Plant cell

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The basic unit of structure and function in nearly all plants. Although plant cells are variously modified in structure and function, they have many common features. The most distinctive attribute of the majority of plant cells is the rigid cell wall, a feature that is typically absent in animal cells. However, any classification system is imperfect and some plant cells, such as those of the green alga *Dunaliella*, lack a rigid cell wall, whereas some animal cells, such as those in the tunicates, have a rigid cellulosic cell wall. The range of specialization and the character of association of plant cells are very wide. In the simplest plant forms, a single cell constitutes a whole organism and carries out all the life functions. In just slightly more complex forms, cells are associated structurally, but the cytoplasm of each cell is separate and each cell appears to carry out the fundamental life functions, although certain ones may be specialized for participation in reproductive processes. In the most advanced plants, cells whose cytoplasms are connected are associated in functionally specialized tissues, and the associated tissues make up organs such as the leaves, stem, and root. Although a substantial body of knowledge exists concerning the features of various types of plant cells, there is a great gap in knowledge of how cells become specialized for particular functions and associations. *See also:* **Cell (biology) (/content/cell-biology/116000)**; **Plant (/content/plant/522400)**

For convenience, this article first considers the structure of the cell in the interphase or nondividing stage and then in the dividing stage. The cell spends the majority of its life in the interphase stage during which the chromatin in the nucleus is decondensed. Interphase is composed of the G1, S, and G2 phases. In the nucleus, DNA synthesis takes place during the S phase and RNA synthesis predominates during either the G1 or G2 phase. During interphase, protein synthesis takes place in the cytoplasm.

Interphase Cell

For many years, it was usual to employ the term protoplasm to refer collectively to the cell components responsible for imparting the characteristics of life. However, techniques such as cytochemistry, light and electron microscopy, and cell fractionation have made it increasingly possible to define structures known as organelles in the protoplasm (**Fig. 1**). Furthermore, it is possible to localize specific enzyme activities in the organelles so that cell functions can be associated with definite cell structures. *See also:* **Cytochemistry (/content/cytochemistry/178700)**; **Electron microscope (/content**

/electron-microscope/224400); **Enzyme (/content/enzyme/236000)**

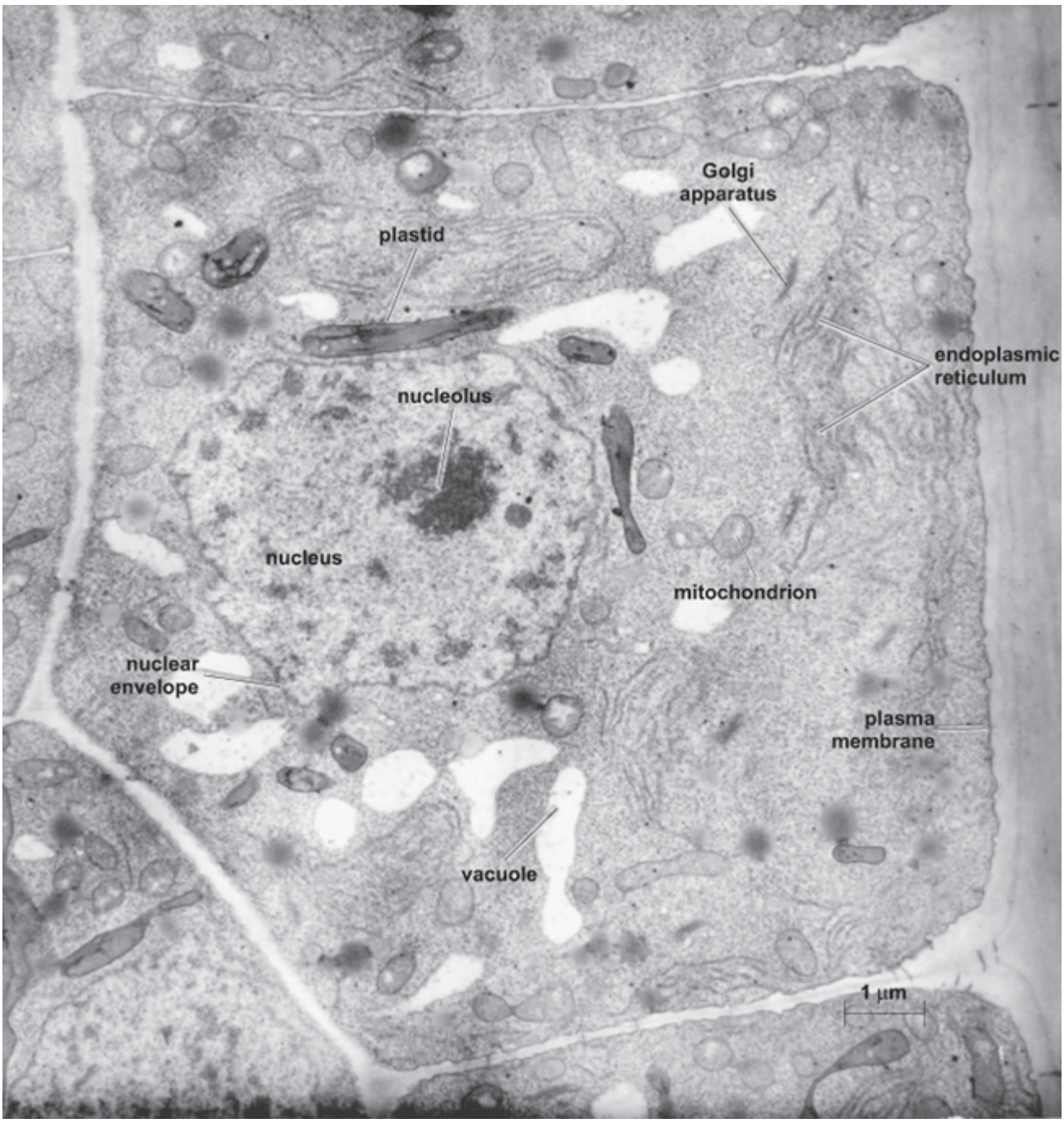

Fig. 1 Spinach (*Spinacia oleracea*) root epidermal cell showing the nucleus and the cytoplasm, which contains various organelles, including the endoplasmic reticulum, the Golgi apparatus, the vacuoles, the mitochondria, and the plastids. In plant cells, vacuole size often determines the position of the nucleus. (*Courtesy of M. Dauwalder*)

Plasma membrane

The cytoplasm is bounded externally by a membrane called the plasma membrane. Whereas the membranes of the compartments in the cytoplasm separate certain activities from the matrix, the plasma membrane separates the activities of the protoplast from the surrounding environment. The plasma membrane is a typical membrane composed of phospholipids and proteins and, as first evidenced from the study of plasmolysis, the plasma membrane is known to be selective with respect to the passage of ions and small molecules into or out of the cytoplasm. The lipids in the plasma membrane form a bilayer that is relatively permeable to hydrophobic molecules, but relatively impermeable to the nutritious hydrophilic charged

ions and polar molecules. Membrane proteins known as channels and carriers facilitate the movement of charged ions and polar molecules across the plasma membrane. While some substances move across the plasma membrane passively down their electrochemical potential gradient, the movement of substances against their electrochemical potential gradient is active and requires the chemical energy of adenosine triphosphate (ATP). The proton-translocating ATPase of the plasma membrane is electrogenic (producing electrical activity in living tissue) and creates an electrochemical potential of over 200 mV across the plasma membrane. The large potential created by this primary transporter drives the movement of cations into the cell and anions out of the cell through secondary transporters. The ion-translocating proteins of the plasma membranes of the sensitive plant (*Mimosa*), Venus' flytrap (*Dionaea*), and the stonewort (*Chara*) are also capable of generating action potentials that are used for communicating changes in the external environment to the cytoplasm and throughout the plant. Indeed, action potentials were characterized in plant cells before they were characterized in animal cells. *See also:* **Ion transport (/content/ion-transport/352000)**; **Lipid rafts (membranes) (/content/lipid-rafts-membranes/800820)**

The transport of macromolecules into and out of the cell occurs by endocytosis and exocytosis, respectively. Exocytosis has been much studied in plant cells, particularly those constituting the aleurone layers of cereal grains that secrete the enzymes necessary to hydrolyze the food in the endosperm necessary for the growing embryo. Endocytosis is not only vital for the uptake of macromolecules, but is also used to ensure that the surface area of the plasma membrane does not increase in nongrowing secretory cells in which exocytosis is active. The vesicles formed during endocytosis are known as endosomes. As endocytosis proceeds, the endocytotic vesicles change their appearance as a result of maturation or vesicle fusion. In soybean cells, the endosomes develop into multivesicular bodies. Endocytosis is less prevalent in turgid plant cells than it is in protoplasts that lack turgor pressure.

