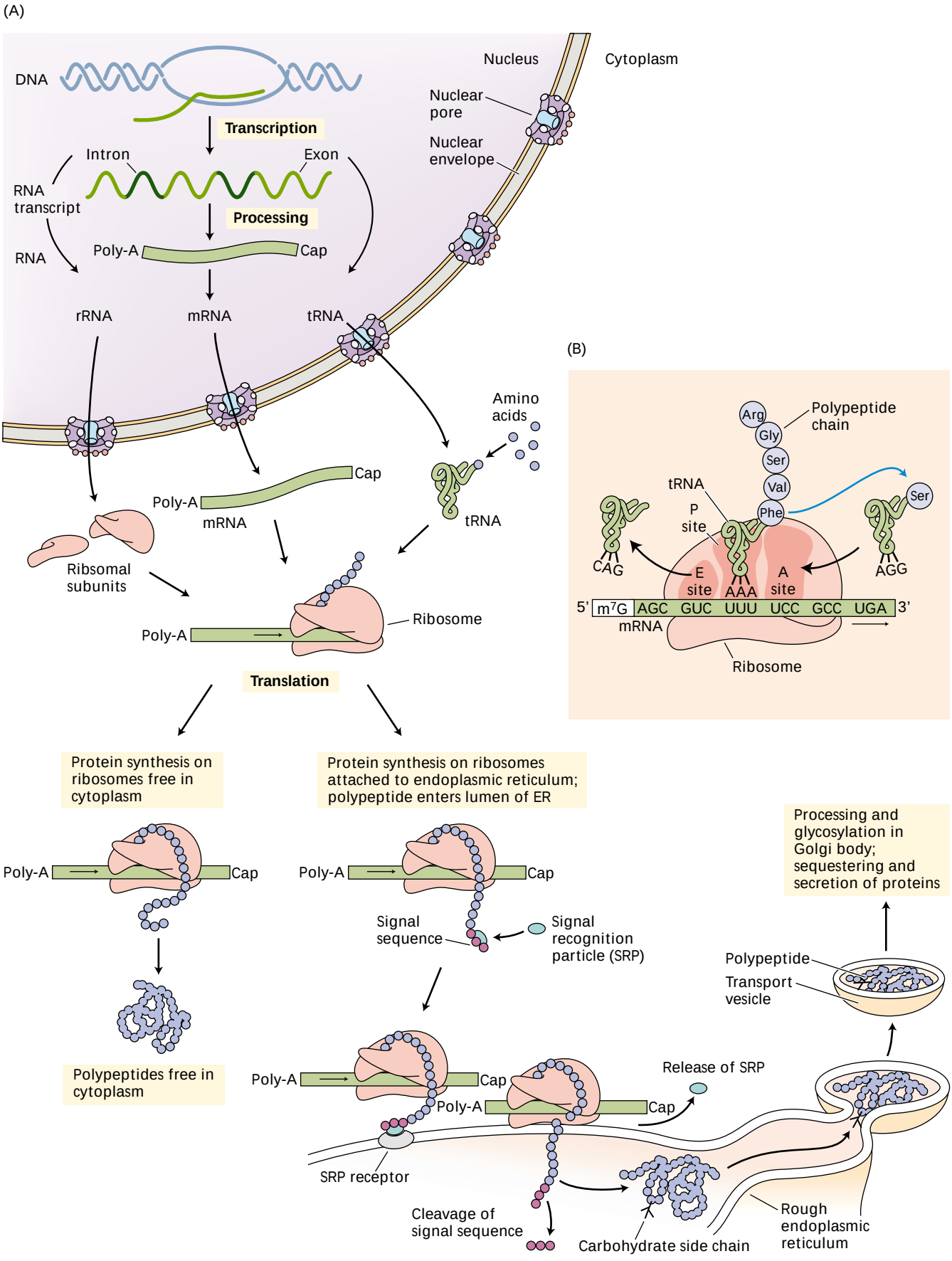
Ultrastructural studies have shown that the ER is continuous with the outer membrane of the nuclear envelope. There are two types of ER—smooth and rough (Figure 1.11)—and the two types are interconnected. **Rough ER** (**RER**) differs from smooth ER in that it is covered with ribosomes that are actively engaged in protein synthesis; in addition, rough ER tends to be lamellar (a flat sheet composed of two unit membranes), while smooth ER tends to be tubular, although a gradation for each type can be observed in almost any cell.

The structural differences between the two forms of ER are accompanied by functional differences. **Smooth ER** functions as a major site of lipid synthesis and membrane assembly. Rough ER is the site of synthesis of membrane proteins and proteins to be secreted outside the cell or into the vacuoles.

Secretion of Proteins from Cells Begins with the Rough ER

Proteins destined for secretion cross the RER membrane and enter the lumen of the ER. This is the first step in the

FIGURE 1.10 (A) Basic steps in gene expression, including transcription, processing, export to the cytoplasm, and translation. Proteins may be synthesized on free or bound ribosomes. Secretory proteins containing a hydrophobic signal sequence bind to the signal recognition particle (SRP) in the cytosol. The SRP–ribosome complex then moves to the endoplasmic reticulum, where it attaches to the SRP receptor. Translation proceeds, and the elongating polypeptide is inserted into the lumen of the endoplasmic reticulum. The signal peptide is cleaved off, sugars are added, and the glycoprotein is transported via vesicles to the Golgi. (B) Amino acids are polymerized on the ribosome, with the help of tRNA, to form the elongating polypeptide chain.


(A)
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Transcription
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RNA transcript
Processing
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Cap
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Nucleus
Cytoplasm
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Amino acids
Cap
Poly-A
mRNA
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Ribosomal subunits
Poly-A
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Translation
(B)
Arg
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Ser
Val
Phe
Polypeptide chain
tRNA
P site
Ser
CAG
E site
AAA
A site
AGG
5'
m7G
AGC
GUC
UUU
UCC
GCC
UGA
3'
mRNA
Ribosome
Protein synthesis on ribosomes free in cytoplasm
Protein synthesis on ribosomes attached to endoplasmic reticulum; polypeptide enters lumen of ER
Poly-A
Cap
Polypeptides free in cytoplasm
Signal sequence
Signal recognition particle (SRP)
Release of SRP
SRP receptor
Cleavage of signal sequence
Carbohydrate side chain
Rough endoplasmic reticulum
Processing and glycosylation in Golgi body; sequestering and secretion of proteins
Polypeptide
Transport vesicle

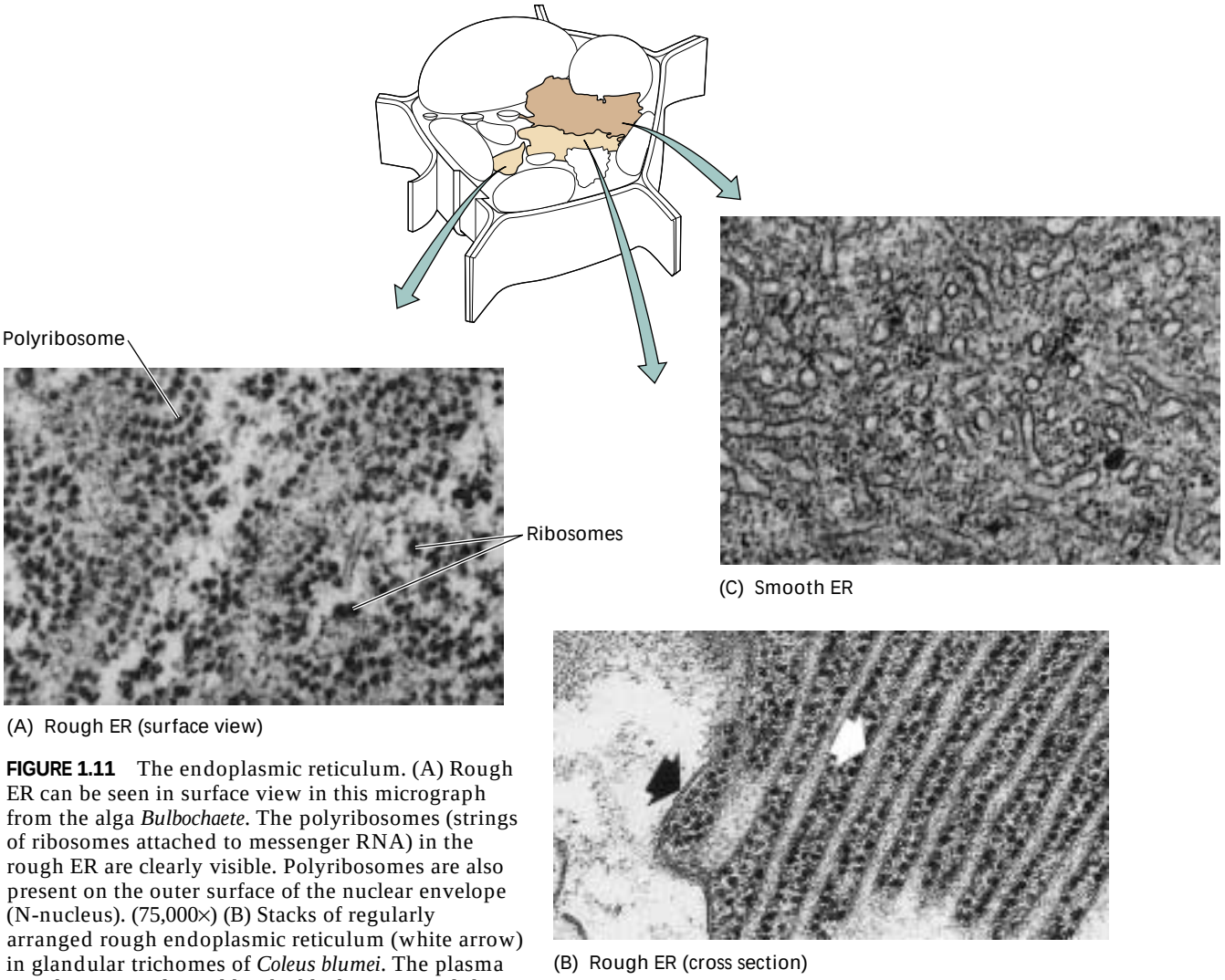

FIGURE 1.11 The endoplasmic reticulum. (A) Rough ER can be seen in surface view in this micrograph from the alga *Bulbochaete*. The polyribosomes (strings of ribosomes attached to messenger RNA) in the rough ER are clearly visible. Polyribosomes are also present on the outer surface of the nuclear envelope (N-nucleus). (75,000×) (B) Stacks of regularly arranged rough endoplasmic reticulum (white arrow) in glandular trichomes of *Coleus blumei*. The plasma membrane is indicated by the black arrow, and the material outside the plasma membrane is the cell wall. (75,000×) (C) Smooth ER often forms a tubular network, as shown in this transmission electron micrograph from a young petal of *Primula kewensis*. (45,000×) (Photos from Gunning and Steer 1996.)

secretion pathway that involves the Golgi body and vesicles that fuse with the plasma membrane.