The plasma membrane is a very dynamic structure due to the rapid turnover of phospholipids and the activation of transport and signaling proteins in response to environment signals. Thus, the membranous barrier between the living cell contents and the environment, once thought to be a more or less passive structure, is really a very dynamic one.

The cells of multicellular plants are not isolated from each other. Instead, the cytoplasms of adjacent cells are often connected by small tunnels called plasmodesmata (singular: plasmodesma), which allow direct cell-to-cell communication. The cells of multicellular animals are often connected by analogous structures known as gap junctions. As a result of the presence of plasmodesmata, the plasma membrane of one plant cell may be continuous with the plasma membrane of the adjacent cell. The continuum of protoplasm is known as the symplast. *See also:* **Cell membranes (/content/cell-membranes/116500)**

Nucleus

The nucleus was first discovered serendipitously by Robert Brown in the 1830s while he was studying pollination in orchids. The nucleus of the undifferentiated plant cell is generally centrally located, whereas in mature plant cells it may be displaced to the edge of the cell by the presence of a large vacuole. The nuclear material consists of clear regions, a fibrillar nuclear matrix, and chromatin, which at the time of division is resolved into chromosomes, a form suitable for transport. Nuclear components of key importance are DNA, RNA, basic proteins known as histones that make up the nucleosomes around which the DNA is wrapped, and other proteins, including DNA polymerase, RNA polymerase, and transcription factors. Continuing syntheses of DNA and RNA are predominant activities in the nucleus, although comparable processes also take place in the mitochondria and the plastids. The singular importance of the relationships of DNA to RNA and proteins lies in the fact that the hereditary characteristics of the cell, encoded in DNA molecules, are transmitted in a complex sequence via RNA to proteins. *See also:* **Deoxyribonucleic acid (DNA) (/content/deoxyribonucleic-acid-dna/186500)**; **Genetic code (/content/genetic-code/284900)**; **Histone (/content/histone/461000)**; **Nucleic acid (/content/nucleic-acid/460600)**; **Protein (/content/protein/550200)**; **Ribonucleic acid (RNA) (/content/ribonucleic-acid-rna/589000)**

Different types of RNA are formed in the nucleus: transfer RNA (tRNA), ribosomal RNA (rRNA), messenger RNA (mRNA), and microRNA (miRNA). The first three participate in the synthesis of proteins by ribosomes and the last is involved in suppressing the synthesis of proteins.

One or more nucleoli are found in the nuclei of all plant cells. Chemically, plant nucleoli contain DNA that codes for rRNA, the rRNA itself, and relatively large amounts of protein that will join with the rRNA to form the large and small subunits of the ribosomes. The appearance of the nucleolus changes through development.

As in animal cells, the nucleus of the plant cell is bounded by an envelope. The envelope is a complex structure, consisting of two membranes with a lumen (called the perinuclear space) between, and with discontinuities (called pores) fairly regularly spaced throughout. These pores are regular in outline and are bounded by proteins known as nucleoporins. They were frequently seen to contain material that stains differently from the adjacent regions, and it had been suggested that interchanges, particularly of large molecules, between nucleus and cytoplasm take place through the pores (**Fig. 2***a*). By tagging proteins and nucleic acids with colloidal gold and microinjecting them into the nucleus or cytoplasm, it has been shown that the nuclear pores transport proteins from the cytoplasm into the nucleus and transport nucleic acids from the nucleus into the cytoplasm. The perinuclear space has been relatively little studied, but some cytochemical studies suggest the presence of enzymes (**Fig. 2***b*). The nuclear envelope, with a metabolically active lumen, apparently is a complex system for controlling nucleocytoplasmic exchanges.

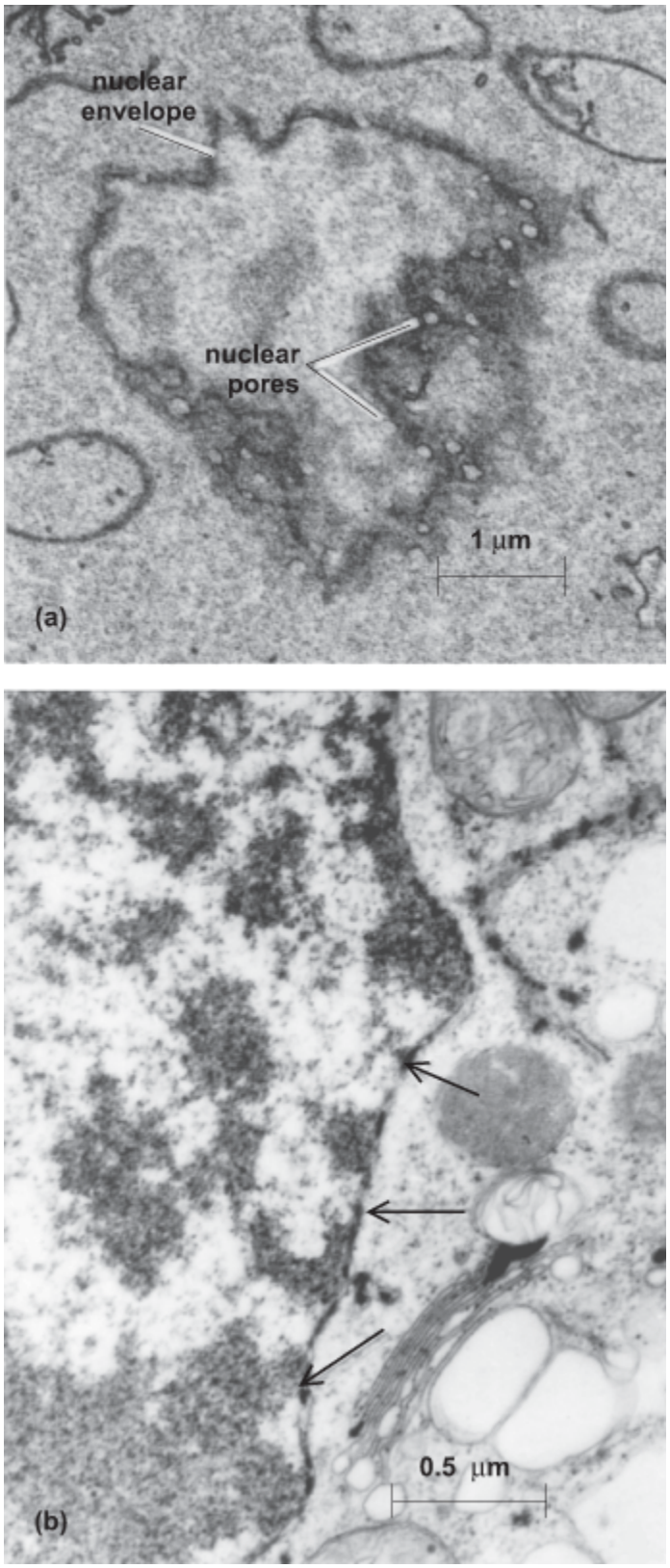

Fig. 2 Cell nucleus. (*a*) Somewhat tangential section (*courtesy of H. H. Mollenhauer*). (*b*) Section showing the nuclear envelope (*courtesy of C. W. Goff*). The dark lead precipitate (arrows) indicates the presence of acid phosphatase within the perinuclear space.