The mechanism of transport across the membrane is complex, involving the ribosomes, the mRNA that codes for the secretory protein, and a special receptor in the ER membrane. All secretory proteins and most integral membrane proteins have been shown to have a hydrophobic sequence of 18 to 30 amino acid residues at the amino-terminal end of the chain. During translation, this hydrophobic leader, called the **signal peptide** sequence, is recognized by a **signal recognition particle** (**SRP**), made up of protein and RNA, which facilitates binding of the free ribosome to **SRP receptor** proteins (or "docking proteins") on the ER (see Figure 1.10A). The signal peptide then mediates the transfer of the elongating polypeptide across the ER membrane into the lumen. (In the case of integral membrane proteins, a portion of the completed polypeptide remains embedded in the membrane.)

Once inside the lumen of the ER, the signal sequence is cleaved off by a signal peptidase. In some cases, a branched oligosaccharide chain made up of *N*-acetylglucosamine (GlcNac), mannose (Man), and glucose (Glc), having the stoichiometry $GlcNac_2Man_9Glc_3$, is attached to the free amino group of a specific asparagine side chain. This carbohydrate assembly is called an *N-linked glycan* (Faye et al. 1992). The three terminal glucose residues are then removed by specific glucosidases, and the processed glycoprotein (i.e., a protein with covalently attached sugars) is ready for transport to the Golgi apparatus. The so-called **N-linked glycoproteins** are then transported to the Golgi apparatus via small vesicles. The vesicles move through the cytosol and fuse with cisternae on the *cis* face of the Golgi apparatus (Figure 1.12).

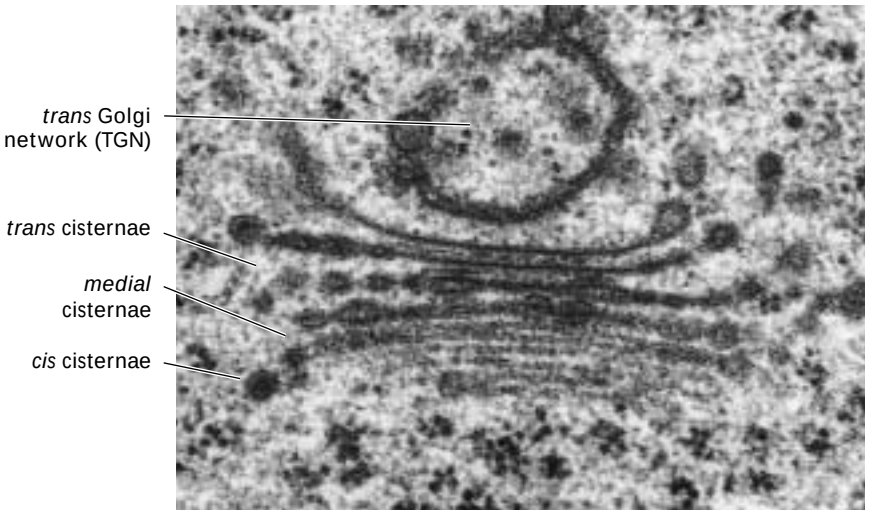

FIGURE 1.12 Electron micrograph of a Golgi apparatus in a tobacco (*Nicotiana tabacum*) root cap cell. The *cis*, *medial*, and *trans* cisternae are indicated. The *trans* Golgi network is associated with the *trans* cisterna. (60,000×) (From Gunning and Steer 1996.)

Proteins and Polysaccharides for Secretion Are Processed in the Golgi Apparatus

The **Golgi apparatus** (also called **Golgi complex**) of plant cells is a dynamic structure consisting of one or more stacks of three to ten flattened membrane sacs, or cisternae, and an irregular network of tubules and vesicles called the ***trans* Golgi network** (**TGN**) (see Figure 1.12). Each individual stack is called a **Golgi body** or **dictyosome**.

As Figure 1.12 shows, the Golgi body has distinct functional regions: The cisternae closest to the plasma membrane are called the *trans* face, and the cisternae closest to the center of the cell are called the *cis* face. The *medial* cisternae are between the *trans* and *cis* cisternae. The *trans* Golgi network is located on the *trans* face. The entire structure is stabilized by the presence of **intercisternal elements**, protein cross-links that hold the cisternae together. Whereas in animal cells Golgi bodies tend to be clustered in one part of the cell and are interconnected via tubules, plant cells contain up to several hundred apparently separate Golgi bodies dispersed throughout the cytoplasm (Driouich et al. 1994).

The Golgi apparatus plays a key role in the synthesis and secretion of complex polysaccharides (polymers composed of different types of sugars) and in the assembly of the oligosaccharide side chains of glycoproteins (Driouich et al. 1994). As noted already, the polypeptide chains of future glycoproteins are first synthesized on the rough ER, then transferred across the ER membrane, and glycosylated on the $—NH_2$ groups of asparagine residues. Further modifications of, and additions to, the oligosaccharide side chains are carried out in the Golgi. Glycoproteins destined for secretion reach the Golgi via vesicles that bud off from the RER.

The exact pathway of glycoproteins through the plant Golgi apparatus is not yet known. Since there appears to be no direct membrane continuity between successive cisternae, the contents of one cisterna are transferred to the next cisterna via small vesicles budding off from the margins, as occurs in the Golgi apparatus of animals. In some cases, however, entire cisternae may progress through the Golgi body and emerge from the *trans* face.

Within the lumens of the Golgi cisternae, the glycoproteins are enzymatically modified. Certain sugars, such as mannose, are removed from the oligosaccharide chains, and other sugars are added. In addition to these modifications, glycosylation of the —OH groups of hydroxyproline, serine, threonine, and tyrosine residues (**O-linked oligosaccharides**) also occurs in the Golgi. After being processed within the Golgi, the glycoproteins leave the organelle in other vesicles, usually from the *trans* side of the stack. All of this processing appears to confer on each protein a specific tag or marker that specifies the ultimate destination of that protein inside or outside the cell.

In plant cells, the Golgi body plays an important role in cell wall formation (see Chapter 15). Noncellulosic cell wall polysaccharides (hemicellulose and pectin) are synthesized, and a variety of glycoproteins, including hydroxyproline-rich glycoproteins, are processed within the Golgi.

Secretory vesicles derived from the Golgi carry the polysaccharides and glycoproteins to the plasma membrane, where the vesicles fuse with the plasma membrane and empty their contents into the region of the cell wall. Secretory vesicles may either be smooth or have a protein coat. Vesicles budding from the ER are generally smooth. Most vesicles budding from the Golgi have protein coats of some type. These proteins aid in the budding process during vesicle formation. Vesicles involved in traffic from the ER to the Golgi, between Golgi compartments, and from the Golgi to the TGN have **protein coats. Clathrin-coated vesicles** (Figure 1.13) are involved in the transport of storage proteins from the Golgi to specialized protein-storing vacuoles. They also participate in **endocytosis,** the process that brings soluble and membrane-bound proteins into the cell.

The Central Vacuole Contains Water and Solutes

Mature living plant cells contain large, water-filled central vacuoles that can occupy 80 to 90% of the total volume of the cell (see Figure 1.4). Each vacuole is surrounded by a **vacuolar membrane**, or **tonoplast**. Many cells also have cytoplasmic strands that run through the vacuole, but each transvacuolar strand is surrounded by the tonoplast.

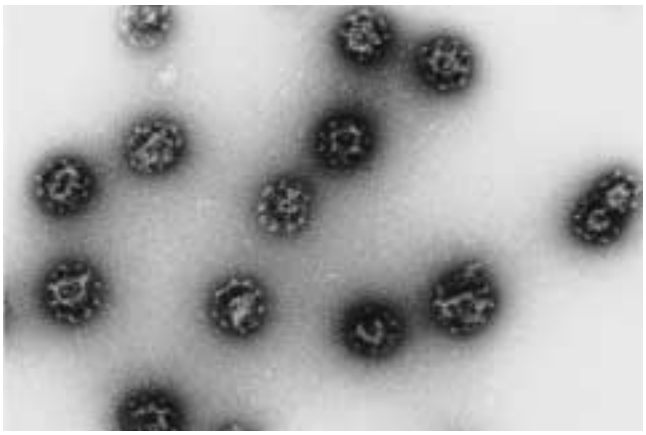

FIGURE 1.13 Preparation of clathrin-coated vesicles isolated from bean leaves. (102,000×) (Photo courtesy of D. G. Robinson.)

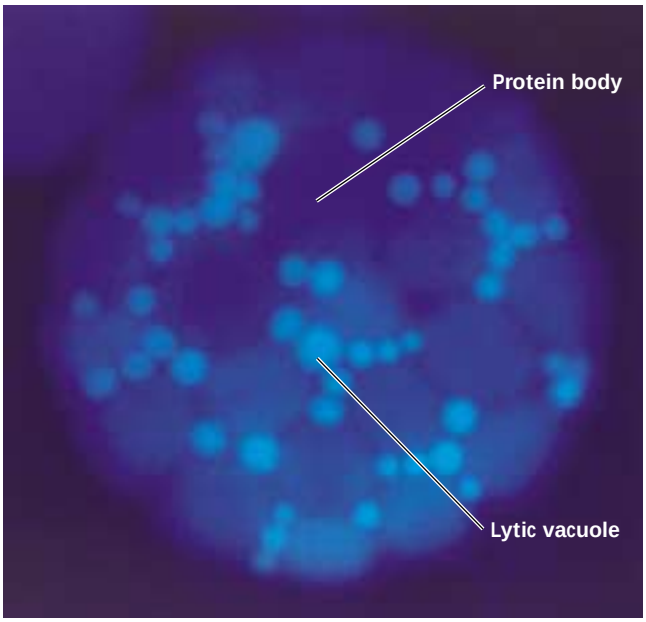

FIGURE 1.14 Light micrograph of a protoplast prepared from the aleurone layer of seeds. The fluorescent stain reveals two types of vacuoles: the larger protein bodies (V_1) and the smaller lytic vacuoles (V_2). (Photo courtesy of P. Bethke and R. L. Jones.)

In meristematic tissue, vacuoles are less prominent, though they are always present as small **provacuoles**. Provacuoles are produced by the *trans* Golgi network (see Figure 1.12). As the cell begins to mature, the provacuoles fuse to produce the large central vacuoles that are characteristic of most mature plant cells. In such cells, the cytoplasm is restricted to a thin layer surrounding the vacuole.

The vacuole contains water and dissolved inorganic ions, organic acids, sugars, enzymes, and a variety of secondary metabolites (see Chapter 13), which often play roles in plant defense. Active solute accumulation provides the osmotic driving force for water uptake by the vacuole, which is required for plant cell enlargement. The turgor pressure generated by this water uptake provides the structural rigidity needed to keep herbaceous plants upright, since they lack the lignified support tissues of woody plants.

Like animal lysosomes, plant vacuoles contain hydrolytic enzymes, including proteases, ribonucleases, and glycosidases. Unlike animal lysosomes, however, plant vacuoles do not participate in the turnover of macromolecules throughout the life of the cell. Instead, their degradative enzymes leak out into the cytosol as the cell undergoes senescence, thereby helping to recycle valuable nutrients to the living portion of the plant.

Specialized protein-storing vacuoles, called **protein bodies**, are abundant in seeds. During germination the storage proteins in the protein bodies are hydrolyzed to amino acids and exported to the cytosol for use in protein synthesis. The hydrolytic enzymes are stored in specialized **lytic vacuoles**, which fuse with the protein bodies to initiate the breakdown process (Figure 1.14).

Mitochondria and Chloroplasts Are Sites of Energy Conversion

A typical plant cell has two types of energy-producing organelles: mitochondria and chloroplasts. Both types are separated from the cytosol by a double membrane (an outer and an inner membrane). **Mitochondria** (singular *mitochondrion*) are the cellular sites of respiration, a process in which the energy released from sugar metabolism is used for the synthesis of ATP (adenosine triphosphate) from ADP (adenosine diphosphate) and inorganic phosphate (P_i) (see Chapter 11).

Mitochondria can vary in shape from spherical to tubular, but they all have a smooth outer membrane and a highly convoluted inner membrane (Figure 1.15). The infoldings of the inner membrane are called **cristae** (singular *crista*). The compartment enclosed by the inner membrane, the mitochondrial **matrix**, contains the enzymes of the pathway of intermediary metabolism called the Krebs cycle.

In contrast to the mitochondrial outer membrane and all other membranes in the cell, the inner membrane of a mitochondrion is almost 70% protein and contains some phospholipids that are unique to the organelle (e.g., cardiolipin). The proteins in and on the inner membrane have special enzymatic and transport capacities.

The inner membrane is highly impermeable to the passage of H^+; that is, it serves as a barrier to the movement of protons. This important feature allows the formation of electrochemical gradients. Dissipation of such gradients by the controlled movement of H^+ ions through the transmembrane enzyme **ATP synthase** is coupled to the phosphorylation of ADP to produce ATP. ATP can then be released to other cellular sites where energy is needed to drive specific reactions.

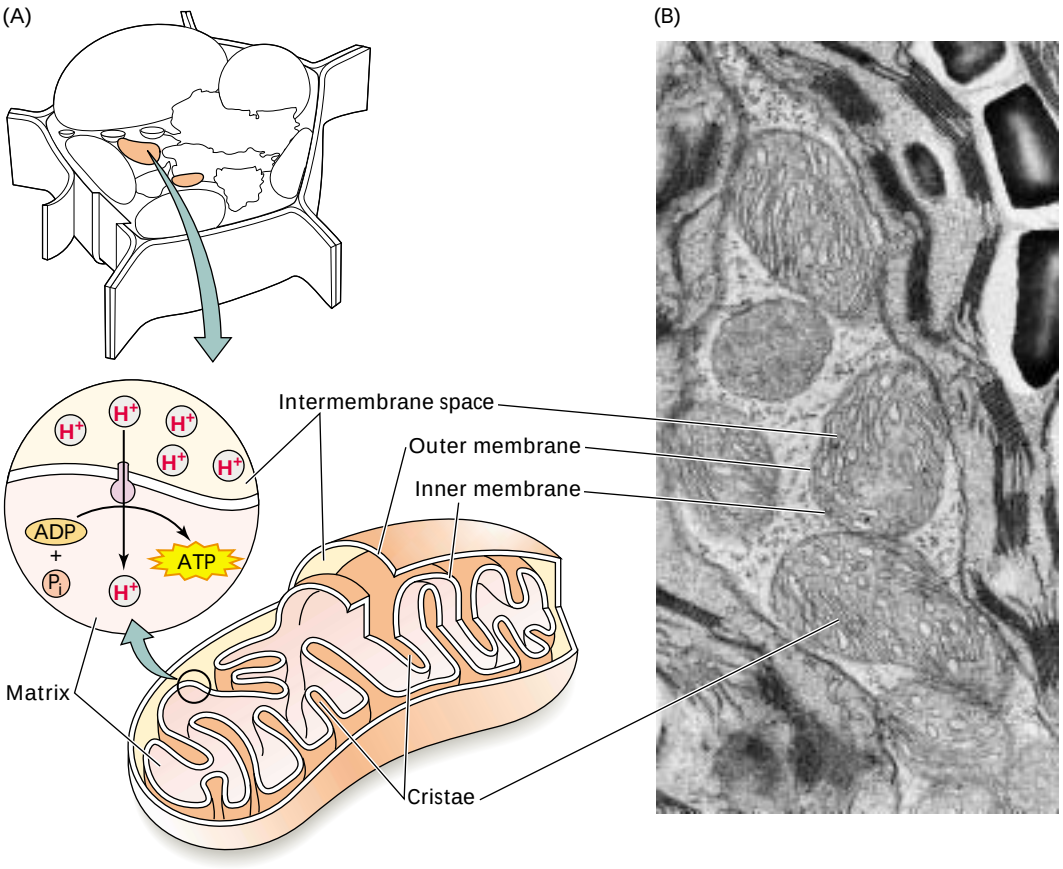

FIGURE 1.15 (A) Diagrammatic representation of a mitochondrion, including the location of the H^+-ATPases involved in ATP synthesis on the inner membrane. (B) An electron micrograph of mitochondria from a leaf cell of Bermuda grass, *Cynodon dactylon*. (26,000×) (Photo by S. E. Frederick, courtesy of E. H. Newcomb.)

Chloroplasts (Figure 1.16A) belong to another group of double membrane–enclosed organelles called **plastids**. Chloroplast membranes are rich in glycosylglycerides (see **Web Topic 1.4**). Chloroplast membranes contain chlorophyll and its associated proteins and are the sites of photosynthesis. In addition to their inner and outer envelope membranes, chloroplasts possess a third system of membranes called **thylakoids**. A stack of thylakoids forms a **granum** (plural *grana*) (Figure 1.16B). Proteins and pigments (chlorophylls and carotenoids) that function in the photochemical events of photosynthesis are embedded in the thylakoid membrane. The fluid compartment surrounding the thylakoids, called the **stroma**, is analogous to the matrix of the mitochondrion. Adjacent grana are connected by unstacked membranes called **stroma lamellae** (singular *lamella*).

The different components of the photosynthetic apparatus are localized in different areas of the grana and the stroma lamellae. The ATP synthases of the chloroplast are located on the thylakoid membranes (Figure 1.16C). During photosynthesis, light-driven electron transfer reactions result in a proton gradient across the thylakoid membrane. As in the mitochondria, ATP is synthesized when the proton gradient is dissipated via the ATP synthase.

Plastids that contain high concentrations of carotenoid pigments rather than chlorophyll are called **chromoplasts**. They are one of the causes of the yellow, orange, or red colors of many fruits and flowers, as well as of autumn leaves (Figure 1.17).

Nonpigmented plastids are called **leucoplasts**. The most important type of leucoplast is the **amyloplast**, a starch-storing plastid. Amyloplasts are abundant in storage tissues of the shoot and root, and in seeds. Specialized amyloplasts in the root cap also serve as gravity sensors that direct root growth downward into the soil (see Chapter 19).

Mitochondria and Chloroplasts Are Semiautonomous Organelles

Both mitochondria and chloroplasts contain their own DNA and protein-synthesizing machinery (ribosomes, transfer RNAs, and other components) and are believed to have evolved from endosymbiotic bacteria. Both plastids and mitochondria divide by fission, and mitochondria can also undergo extensive fusion to form elongated structures or networks.

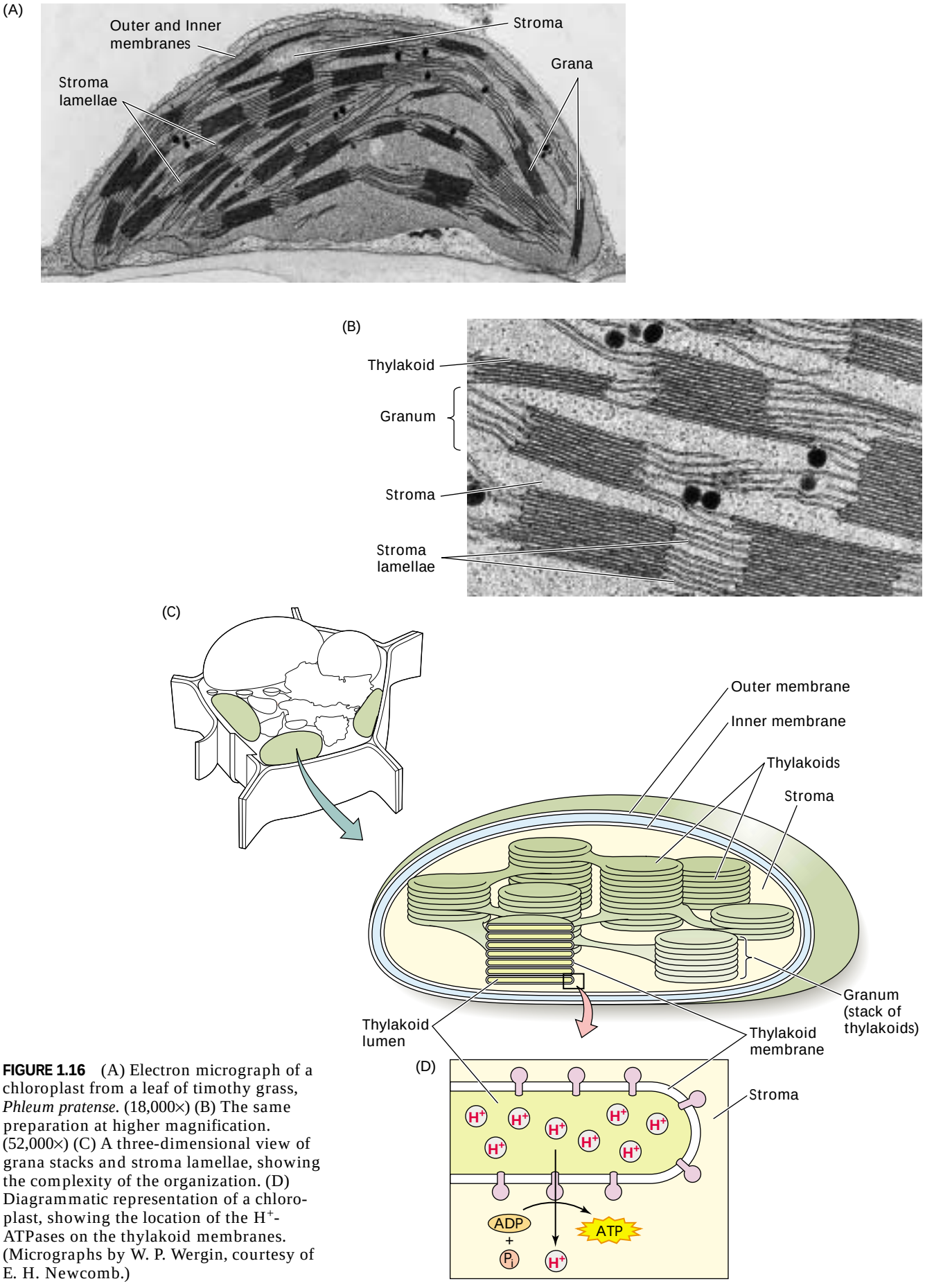

FIGURE 1.16 (A) Electron micrograph of a chloroplast from a leaf of timothy grass, *Phleum pratense*. (18,000×) (B) The same preparation at higher magnification. (52,000×) (C) A three-dimensional view of grana stacks and stroma lamellae, showing the complexity of the organization. (D) Diagrammatic representation of a chloroplast, showing the location of the H^+-ATPases on the thylakoid membranes. (Micrographs by W. P. Wergin, courtesy of E. H. Newcomb.)