The inner membrane of the nuclear envelope is frequently in close association with portions of the chromatin, particularly the telomeric and centromeric regions. The outer membrane may be studded with ribosomes. In some instances, extensions of the nuclear envelope continue outward into the cytoplasm, often in specific association with particular organelles (**Fig. 3**). In instances in which segments of nuclear envelope have particular architectural modifications, and these same modifications are seen elsewhere in the cell, it has been suggested that the membrane may be transferred from the nuclear envelope,

perhaps transporting perinuclear material with it. No substantial experimental evidence has been provided for this, but it does seem clear that the nuclear envelope is a dynamic structure from which vesicles may be evolved in certain stages of cellular activity. One example is the frequent appearance of what appear to be vesicles being pinched off from the nuclear envelope and transported to the Golgi apparatus. *See also:* **Cell nucleus (/content/cell-nucleus/116800)**

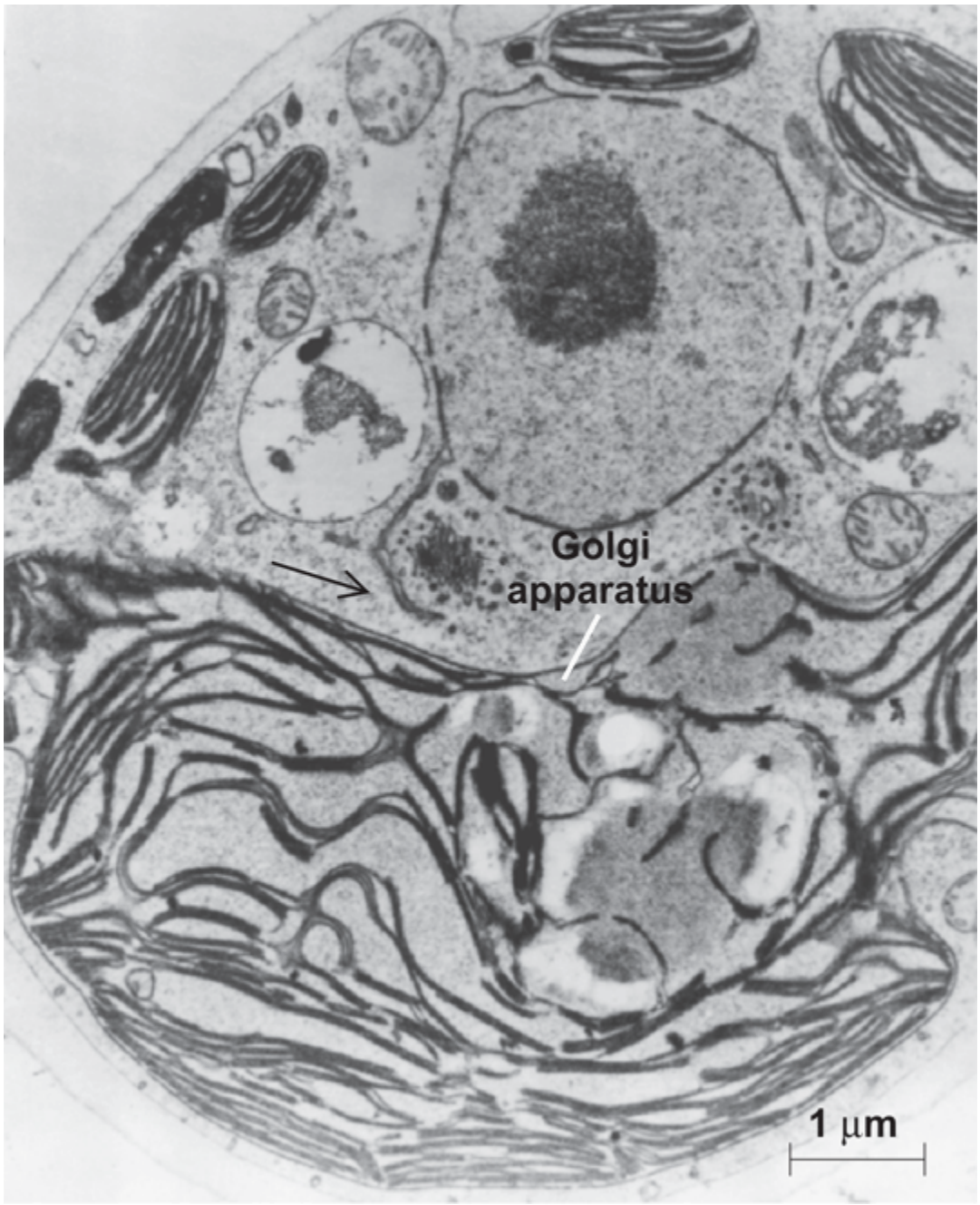

Fig. 3 Section of a *Chlamydomonas* cell showing extension of the nuclear envelope (arrow) to the vicinity of the Golgi apparatus. (*Courtesy of P. L. Walne*)

Cytoplasm

The cytoplasm is the region of the cell between the nuclear envelope and the plasma membrane. It consists of a non-newtonian, thixotropic matrix throughout which are distributed various organelles and through which these organelles move. [A non-newtonian fluid does not have a constant viscosity in accordance with Newton's law; thixotropy is a property of certain gels or fluids that are thick (viscous) under standing conditions, but liquefy (become less viscous) when subjected to agitation or stress.] Metabolic activities may be generally distributed throughout the cytoplasm, confined to specific regions, or clearly

carried out within the organelles. Although more research has been directed to the analysis of the chemical composition and activities of the organelles than of the cytoplasm, it is apparent that the cytoplasm is composed in part of cytoskeletal elements and chains of functionally related enzymes surrounded by the cytosol, which includes water, ions, small metabolites, and proteins.

The organelles, which are compartments in which certain metabolic activities are localized, are bounded by membranes similar to the plasma membrane. The molecular components (phospholipids and proteins) of the membranes are subject to rapid turnover. The membranes act as sites for the synthesis or breakdown of materials and frequently, as in mitochondria, are structurally highly specialized for these activities. Therefore, far from being simply selective barriers to the movement of materials, the membranes of the plant cell are dynamic structures that play key roles in metabolism. *See also:* **Cytoplasm (/content/cytoplasm/179300)**

Ribosomes

Conspicuous among the components of the cytoplasmic matrix are millions of particles, approximately 20 nanometers in diameter, known as ribosomes. Each ribosome is composed of a small subunit and a large subunit that are formed separately in the nucleolus from rRNA and proteins and brought together in the cytoplasm. The ribosomes are the sites of protein synthesis and function in translating the sequence of nucleotides in mRNA into the sequence of amino acids that make up the protein encoded by the mRNA. Translation of the genetic code in the ribosomes also requires tRNA. Some of the rRNAs that make up the ribosome acts as a ribozyme in the translation process. Smaller ribosomes are also present in the mitochondria and plastids, where they translate RNA encoded by the DNA that resides in these organelles.

In many instances, the cytoplasmic ribosomes are seen in spiral or helical arrangements called polyribosomes or polysomes, in which the ribosomes are interconnected by thin strands of mRNA. These arrangements represent ribosomes moving along strands of mRNA. In all types of cells, some of the ribosomes in the cytoplasm appear to be free, whereas others are attached to the surface of the membranes of the endoplasmic reticulum or to the outer membrane of the nuclear envelope. *See also:* **Ribosomes (/content/ribosomes/589200)**

Endoplasmic reticulum

The character of the cytoplasmic compartment known as the endoplasmic reticulum has been known only since electron microscopy has been adapted to the study of cells. This compartment may be tubular or lamellar; in thin sections, each form appears to be a profile of two membranes with a lumen between.

The endoplasmic reticulum is an architecturally regular structure only in a few types of plant cells. It frequently shows dilatations, sometimes containing crystals or other distinctively staining material. The endoplasmic reticulum is a protean (highly variable) structure, and the manners in which its profiles are associated differ with the stage of development and metabolic activity. In certain stages, numbers of profiles are seen to be stacked, frequently parallel to the surface of the cell (**Fig. 4**). The profiles may also surround the nucleus or seem to encompass any of several types of organelles. The endoplasmic reticulum may be smooth or rough; that is, the outer surfaces of the membranes may be studded with ribosomes. While all plant cells have rough and smooth endoplasmic reticulum to synthesize the proteins and lipids necessary to construct many of the membranes of the cell, the rough endoplasmic reticulum is enriched in cells that are specialized for protein synthesis, including the cells of the aleurone layer of cereal seeds, and the smooth endoplasmic reticulum is enriched in cells specialized for lipid production, including oil gland cells and some stigmatic cells. Transitional endoplasmic reticulum, which is intermediate in structure between the smooth and rough endoplasmic reticulum, is rich in cells of the tapetum and the cells of seeds that store lipids in the form of osmotically active lipid bodies.

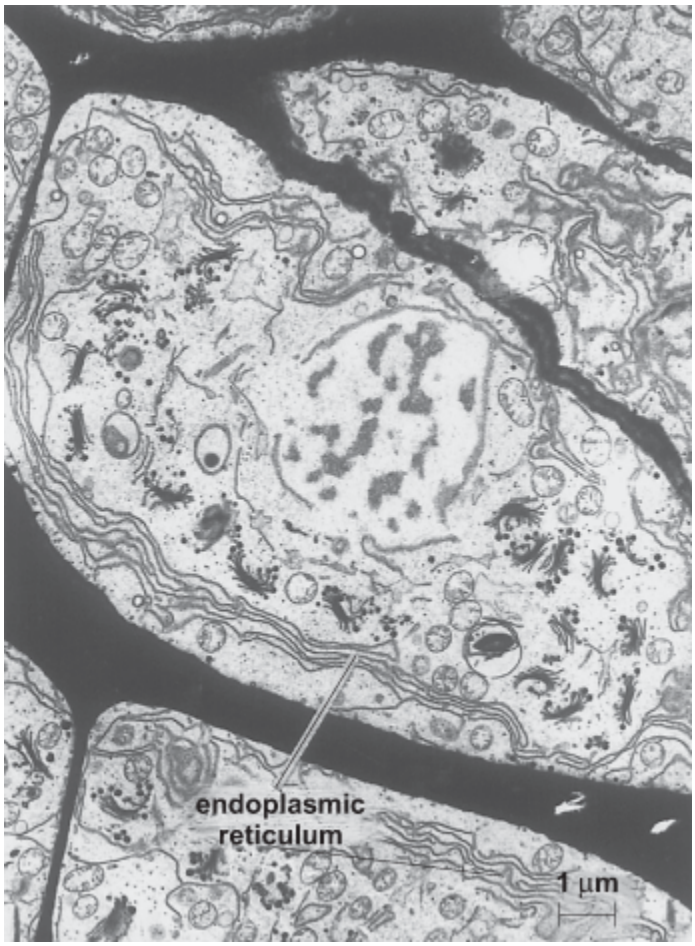

Fig. 4 Portions of maize root cap cells showing profiles of endoplasmic reticulum stacked more or less parallel to the cell surface. (*Courtesy of M. Dauwalder*)

It is known that certain substances are transferred through the endomembrane system from the endoplasmic reticulum to other sites in the cell. For example, in many secreting cells, it can be shown by autoradiography and cell fractionation studies that proteins or protein precursors move from the endoplasmic reticulum to the Golgi apparatus by way of vesicles; then, from the Golgi apparatus, vesicles bleb off and move to either the vacuole or the plasma membrane where the contents of the vesicles are secreted into the cell wall. Amino acid sequences in the transported protein known as molecular zip codes determine the final destination of the transported protein. The movement of proteins from organelle to organelle through the endomembrane pathway occurs as a result of vesicle formation from the donor membrane and vesicle fusion with the acceptor membrane. The transfer of vesicles between membranes requires guanosine 5′-triphosphate (GTP)–binding proteins. Much work is under way in order to elucidate the secretory process and to make it more efficient as more plant cells are being used as light-powered bioreactors to produce fine pharmaceuticals as well as vaccines that are targeted against viruses that plague humans and animals. *See also:* **Autoradiography (/content/autoradiography/065200)**

The introduction of toxic substances such as herbicides sometimes causes extensive proliferation of the endoplasmic reticulum. This development appears to be a compensatory response to deleterious conditions. It may well be that proliferation of the endoplasmic reticulum provides additional reaction surface and more enzymes that increase the capacity of the cell to detoxify substances or otherwise adjust to unfavorable circumstances.

In multicellular plants, the endoplasmic reticulum passes through the cell-to-cell connections known as plasmodesmata and thus can be continuous between adjacent cells. The endoplasmic reticulum forms the center of the plasmodesma so that the cytoplasm within the plasmodesmata takes the form of a hollow cylinder. While the membrane of the endoplasmic reticulum is continuous between adjacent cells, the lumen is not (**Fig. 5**). *See also:* **Endoplasmic reticulum (/content/endoplasmic-**

reticulum/232300)

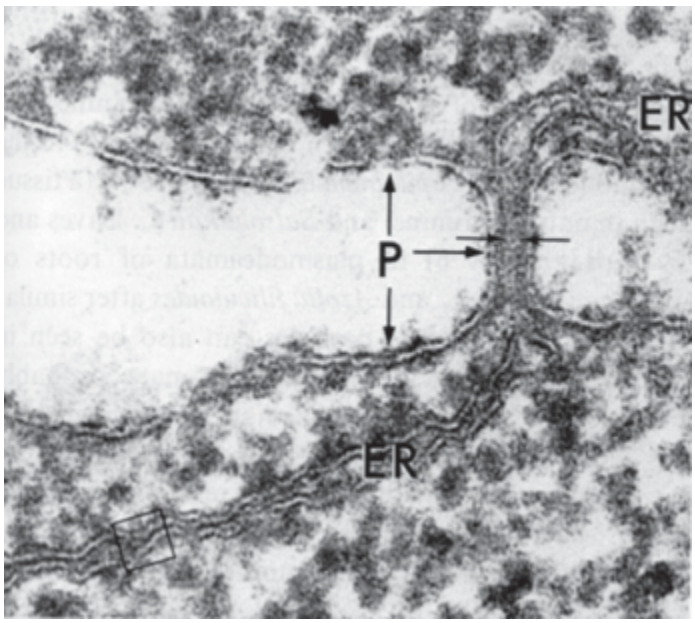

Fig. 5 Longitudinal view of a plasmodesma passing from cell to cell through the wall in *Azolla pinnata* root cells [×175,000]. ER, endoplasmic reticulum; P, plasma membrane. (*From R. L. Overall, J. Wolfe, and B. E. S. Gunning, Intercellular communication in Azolla roots: I. Ultrastructure of plasmodesmata, Protoplasma, 111:134–150, 1982*)

Golgi apparatus

The Golgi apparatus is a component of all plant cells, with the possible exception of certain fungi and some highly specialized cells such as mature sperm. In many plant cells, the Golgi apparatus clearly functions in secretion, but the ubiquitous occurrence of the organelle suggests that it may have other roles in cellular activity. Although many aspects of its function are still obscure, it is apparent that certain materials are sequestered into its cisternae or saccules (**Fig. 6**), synthesized there, or variously combined in the cisternae to form complex secretion products. Many of the secretory proteins that pass through the Golgi apparatus are glycosylated there. The secretory products are then separated from the cisternae as membrane-bound vesicles and transported to and through the plasma membrane or to the vacuolar compartment where they remain inside the cell. While the Golgi apparatus is important in the secretion of many proteins, including the fucose-rich mucilage secreted by root cap cells, the digestive enzymes secreted by insectivorous plants, and the wall-degrading enzymes released by the cells in the abscission zone, it is bypassed in the secretion of some proteins, including the prolamin proteins that make up some of the protein vacuoles in the seeds of cereals. In the majority of plant cells, the Golgi apparatus is responsible for packaging and exporting the hemicelluloses, pectins, and hydroxyproline-rich glycoproteins of the wall that is built up around the cell.
See also: **Golgi apparatus (/content/golgi-apparatus/295200)**