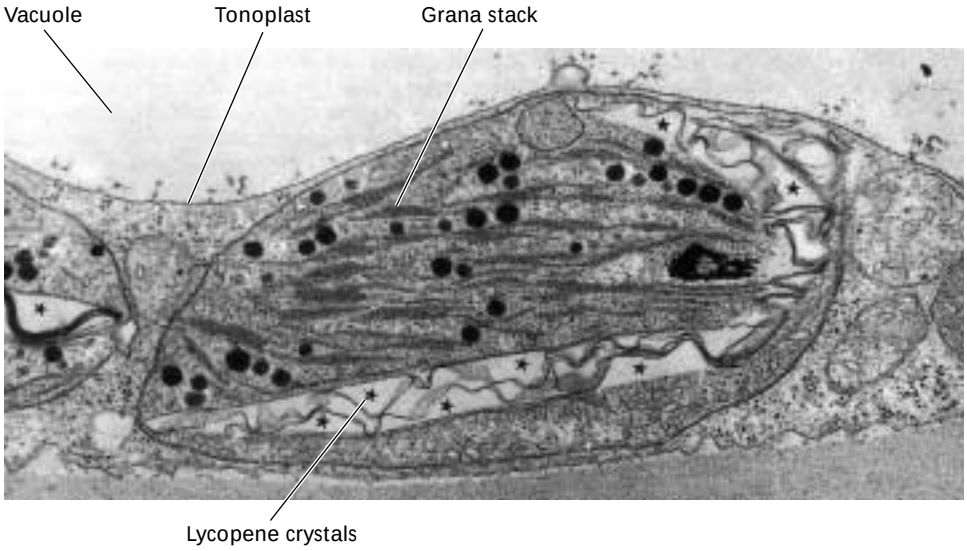

FIGURE 1.17 Electron micrograph of a chromoplast from tomato (*Lycopersicon esculentum*) fruit at an early stage in the transition from chloroplast to chromoplast. Small grana stacks are still visible. Crystals of the carotenoid lycopene are indicated by the stars. (27,000×) (From Gunning and Steer 1996.)

The DNA of these organelles is in the form of circular chromosomes, similar to those of bacteria and very different from the linear chromosomes in the nucleus. These DNA circles are localized in specific regions of the mitochondrial matrix or plastid stroma called **nucleoids**. DNA replication in both mitochondria and chloroplasts is independent of DNA replication in the nucleus. On the other hand, the numbers of these organelles within a given cell type remain approximately constant, suggesting that some aspects of organelle replication are under cellular regulation.

The mitochondrial genome of plants consists of about 200 kilobase pairs (200,000 base pairs), a size considerably larger than that of most animal mitochondria. The mitochondria of meristematic cells are typically polyploid; that is, they contain multiple copies of the circular chromosome. However, the number of copies per mitochondrion gradually decreases as cells mature because the mitochondria continue to divide in the absence of DNA synthesis.

Most of the proteins encoded by the mitochondrial genome are prokaryotic-type 70S ribosomal proteins and components of the electron transfer system. The majority of mitochondrial proteins, including Krebs cycle enzymes, are encoded by nuclear genes and are imported from the cytosol.

The chloroplast genome is smaller than the mitochondrial genome, about 145 kilobase pairs (145,000 base pairs). Whereas mitochondria are polyploid only in the meristems, chloroplasts become polyploid during cell maturation. Thus the average amount of DNA per chloroplast in the plant is much greater than that of the mitochondria. The total amount of DNA from the mitochondria and plastids combined is about one-third of the nuclear genome (Gunning and Steer 1996).

Chloroplast DNA encodes rRNA; transfer RNA (tRNA); the large subunit of the enzyme that fixes CO_2, ribulose-1,5-bisphosphate carboxylase / oxygenase (rubisco); and several of the proteins that participate in photosynthesis. Nevertheless, the majority of chloroplast proteins, like those of mitochondria, are encoded by nuclear genes, synthesized in the cytosol, and transported to the organelle. Although mitochondria and chloroplasts have their own genomes and can divide independently of the cell, they are characterized as *semiautonomous organelles* because they depend on the nucleus for the majority of their proteins.

Different Plastid Types Are Interconvertible

Meristem cells contain **proplastids**, which have few or no internal membranes, no chlorophyll, and an incomplete complement of the enzymes necessary to carry out photosynthesis (Figure 1.18A). In angiosperms and some gymnosperms, chloroplast development from proplastids is triggered by light. Upon illumination, enzymes are formed inside the proplastid or imported from the cytosol, light-absorbing pigments are produced, and membranes proliferate rapidly, giving rise to stroma lamellae and grana stacks (Figure 1.18B).

Seeds usually germinate in the soil away from light, and chloroplasts develop only when the young shoot is exposed to light. If seeds are germinated in the dark, the proplastids differentiate into **etioplasts**, which contain semicrystalline tubular arrays of membrane known as **prolamellar bodies** (Figure 1.18C). Instead of chlorophyll, the etioplast contains a pale yellow green precursor pigment, **protochlorophyll**.

Within minutes after exposure to light, the etioplast differentiates, converting the prolamellar body into thylakoids and stroma lamellae, and the protochlorophyll into chlorophyll. The maintenance of chloroplast structure depends on the presence of light, and mature chloroplasts can revert to etioplasts during extended periods of darkness.

Chloroplasts can be converted to chromoplasts, as in the case of autumn leaves and ripening fruit, and in some cases

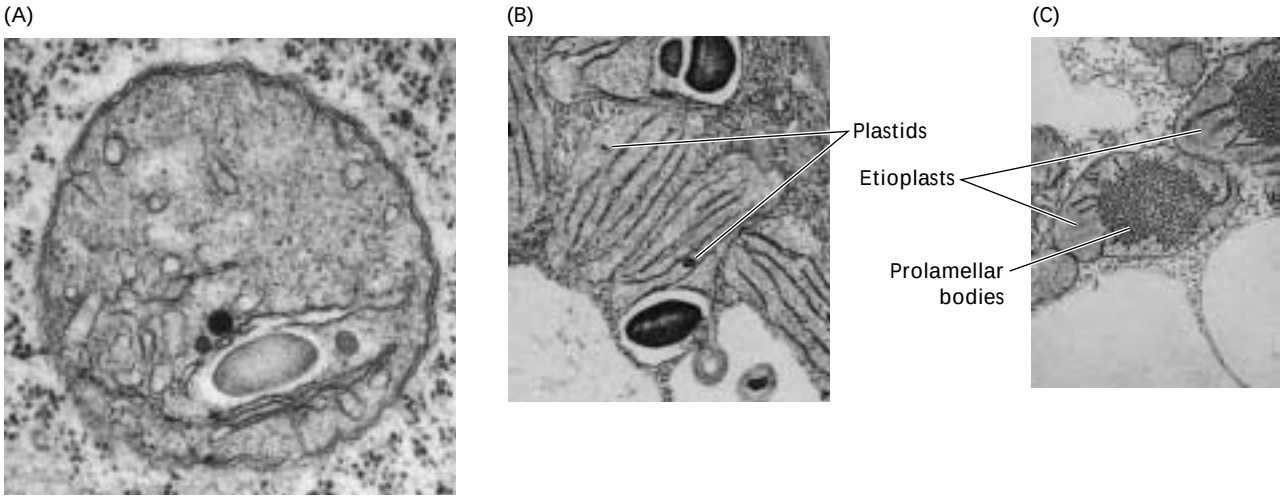

FIGURE 1.18 Electron micrographs illustrating several stages of plastid development. (A) A higher-magnification view of a proplastid from the root apical meristem of the broad bean (*Vicia faba*). The internal membrane system is rudimentary, and grana are absent. (47,000×) (B) A mesophyll cell of a young oat leaf at an early stage of differentiation in the light. The plastids are developing grana stacks. (C) A cell from a young oat leaf from a seedling grown in the dark. The plastids have developed as etioplasts, with elaborate semicrystalline lattices of membrane tubules called prolamellar bodies. When exposed to light, the etioplast can convert to a chloroplast by the disassembly of the prolamellar body and the formation of grana stacks. (7,200×) (From Gunning and Steer 1996.)

this process is reversible. And amyloplasts can be converted to chloroplasts, which explains why exposure of roots to light often results in greening of the roots.

Microbodies Play Specialized Metabolic Roles in Leaves and Seeds

Plant cells also contain **microbodies**, a class of spherical organelles surrounded by a single membrane and specialized for one of several metabolic functions. The two main types of microbodies are peroxisomes and glyoxysomes.

Peroxisomes are found in all eukaryotic organisms, and in plants they are present in photosynthetic cells (Figure 1.19). Peroxisomes function both in the removal of hydrogens from organic substrates, consuming O_2 in the process, according to the following reaction:

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

where R is the organic substrate. The potentially harmful peroxide produced in these reactions is broken down in peroxisomes by the enzyme catalase, according to the following reaction:

$$H_2O_2 \rightarrow H_2O + \tfrac{1}{2}O_2$$

Although some oxygen is regenerated during the catalase reaction, there is a net consumption of oxygen overall.

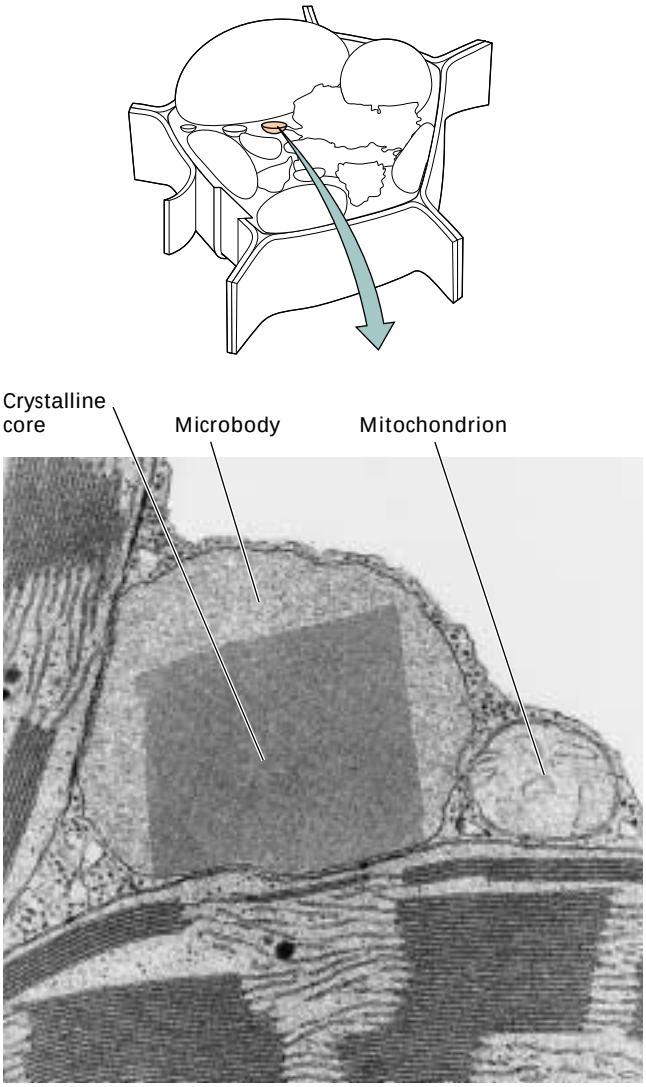

FIGURE 1.19 Electron micrograph of a peroxisome from a mesophyll cell, showing a crystalline core. (27,000×) This peroxisome is seen in close association with two chloroplasts and a mitochondrion, probably reflecting the cooperative role of these three organelles in photorespiration. (From Huang 1987.)