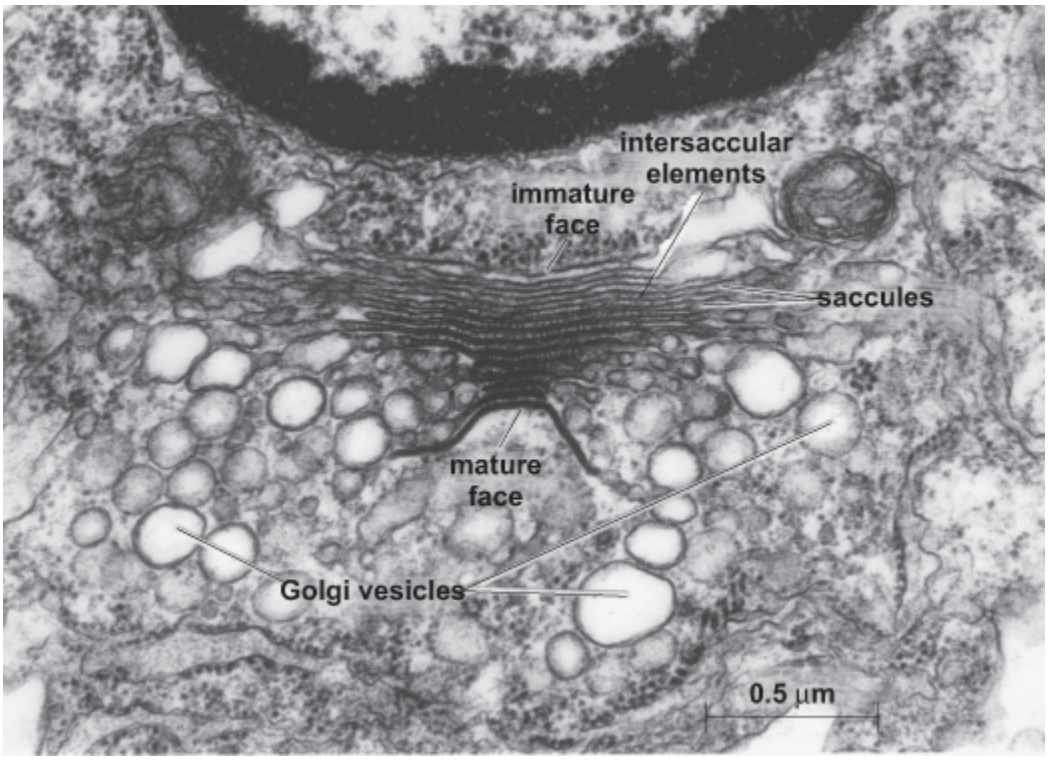

Fig. 6 Portion of a *Nitella* cell showing a Golgi apparatus composed of a stack of cisternae/saccules, the contents of which stain differentially from the immature face to the mature face. Note also the intersaccular elements and the associated Golgi vesicles produced from the saccules. (*Courtesy of R. Turner*)

Vacuoles

The vacuole is a membrane-bound compartment in the cell that contains the cell sap. In meristematic cells, vacuoles are generally small and are characterized by contents that stain darkly with certain procedures. The contents of these vacuoles seem to be utilized in the process of development and then are replaced by water. At a certain stage in this process, the vacuoles fuse to form the large central vacuole, and most mature plant cells have large, centrally located vacuoles that make up the greatest part of the total volume of the cell. The cell sap is typically clear, making the vacuole look empty or vacuous. The increase in volume of this vacuole is important in the growth of the plant cell. Moreover, the presence of water in the vacuole allows plants to have a large open dendritic form with a minimum investment of energy-intensive compounds in order to help the plants acquire light and the necessary nutrients that are dilute in the environment. In plant cells, vacuoles of different sorts are known to have different origins, with the endoplasmic reticulum, the Golgi apparatus, and the plasma membrane being involved.

Vacuoles participate in the homeostasis of the cytosol by acting as large reversible stores of water, protons and other ions, amino acids, and other metabolites. The vacuoles in cells of many seeds function in the storage of proteins, and the vacuoles in the cells of many desert plants function in the storage of water as well as the storage of carbon in the form of organic acids.

The colors of many flowers and fruits result from the presence of pigments dissolved in the vacuolar fluid. Anthocyanins in the vacuoles produce red-blue colors, depending upon the relative acidity of the fluid in the vacuole. By observing the presence or absence of anthocyanins in the vacuoles of the aleurone cells of maize kernels, transposable elements have been discovered. Observation of anthocyanins in the vacuoles of cells in the petals of transformed *Petunia* plants also led to the discovery of microRNA. *See also:* **Plant pigment (/content/plant-pigment/524550)**

Since vacuoles typically take up the majority of the space in a mature cell, they have the volume necessary to store organic molecules that would be toxic if they were stored in the cytosol. Many of these compounds, including nicotine, caffeine,

colchicine, vinblastine, trypsin inhibitor, and calcium oxalate, which would be harmful if kept in the cytosol, protect the plant from potential predators (**Fig. 7**).

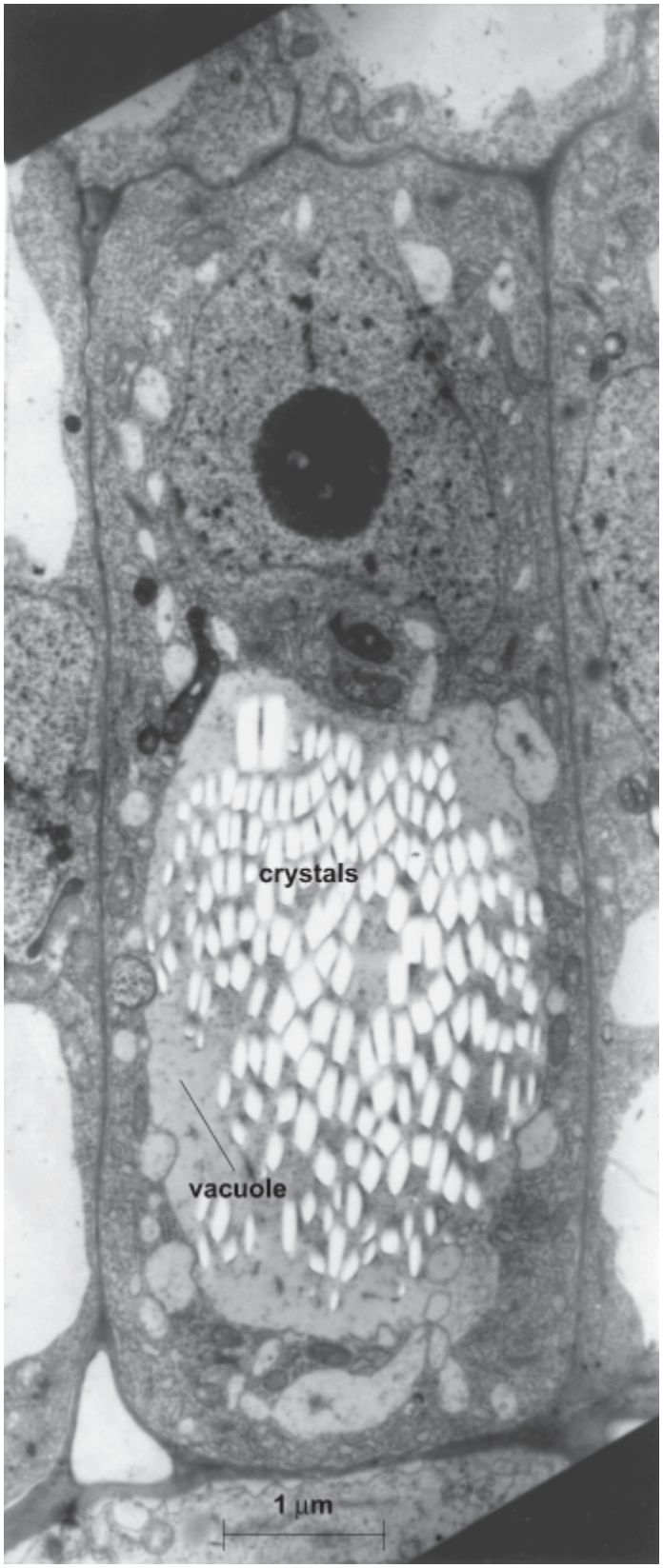

Fig. 7 *Eichhornia* cell showing crystals developing within the vacuole. (*Courtesy of H. J. Arnott*)