Another type of microbody, the **glyoxysome**, is present in oil-storing seeds. Glyoxysomes contain the *glyoxylate cycle* enzymes, which help convert stored fatty acids into sugars that can be translocated throughout the young plant to provide energy for growth (see Chapter 11). Because both types of microbodies carry out oxidative reactions, it has been suggested they may have evolved from primitive respiratory organelles that were superseded by mitochondria.

Oleosomes Are Lipid-Storing Organelles

In addition to starch and protein, many plants synthesize and store large quantities of triacylglycerol in the form of oil during seed development. These oils accumulate in organelles called **oleosomes**, also referred to as *lipid bodies* or *spherosomes* (Figure 1.20A).

Oleosomes are unique among the organelles in that they are surrounded by a "half–unit membrane"—that is, a phospholipid monolayer—derived from the ER (Harwood 1997). The phospholipids in the half–unit membrane are oriented with their polar head groups toward the aqueous phase and their hydrophobic fatty acid tails facing the lumen, dissolved in the stored lipid. Oleosomes are thought to arise from the deposition of lipids within the bilayer itself (Figure 1.20B).

Proteins called **oleosins** are present in the half–unit membrane (see Figure 1.20B). One of the functions of the oleosins may be to maintain each oleosome as a discrete organelle by preventing fusion. Oleosins may also help other proteins bind to the organelle surface. As noted earlier, during seed germination the lipids in the oleosomes are broken down and converted to sucrose with the help of the glyoxysome. The first step in the process is the hydrolysis of the fatty acid chains from the glycerol backbone by the enzyme lipase. Lipase is tightly associated with the surface of the half–unit membrane and may be attached to the oleosins.

THE CYTOSKELETON

The cytosol is organized into a three-dimensional network of filamentous proteins called the **cytoskeleton**. This network provides the spatial organization for the organelles and serves as a scaffolding for the movements of organelles and other cytoskeletal components. It also plays fundamental roles in mitosis, meiosis, cytokinesis, wall deposition, the maintenance of cell shape, and cell differentiation.

Plant Cells Contain Microtubules, Microfilaments, and Intermediate Filaments

Three types of cytoskeletal elements have been demonstrated in plant cells: microtubules, microfilaments, and intermediate filament–like structures. Each type is filamentous, having a fixed diameter and a variable length, up to many micrometers.

Microtubules and microfilaments are macromolecular assemblies of globular proteins. **Microtubules** are hollow

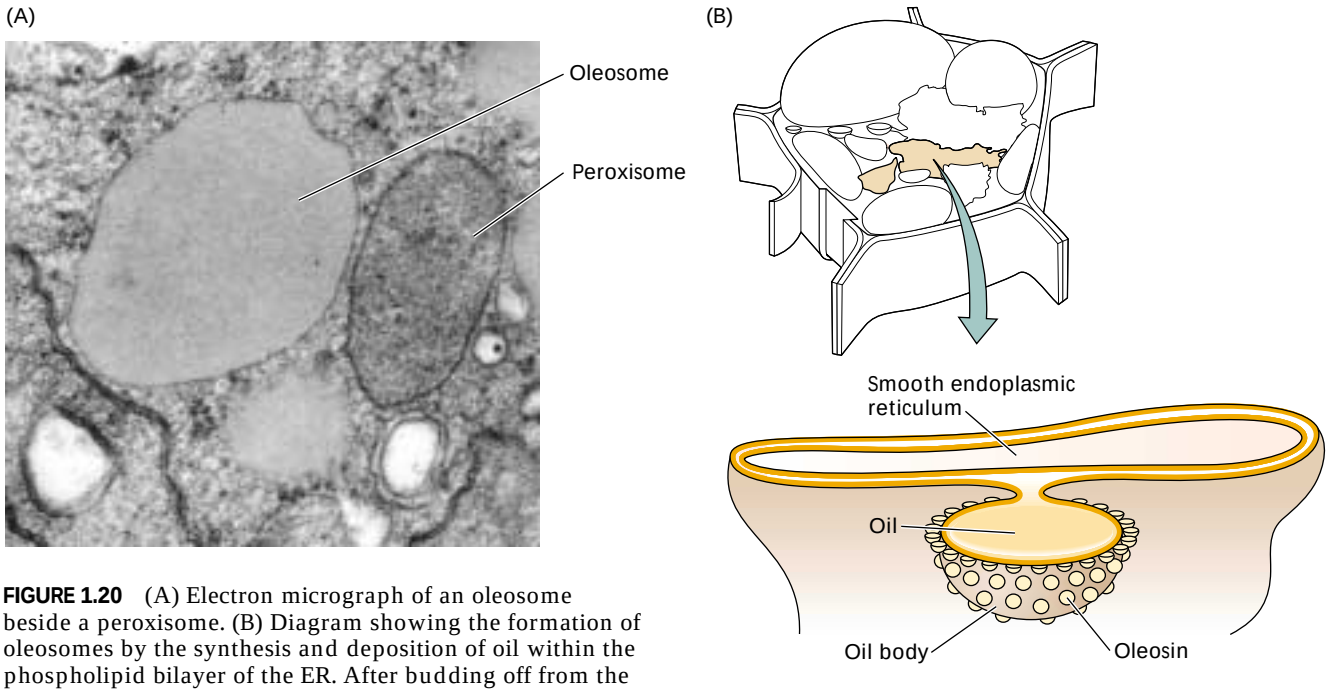

FIGURE 1.20 (A) Electron micrograph of an oleosome beside a peroxisome. (B) Diagram showing the formation of oleosomes by the synthesis and deposition of oil within the phospholipid bilayer of the ER. After budding off from the ER, the oleosome is surrounded by a phospholipid monolayer containing the protein oleosin. (A from Huang 1987; B after Buchanan et al. 2000.)

cylinders with an outer diameter of 25 nm; they are composed of polymers of the protein **tubulin**. The tubulin monomer of microtubules is a heterodimer composed of two similar polypeptide chains (α- and β-tubulin), each having an apparent molecular mass of 55,000 daltons (Figure 1.21A). A single microtubule consists of hundreds of thousands of tubulin monomers arranged in 13 columns called *protofilaments*.

Microfilaments are solid, with a diameter of 7 nm; they are composed of a special form of the protein found in muscle: globular actin, or **G-actin**. Each actin molecule is composed of a single polypeptide with a molecular mass of approximately 42,000 daltons. A microfilament consists of two chains of polymerized actin subunits that intertwine in a helical fashion (Figure 1.21B).

Intermediate filaments are a diverse group of helically wound fibrous elements, 10 nm in diameter. Intermediate filaments are composed of linear polypeptide monomers of various types. In animal cells, for example, the **nuclear lamins** are composed of a specific polypeptide monomer, while the **keratins**, a type of intermediate filament found in the cytoplasm, are composed of a different polypeptide monomer.

In animal intermediate filaments, pairs of parallel monomers (i.e., aligned with their —NH_2 groups at the same ends) are helically wound around each other in a **coiled coil.** Two coiled-coil dimers then align in an antiparallel fashion (i.e., with their —NH_2 groups at opposite ends) to form a tetrameric unit. The tetrameric units then assemble into the final intermediate filament (Figure 1.22).

Although nuclear lamins appear to be present in plant cells, there is as yet no convincing evidence for plant keratin intermediate filaments in the cytosol. As noted earlier, integral proteins cross-link the plasma membrane of plant cells to the rigid cell wall. Such connections to the wall undoubtedly stabilize the protoplast and help maintain cell shape. The plant cell wall thus serves as a kind of cellular exoskeleton, perhaps obviating the need for keratin-type intermediate filaments for structural support.

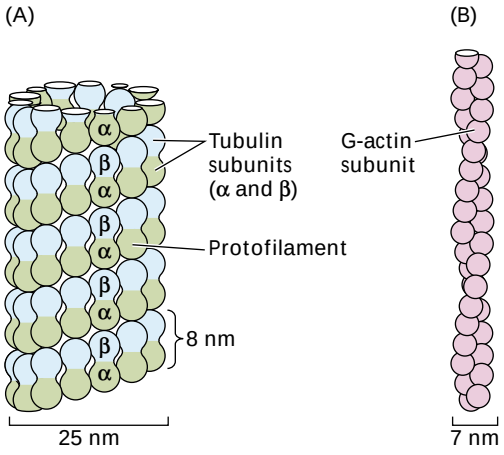

FIGURE 1.21 (A) Drawing of a microtubule in longitudinal view. Each microtubule is composed of 13 protofilaments. The organization of the α and β subunits is shown. (B) Diagrammatic representation of a microfilament, showing two strands of G-actin subunits.

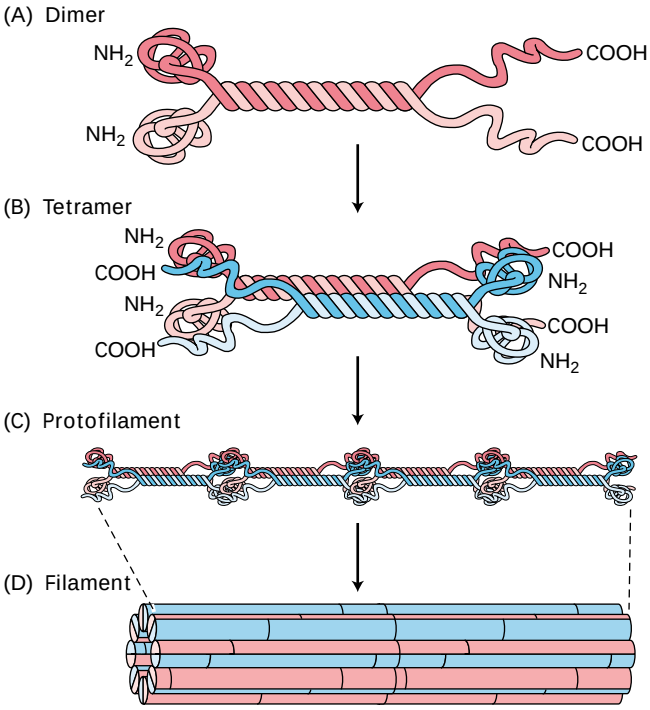

FIGURE 1.22 The current model for the assembly of intermediate filaments from protein monomers. (A) Coiled-coil dimer in parallel orientation (i.e., with amino and carboxyl termini at the same ends). (B) A tetramer of two dimers. Note that the dimers are arranged in an antiparallel fashion, and that one is slightly offset from the other. (C) Two tetramers. (D) Tetramers packed together to form the 10 nm intermediate filament. (After Alberts et al. 2002.)