The vacuoles of plant cells contain many nonspecific hydrolytic or lysosomal enzymes, including proteases with acidic pH optima. These hydrolytic enzymes catalyze the breakdown of molecules so that they can be recycled back to the cytosol. The vacuolar compartment of animal cells functions primarily as a lysosome. In plant cells in which digestive activity is a

predominant process, lysosomal enzymes are abundant, for example, in cells containing aleurone grains from which protein is released to support early growth of the germinating seedling. Some lower plant cells, for example, *Euglena*, contain bodies with lysosomal activity that is more nearly comparable to those of the animal cell. *See also:* **Lysosome (/content/lysosome/394100)**; **Vacuole (/content/vacuole/725300)**

Lipid bodies

Another conspicuous feature of many types of plant cells is the presence of large numbers of lipid bodies or spherosomes (**Fig. 8**). They frequently are abundant in cells of embryos or in root or shoot apices and less numerous in more mature plant cells. These bodies are unique in having a structural boundary that is composed of a monolayer instead of a bilayer that is typical of most membranes. The lipid bodies provide a carbon source for the production of biofuels.

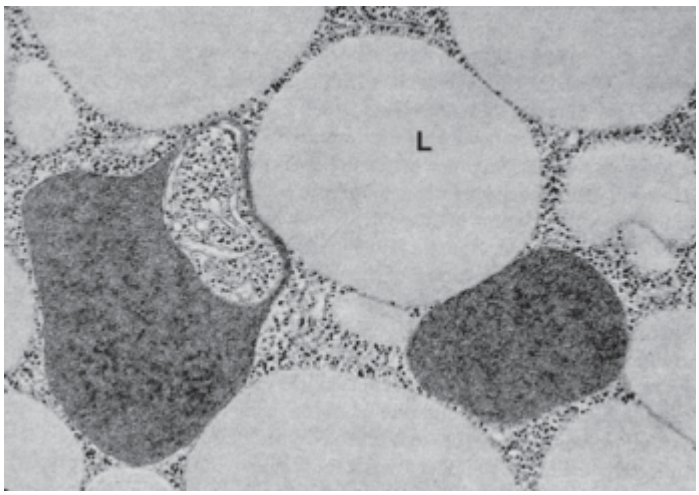

Fig. 8 Glyoxysome next to lipid bodies (L) in a tomato cotyledon cell [×29,000]. Notice how the peroxisome on the left encloses a mitochondrion. (*From S. E. Frederick, P. J. Gruber, and E. H. Newcomb, Plant microbodies, Protoplasma, 84:1–29, 1975*)

Glyoxysomes and peroxisomes

Microbodies are single membrane-enclosed organelles that contain an oxidase that generates hydrogen peroxide and a catalase that breaks it down. Microbodies exist as glyoxysomes or peroxisomes. Glyoxysomes contain the glyoxylate cycle enzymes necessary to convert insoluble lipids into soluble carbohydrates. They are prominent in the cells of oil-rich seeds and spores and are often associated with lipid bodies and mitochondria (Fig. 8). During the greening process, glyoxysomes develop into peroxisomes by degrading the enzymes involved in the glyoxylate cycle and acquiring the enzymes necessary for the photorespiratory process that recovers a portion of the carbon lost when ribulose bisphosphate carboxylase-oxygenase (Rubisco) in the chloroplast catalyzes the addition of oxygen instead of carbon dioxide to ribulose bisphosphate (RuBP). The peroxisomes are often associated with chloroplasts and mitochondria. During the senescence of leaves, peroxisomes transform back to glyoxysomes so that the fatty acids in the cells of the leaf can be translocated back to the plant in soluble form. *See also:* **Peroxisome (/content/peroxisome/757495)**

Mitochondria

Mitochondria typically are ellipsoidal bodies bounded by a double-membrane system with the inner membrane projecting into the lumen to form cristae (**Figs. 9** and **10**), which may be either tubular or sheetlike, depending upon the type of cell and its activity. In general, there is less extensive development of the cristae in the mitochondria of plant cells than in those of animals. This may reflect the fact that plant cells generally have substantially lower respiratory rates. In the few types of plant cells characterized by relatively high respiratory rates, the extent of the cristae more nearly resembles that in animal cells.

The inner membrane of the mitochondria surrounds the matrix. The mitochondria can often be observed to move incessantly throughout the plant cell.

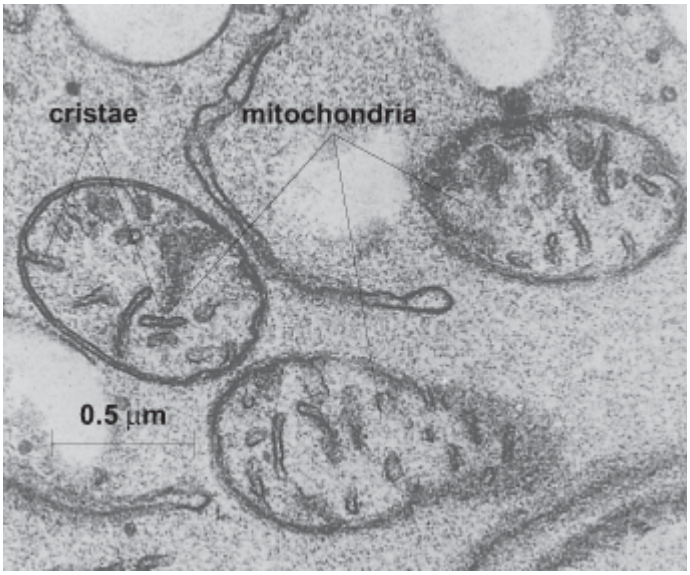

Fig. 9 Three mitochondria showing two bounding membranes and cristae formed by extension of the inner membrane into the lumen. (*Courtesy of H. H. Mollenhauer*)