Microtubules and Microfilaments Can Assemble and Disassemble

In the cell, actin and tubulin monomers exist as pools of free proteins that are in dynamic equilibrium with the polymerized forms. Polymerization requires energy: ATP is required for microfilament polymerization, GTP (guanosine triphosphate) for microtubule polymerization. The attachments between subunits in the polymer are noncovalent, but they are strong enough to render the structure stable under cellular conditions.

Both microtubules and microfilaments are polarized; that is, the two ends are different. In microtubules, the polarity arises from the polarity of the α- and β-tubulin heterodimer; in microfilaments, the polarity arises from the polarity of the actin monomer itself. The opposite ends of microtubules and microfilaments are termed *plus* and *minus*, and polymerization is more rapid at the positive end.

Once formed, microtubules and microfilaments can disassemble. The overall *rate* of assembly and disassembly of these structures is affected by the relative concentrations of free or assembled subunits. In general, microtubules are more unstable than microfilaments. In animal cells, the half-life of an individual microtubule is about 10 minutes. Thus microtubules are said to exist in a state of *dynamic instability*.

In contrast to microtubules and microfilaments, intermediate filaments lack polarity because of the antiparallel orientation of the dimers that make up the tetramers. In addition, intermediate filaments appear to be much more stable than either microtubules or microfilaments. Although very little is known about intermediate filament–like structures in plant cells, in animal cells nearly all of the intermediate-filament protein exists in the polymerized state.

Microtubules Function in Mitosis and Cytokinesis

Mitosis is the process by which previously replicated chromosomes are aligned, separated, and distributed in an orderly fashion to daughter cells (Figure 1.23). Microtubules are an integral part of mitosis. Before mitosis begins, microtubules in the cortical (outer) cytoplasm depolymerize, breaking down into their constituent subunits. The subunits then repolymerize before the start of prophase to form the **preprophase band** (**PPB**), a ring of microtubules encircling the nucleus (see Figure 1.23C–F). The PPB appears in the region where the future cell wall will form after the completion of mitosis, and it is thought to be involved in regulating the plane of cell division.

During prophase, microtubules begin to assemble at two foci on opposite sides of the nucleus, forming the **prophase spindle** (Figure 1.24). Although not associated with any specific structure, these foci serve the same function as animal cell centrosomes in organizing and assembling microtubules.

In early metaphase the nuclear envelope breaks down, the PPB disassembles, and new microtubules polymerize to form the mitotic spindle. In animal cells the spindle microtubules radiate toward each other from two discrete foci at the poles (the centrosomes), resulting in an ellipsoidal, or football-shaped, array of microtubules. The mitotic spindle of plant cells, which lack centrosomes, is more boxlike in shape because the spindle microtubules arise from a diffuse zone consisting of multiple foci at opposite ends of the cell and extend toward the middle in nearly parallel arrays (see Figure 1.24).

Some of the microtubules of the spindle apparatus become attached to the chromosomes at their **kinetochores**, while others remain unattached. The kinetochores are located in the **centromeric** regions of the chromosomes. Some of the unattached microtubules overlap with microtubules from the opposite polar region in the spindle midzone.

Cytokinesis is the process whereby a cell is partitioned into two progeny cells. Cytokinesis usually begins late in mitosis. The precursor of the new wall, the **cell plate** that

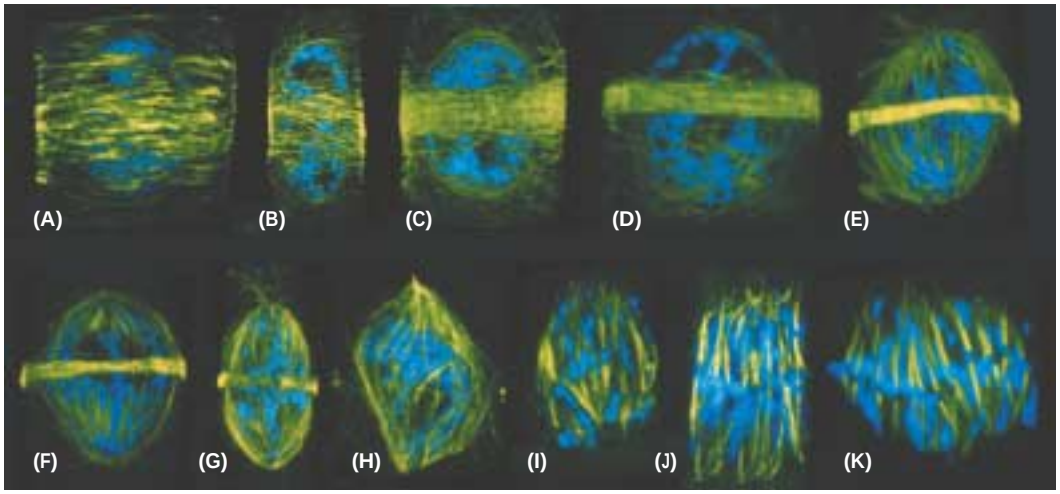

FIGURE 1.23 Fluorescence micrograph taken with a confocal microscope showing changes in microtubule arrangements at different stages in the cell cycle of wheat root meristem cells. Microtubules stain green and yellow; DNA is blue. (A–D) Cortical microtubules disappear and the preprophase band is formed around the nucleus at the site of the future cell plate. (E–H) The prophase spindle forms from foci of microtubules at the poles. (G, H) The preprophase band disappears in late prophase. (I–K) The nuclear membrane breaks down, and the two poles become more diffuse. The mitotic spindle forms in parallel arrays and the kinetochores bind to spindle microtubules. (From Gunning and Steer 1996.)

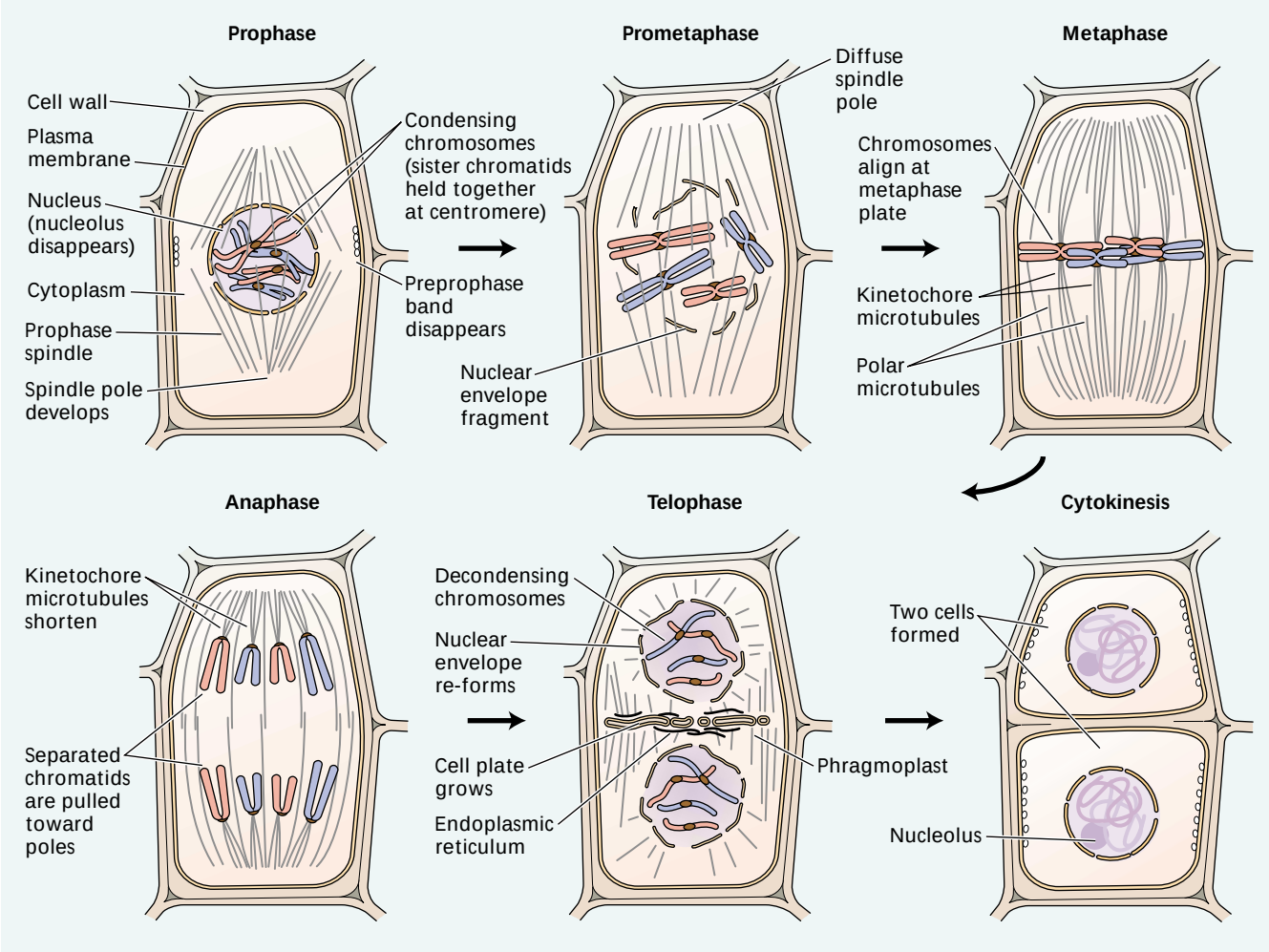

FIGURE 1.24 Diagram of mitosis in plants.

forms between incipient daughter cells, is rich in pectins (Figure 1.25). Cell plate formation in higher plants is a multistep process (see **Web Topic 1.5**). Vesicle aggregation in the spindle midzone is organized by the **phragmoplast**, a complex of microtubules and ER that forms during late anaphase or early telophase from dissociated spindle subunits.

Microfilaments Are Involved in Cytoplasmic Streaming and in Tip Growth

Cytoplasmic streaming is the coordinated movement of particles and organelles through the cytosol in a helical path down one side of a cell and up the other side. Cytoplasmic streaming occurs in most plant cells and has been studied extensively in the giant cells of the green algae *Chara* and *Nitella*, in which speeds up to 75 μm s^{-1} have been measured.

The mechanism of cytoplasmic streaming involves bundles of microfilaments that are arranged parallel to the longitudinal direction of particle movement. The forces necessary for movement may be generated by an interaction of the microfilament protein actin with the protein myosin in a fashion comparable to that of the protein interaction that occurs during muscle contraction in animals.

Myosins are proteins that have the ability to hydrolyze ATP to ADP and P_i when activated by binding to an actin microfilament. The energy released by ATP hydrolysis propels myosin molecules along the actin microfilament from the minus end to the plus end. Thus, myosins belong to the general class of **motor proteins** that drive cytoplasmic streaming and the movements of organelles within the cell. Examples of other motor proteins include the **kinesins** and **dyneins**, which drive movements of organelles and other cytoskeletal components along the surfaces of microtubules.

Actin microfilaments also participate in the growth of the pollen tube. Upon germination, a pollen grain forms a tubular extension that grows down the style toward the embryo sac. As the tip of the pollen tube extends, new cell wall material is continually deposited to maintain the integrity of the wall.

A network of microfilaments appears to guide vesicles containing wall precursors from their site of formation in the Golgi through the cytosol to the site of new wall formation at the tip. Fusion of these vesicles with the plasma membrane deposits wall precursors outside the cell, where they are assembled into wall material.

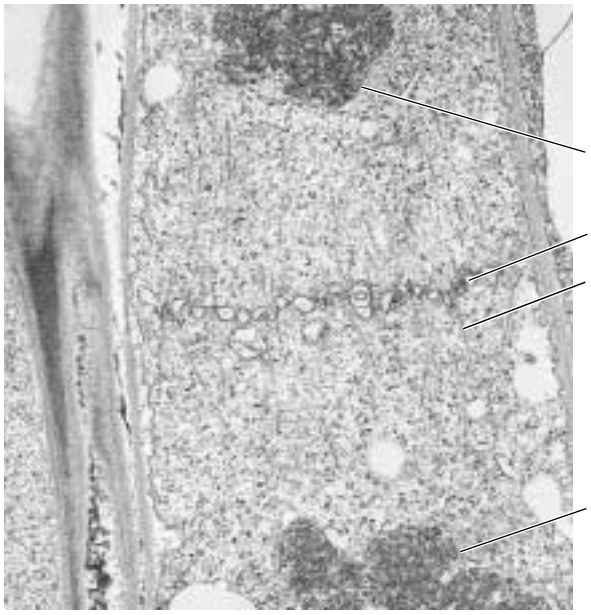

FIGURE 1.25 Electron micrograph of a cell plate forming in a maple seedling (10,000×). (© E. H. Newcomb and B. A. Palevitz / Biological Photo Service.)

Intermediate Filaments Occur in the Cytosol and Nucleus of Plant Cells

Relatively little is known about plant intermediate filaments. Intermediate filament–like structures have been identified in the cytoplasm of plant cells (Yang et al. 1995), but these may not be based on keratin, as in animal cells, since as yet no plant keratin genes have been found. Nuclear lamins, intermediate filaments of another type that form a dense network on the inner surface of the nuclear membrane, have also been identified in plant cells (Frederick et al. 1992), and genes encoding laminlike proteins are present in the *Arabidopsis* genome. Presumably, plant lamins perform functions similar to those in animal cells as a structural component of the nuclear envelope.

CELL CYCLE REGULATION

The cell division cycle, or cell cycle, is the process by which cells reproduce themselves and their genetic material, the nuclear DNA. The four phases of the cell cycle are designated G_1, S, G_2, and M (Figure 1.26A).

Each Phase of the Cell Cycle Has a Specific Set of Biochemical and Cellular Activities

Nuclear DNA is prepared for replication in G_1 by the assembly of a prereplication complex at the origins of replication along the chromatin. DNA is replicated during the S phase, and G_2 cells prepare for mitosis.

The whole architecture of the cell is altered as cells enter mitosis: The nuclear envelope breaks down, chromatin condenses to form recognizable chromosomes, the mitotic spindle forms, and the replicated chromosomes attach to the spindle fibers. The transition from metaphase to anaphase of mitosis marks a major transition point when the two chromatids of each replicated chromosome, which were held together at their kinetochores, are separated and the daughter chromosomes are pulled to opposite poles by spindle fibers.

At a key regulatory point early in G_1 of the cell cycle, the cell becomes committed to the initiation of DNA synthesis. In yeasts, this point is called START. Once a cell has passed START, it is irreversibly committed to initiating DNA synthesis and completing the cell cycle through mitosis and cytokinesis. After the cell has completed mitosis, it may initiate another complete cycle (G_1 through mitosis), or it may leave the cell cycle and differentiate. This choice is made at the critical G_1 point, before the cell begins to replicate its DNA.

DNA replication and mitosis are linked in mammalian cells. Often mammalian cells that have stopped dividing can be stimulated to reenter the cell cycle by a variety of hormones and growth factors. When they do so, they reenter the cell cycle at the critical point in early G_1. In contrast, plant cells can leave the cell division cycle either before or after replicating their DNA (i.e., during G_1 or G_2). As a consequence, whereas most animal cells are diploid (having two sets of chromosomes), plant cells frequently are tetraploid (having four sets of chromosomes), or even polyploid (having many sets of chromosomes), after going through additional cycles of nuclear DNA replication without mitosis.

The Cell Cycle Is Regulated by Protein Kinases

The mechanism regulating the progression of cells through their division cycle is highly conserved in evolution, and plants have retained the basic components of this mechanism (Renaudin et al. 1996). The key enzymes that control the transitions between the different states of the cell cycle, and the entry of nondividing cells into the cell cycle, are the **cyclin-dependent protein kinases,** or **CDKs** (Figure 1.26B). Protein kinases are enzymes that phosphorylate proteins using ATP. Most multicellular eukaryotes use several protein kinases that are active in different phases of the cell cycle. All depend on regulatory subunits called cyclins for their activities. The regulated activity of CDKs is essential for the transitions from G_1 to S and from G_2 to M, and for the entry of nondividing cells into the cell cycle.

CDK activity can be regulated in various ways, but two of the most important mechanisms are (1) cyclin synthesis and destruction and (2) the phosphorylation and dephosphorylation of key amino acid residues within the CDK protein. CDKs are inactive unless they are associated

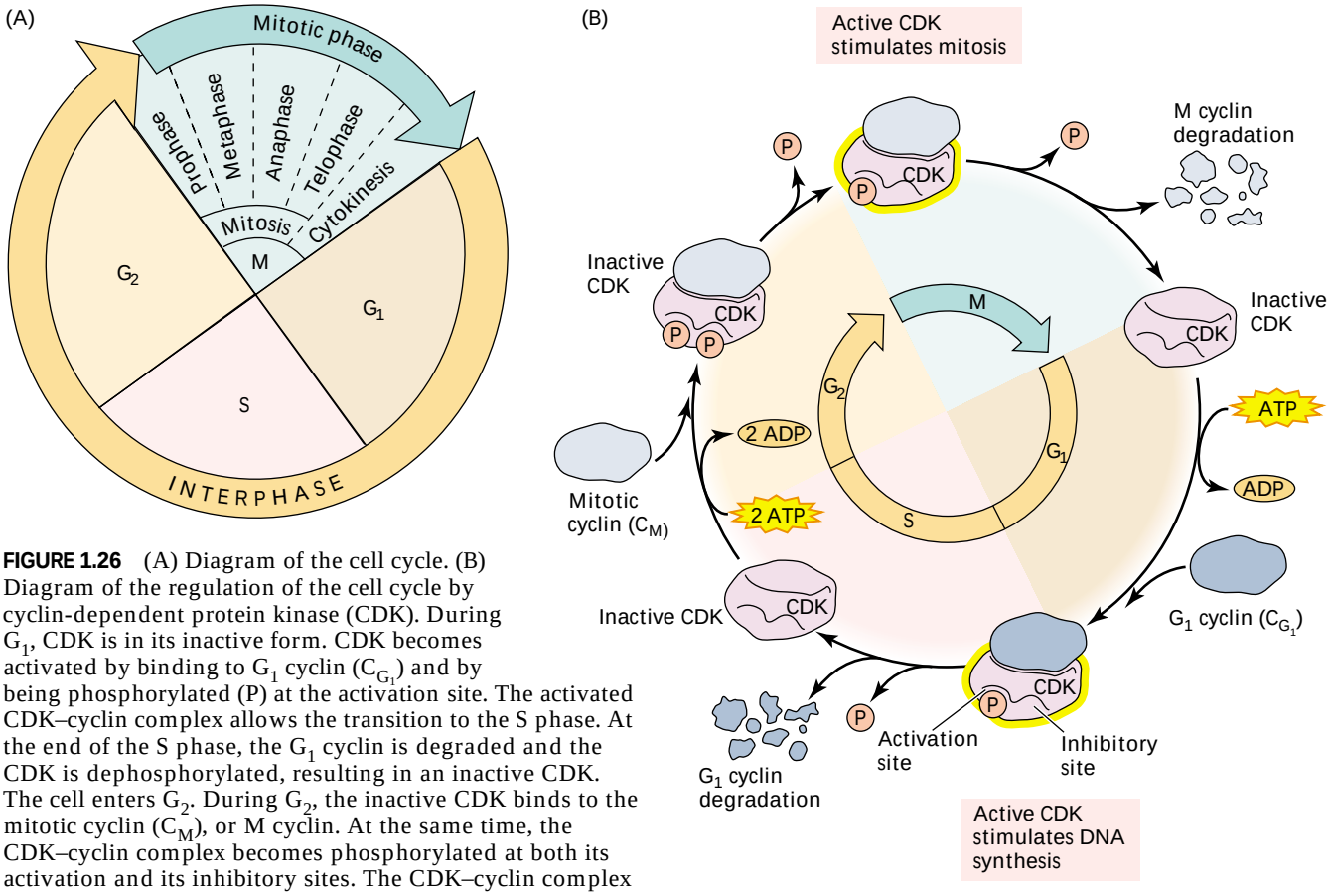

FIGURE 1.26 (A) Diagram of the cell cycle. (B) Diagram of the regulation of the cell cycle by cyclin-dependent protein kinase (CDK). During G_1, CDK is in its inactive form. CDK becomes activated by binding to G_1 cyclin (C_{G_1}) and by being phosphorylated (P) at the activation site. The activated CDK–cyclin complex allows the transition to the S phase. At the end of the S phase, the G_1 cyclin is degraded and the CDK is dephosphorylated, resulting in an inactive CDK. The cell enters G_2. During G_2, the inactive CDK binds to the mitotic cyclin (C_M), or M cyclin. At the same time, the CDK–cyclin complex becomes phosphorylated at both its activation and its inhibitory sites. The CDK–cyclin complex is still inactive because the inhibitory site is phosphorylated. The inactive complex becomes activated when the phosphate is removed from the inhibitory site by a protein phosphatase. The activated CDK then stimulates the transition from G_2 to mitosis. At the end of mitosis, the mitotic cyclin is degraded and the remaining phosphate at the activation site is removed by the phosphatase, and the cell enters G_1 again.

with a cyclin. Most cyclins turn over rapidly. They are synthesized and then actively degraded (using ATP) at specific points in the cell cycle. Cyclins are degraded in the cytosol by a large proteolytic complex called the **proteasome**. Before being degraded by the proteasome, the cyclins are marked for destruction by the attachment of a small protein called *ubiquitin*, a process that requires ATP. Ubiquitination is a general mechanism for tagging cellular proteins destined for turnover (see Chapter 14).

The transition from G_1 to S requires a set of cyclins (known as **G_1 cyclins**) different from those required in the transition from G_2 to mitosis, where **mitotic cyclins** activate the CDKs (see Figure 1.26B). CDKs possess two tyrosine phosphorylation sites: One causes activation of the enzyme; the other causes inactivation. Specific kinases carry out both the stimulatory and the inhibitory phosphorylations.