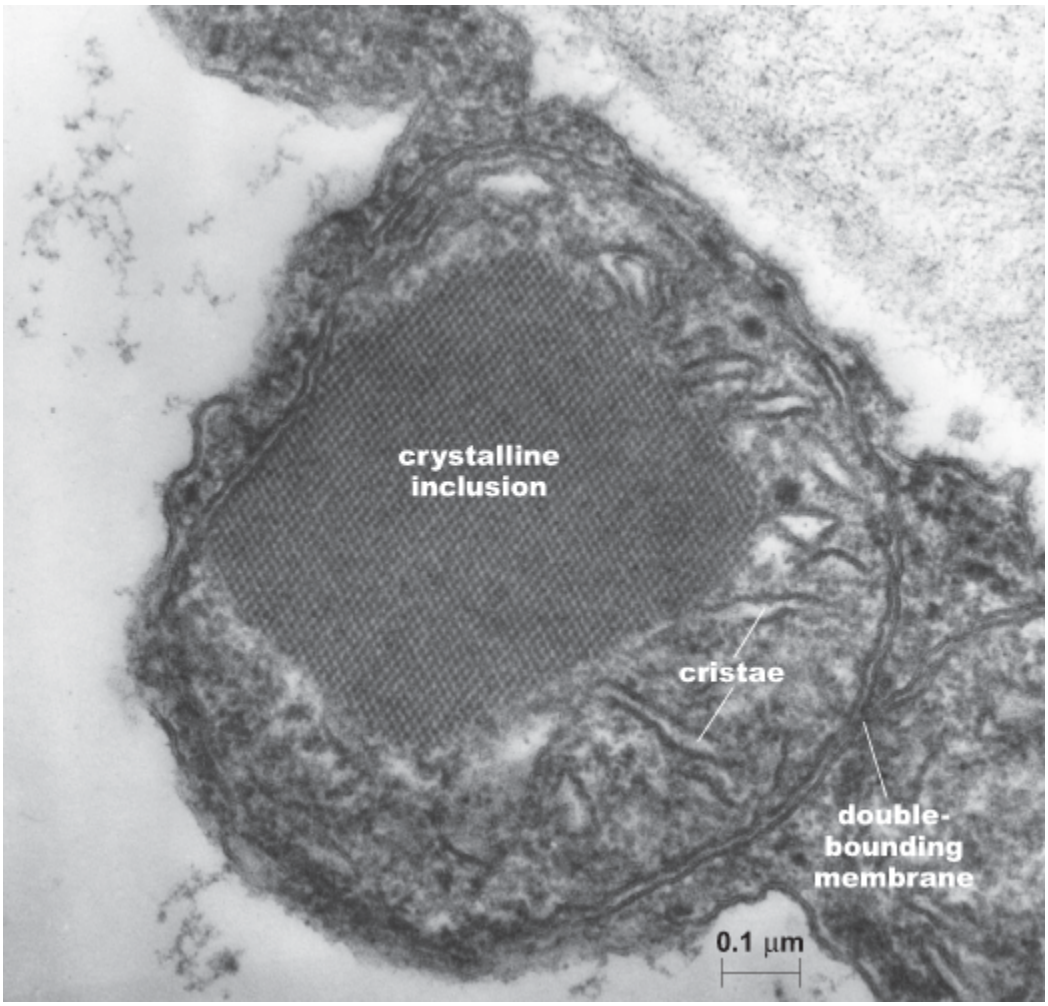

Fig. 10 A highly magnified mitochondrion. Components of crystalline inclusion are in an ordered array. (*Courtesy of H. J. Arnott*)

The mitochondria are the respiratory centers of the cell where the energy released by the combustion of carbohydrates is conserved in the synthesis of adenosine triphosphate (ATP) from adenosine diphosphate (ADP) and inorganic phosphate (P_i). The conversion of the chemical energy of carbohydrate to the chemical energy of ATP requires a few associated processes. The pyruvate formed during glycolysis, which takes place in the cytosol, is oxidized to CO_2 in the matrix of the mitochondria in a process known as the Krebs cycle or the citric acid cycle. The electrons captured in the oxidation process are transported down electron transport chains that exist as iron-containing protein complexes in the inner membrane. Molecular oxygen is the final receptor for these electrons. The transfer of electrons from molecules with high reduction potentials to molecules with low reduction potentials provides enough energy to transport protons against their electrochemical potential from the matrix across the inner membrane, and this transfer of protons results in a proton-motive force. ATP synthases, which are lollipop-shaped structures on the inner membrane, provide a pathway in which the protons can move down their electrochemical gradient back into the matrix. The energy extracted by the ATP synthase as protons flow through them is used for the production of ATP. Since oxygen is required for the synthesis of the majority of ATP in the mitochondria, this process is known as oxidative phosphorylation.

The mitochondria contain a complete genetic system, including DNA, RNA, ribosomes, and the enzymes necessary to synthesize DNA, RNA, and proteins. The mitochondria are also capable of dividing. The DNA in the mitochondria participates in non-Mendelian cytoplasmic inheritance and is responsible for such agronomically important traits as male sterility. The genetic system of the mitochondria produces only a portion of the proteins required by the mitochondria. The rest are transported into the mitochondria after being synthesized on cytoplasmic ribosomes using mRNA transcribed from DNA in the nucleus. The presence of nucleic acids and ribosomes within the mitochondria provides evidence for the endosymbiotic origin of the mitochondria. *See also:* **Citric acid cycle (/content/citric-acid-cycle/366100)**; **Mitochondria (/content/mitochondria/428200)**

Plastids

Perhaps the most conspicuous and certainly the most studied of the features peculiar to plant cells is the presence of plastids. The plastids are bounded by an envelope consisting of two membranes that touch in regions known as contact sites and an inner membrane system immersed in a viscous gel known as the stroma. Chlorophylls and other pigments are associated with the inner-membrane system. The extensiveness of the inner membrane varies greatly with the functional state of the plastid. The inner membranes of chloroplasts known as the thylakoids are characterized in most plants as associations of stacked disk-shaped granal lamellae and interconnecting stromal lamellae (**Fig. 11**). The chlorophylls, or green pigments, have been the most studied of the plant pigments because of their conspicuous role in photosynthesis, the process in which radiant energy is converted into the chemical energy of carbohydrates. *See also:* **Chlorophyll (/content/chlorophyll/132200)**; **Photosynthesis (/content/photosynthesis/511700)**

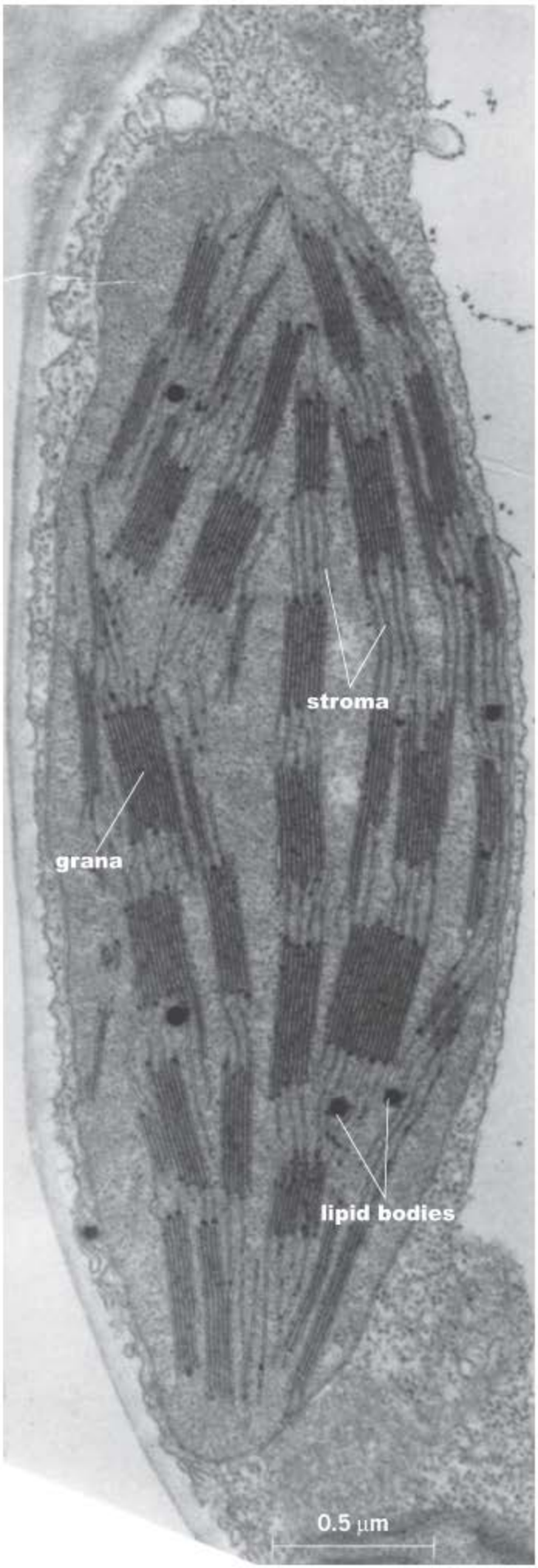
stroma
grana
lipid bodies
0.5 μm

Fig. 11 Electron micrograph of chloroplast of a tomato fruit cell showing granal and stromal lamellae. (*Courtesy of S. W. Rosso*)

The plastids, which can metamorphose into each other, exist in a splendid array of shapes and colors. The green plastids, which are known as chloroplasts, contain chlorophyll, which is responsible for the green color of many parts of plants. In higher plants, chloroplasts are typically ellipsoidal; in contrast, in the algae, they may appear as plates, stars, or spirals. The orange plastids, which are known as chromoplasts, contain carotenoids and are responsible for certain colors in flowers, fruits, the roots of carrots and sweet potatoes (*Ipomoea batatas*), and the stem tubers of yams (*Solanum tuberosum*). The translucent plastids also known as leucoplasts include the amyloplasts and the elaioplasts, in which starch and lipids, respectively, are stored. In higher plants, the plastids originate as small proplastids in the meri-stematic cells. The transformation of proplastids into chloroplasts in higher plants requires light. In the absence of light, the proplastids transform into etioplasts, which will rapidly become chloroplasts upon exposure to light.