Similarly, protein phosphatases can remove phosphate from CDKs, either stimulating or inhibiting their activity, depending on the position of the phosphate. The addition or removal of phosphate groups from CDKs is highly regulated and an important mechanism for the control of cell cycle progression (see Figure 1.26B). Cyclin inhibitors play an important role in regulating the cell cycle in animals, and probably in plants as well, although little is known about plant cyclin inhibitors.

Finally, as we will see later in the book, certain plant hormones are able to regulate the cell cycle by regulating the synthesis of key enzymes in the regulatory pathway.

PLASMODESMATA

Plasmodesmata (singular *plasmodesma*) are tubular extensions of the plasma membrane, 40 to 50 nm in diameter, that traverse the cell wall and connect the cytoplasms of adjacent cells. Because most plant cells are interconnected in this way, their cytoplasms form a continuum referred to as the **symplast**. Intercellular transport of solutes through plasmodesmata is thus called **symplastic transport** (see Chapters 4 and 6).

There Are Two Types of Plasmodesmata: Primary and Secondary

Primary plasmodesmata form during cytokinesis when Golgi-derived vesicles containing cell wall precursors fuse to form the cell plate (the future middle lamella). Rather than forming a continuous uninterrupted sheet, the newly deposited cell plate is penetrated by numerous pores (Figure 1.27A), where remnants of the spindle apparatus, consisting of ER and microtubules, disrupt vesicle fusion. Further deposition of wall polymers increases the thickness of the two primary cell walls on either side of the middle lamella, generating linear membrane-lined channels (Figure 1.27B). Development of primary plasmodesmata thus provides direct continuity and communication between cells that are clonally related (i.e., derived from the same mother cell).

Secondary plasmodesmata form between cells after their cell walls have been deposited. They arise either by evagination of the plasma membrane at the cell surface, or by branching from a primary plasmodesma (Lucas and Wolf 1993). In addition to increasing the communication between cells that are clonally related, secondary plasmodesmata allow symplastic continuity between cells that are not clonally related.

Plasmodesmata Have a Complex Internal Structure

Like nuclear pores, plasmodesmata have a complex internal structure that functions in regulating macromolecular traffic from cell to cell. Each plasmodesma contains a narrow tubule of ER called a **desmotubule** (see Figure 1.27). The desmotubule is continuous with the ER of the adjacent cells. Thus the symplast joins not only the cytosol of neighboring cells, but the contents of the ER lumens as well. However, it is not clear that the desmotubule actually represents a passage, since there does not appear to be a space between the membranes, which are tightly appressed.

Globular proteins are associated with both the desmotubule membrane and the plasma membrane within the pore (see Figure 1.27B). These globular proteins appear to be interconnected by spokelike extensions, dividing the pore into eight to ten microchannels (Ding et al. 1992). Some molecules can pass from cell to cell through plasmodesmata, probably by flowing through the microchannels, although the exact pathway of communication has not been established.

By following the movement of fluorescent dye molecules of different sizes through plasmodesmata connecting leaf epidermal cells, Robards and Lucas (1990) determined

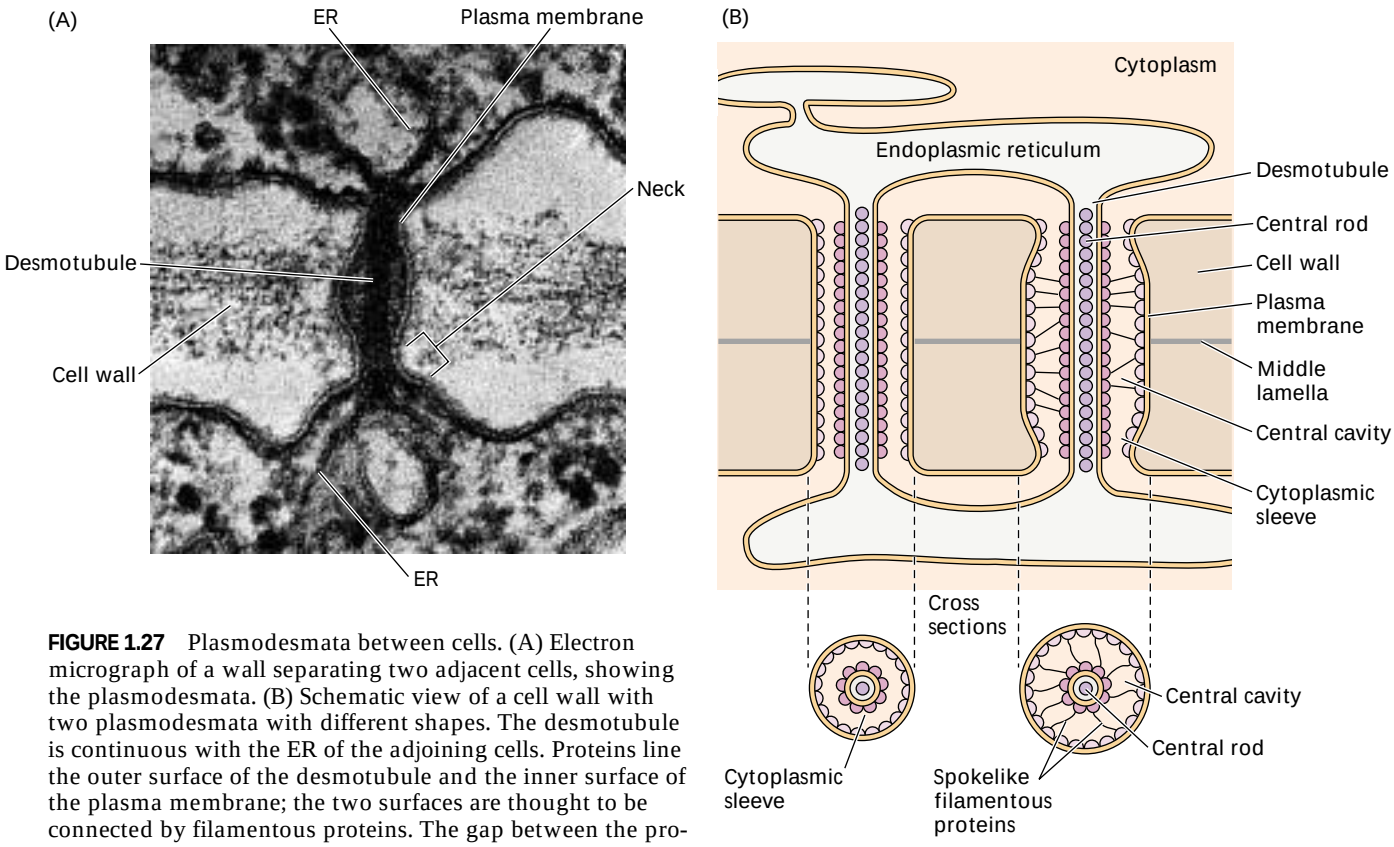

FIGURE 1.27 Plasmodesmata between cells. (A) Electron micrograph of a wall separating two adjacent cells, showing the plasmodesmata. (B) Schematic view of a cell wall with two plasmodesmata with different shapes. The desmotubule is continuous with the ER of the adjoining cells. Proteins line the outer surface of the desmotubule and the inner surface of the plasma membrane; the two surfaces are thought to be connected by filamentous proteins. The gap between the proteins lining the two membranes apparently controls the molecular sieving properties of plasmodesmata. (A from Tilney et al. 1991; B after Buchanan et al. 2000.)

the limiting molecular mass for transport to be about 700 to 1000 daltons, equivalent to a molecular size of about 1.5 to 2.0 nm. This is the **size exclusion limit**, or **SEL**, of plasmodesmata.

If the width of the cytoplasmic sleeve is approximately 5 to 6 nm, how are molecules larger than 2.0 nm excluded? The proteins attached to the plasma membrane and the ER within the plasmodesmata appear to act to restrict the size of molecules that can pass through the pore. As we'll see in Chapter 16, the SELs of plasmodesmata can be regulated. The mechanism for regulating the SEL is poorly understood, but the localization of both actin and myosin within plasmodesmata, possibly forming the "spoke" extensions (see Figure 1.27B), suggests that they may participate in the process (White et al. 1994; Radford and White 1996). Recent studies have also implicated calcium-dependent protein kinases in the regulation of plasmodesmatal SEL.

SUMMARY

Despite their great diversity in form and size, all plants carry out similar physiological processes. As primary producers, plants convert solar energy to chemical energy. Being nonmotile, plants must grow toward light, and they must have efficient vascular systems for movement of water, mineral nutrients, and photosynthetic products throughout the plant body. Green land plants must also have mechanisms for avoiding desiccation.

The major vegetative organ systems of seed plants are the shoot and the root. The shoot consists of two types of organs: stems and leaves. Unlike animal development, plant growth is indeterminate because of the presence of permanent meristem tissue at the shoot and root apices, which gives rise to new tissues and organs during the entire vegetative phase of the life cycle. Lateral meristems (the vascular cambium and the cork cambium) produce growth in girth, or secondary growth.

Three major tissue systems are recognized: dermal, ground, and vascular. Each of these tissues contains a variety of cell types specialized for different functions.

Plants are eukaryotes and have the typical eukaryotic cell organization, consisting of nucleus and cytoplasm. The nuclear genome directs the growth and development of the organism. The cytoplasm is enclosed by a plasma membrane and contains numerous membrane-enclosed organelles, including plastids, mitochondria, microbodies, oleosomes, and a large central vacuole. Chloroplasts and mitochondria are semiautonomous organelles that contain their own DNA. Nevertheless, most of their proteins are encoded by nuclear DNA and are imported from the cytosol.

The cytoskeletal components—microtubules, microfilaments, and intermediate filaments—participate in a variety of processes involving intracellular movements, such as mitosis, cytoplasmic streaming, secretory vesicle transport, cell plate formation, and cellulose microfibril deposition. The process by which cells reproduce is called the cell cycle. The cell cycle consists of the G_1, S, G_2, and M phases. The transition from one phase to another is regulated by cyclin-dependent protein kinases. The activity of the CDKs is regulated by cyclins and by protein phosphorylation.

During cytokinesis, the phragmoplast gives rise to the cell plate in a multistep process that involves vesicle fusion. After cytokinesis, primary cell walls are deposited. The cytosol of adjacent cells is continuous through the cell walls because of the presence of membrane-lined channels called plasmodesmata, which play a role in cell–cell communication.

Web Material

Web Topics

1.1 The Plant Kingdom
The major groups of the plant kingdom are surveyed and described.

1.2 Flower Structure and the Angiosperm Life Cycle
The steps in the reproductive style of angiosperms are discussed and illustrated.

1.3 Plant Tissue Systems: Dermal, Ground, and Vascular
A more detailed treatment of plant anatomy is given.

1.4 The Structures of Chloroplast Glycosylglycerides
The chemical structures of the chloroplast lipids are illustrated.

1.5 The Multiple Steps in Construction of the Cell Plate Following Mitosis
Details of the production of the cell plate during cytokinesis in plants are described.

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