Like the mitochondria, the plastids are capable of dividing and they contain a complete genetic system. Mutations in the plastid DNA can often be visualized as the colorless regions of variegated plants. As in the mitochondria, the genetic system of the plastids produces only a portion of the proteins that they require. The rest are transported into the plastid after being synthesized on cytoplasmic ribosomes using mRNA transcribed from the DNA in the nucleus.

Changes in plastid form, distribution, and quite possibly metabolic efficiency have been conspicuous features of plant evolution. At any evolutionary level, however, the presence of plastids, and all that this implies metabolically, provides a nearly sharp distinction between a plant and an animal cell. The one exception is the presence of plastids, known as apicoplasts, in the apicomplexan parasites that include *Plasmodium*, the cause of malaria in humans. Even so, plastids impart to plants their unique status in the biotic world by creating concentrated organic matter from dilute inorganic molecules using the radiant energy of sunlight. *See also:* **Cell plastids (/content/cell-plastids/117100)**; **Plant evolution (/content/plant-evolution/522800)**; **Plant kingdom (/content/plant-kingdom/523300)**

Microtubules and microfilaments

Plant cells contain a network of filaments that is known as the cytoskeleton. Microfilaments are one component of the cytoskeleton. Actin microfilaments are polymers of the protein actin and are similar to the 5–6-nm-diameter thin filaments found in the muscle cells of animals. Likewise, plant cells also contain myosin, a mechanochemical protein that converts the chemical energy of ATP into the mechanical energy of movement. Actin microfilaments provide the track upon which myosin moves in order to drive many motile events in plant cells, including cytoplasmic streaming, the movement of Golgi-derived vesicles to the tip of growing pollen tubes, and the movement of chloroplasts to maximize photosynthesis and minimize photodamage.

Plant cells also contain microtubules, which are hollow tubular polymers, 24 nm in diameter, and composed of the protein tubulin. Microtubules provide the tracks upon which the mechanochemical proteins dynein and kinesin move to drive motile events, particularly mitosis, cell plate formation, and the ciliary and flagellar movements that occur in the sperm of lower plants (**Fig. 12**). *See also:* **Cilia and flagella (/content/cilia-and-flagella/136100)**

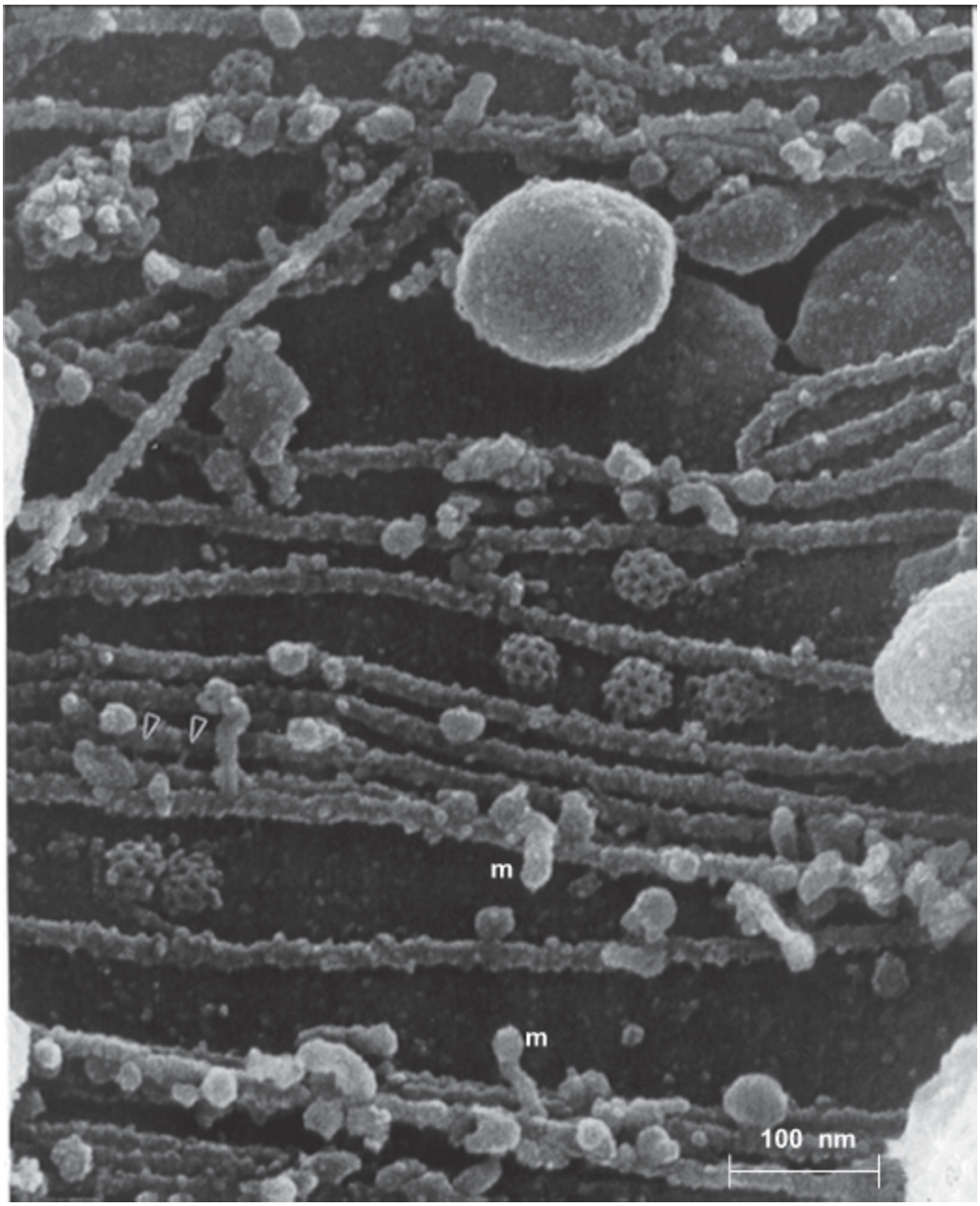

Fig. 12 Cortical microtubules in an onion root cell that have been freeze-fixed, freeze-fractured, dried, and observed with a field-emission scanning electron microscope. There are many cross-bridges (arrowheads) and appendages (m) on the microtubules. The plasma membrane is in the background and coated vesicles can be seen. (*From P. A. Vesk, M. Vesk, and B. E. S. Gunning, Field emission scanning electron microscopy of microtubule arrays in higher plant cells, Protoplasma, 195:168–182, 1996*)

The microtubules control in part the orientation of the cellulose microfibrils in the cell wall that are synthesized by a cellulose synthase complex on the plasma membrane. The microtubules adjacent to the cytoplasmic side of the plasma membrane and the cellulose microfibrils adjacent to the external surface of the plasma membrane are typically coparallel. Moreover, when plant cells are treated with drugs that cause the depolymerization of microtubules, the cellulose microfibrils become randomly oriented. The plant hormones auxin and gibberellin cause the microtubules underlying the plasma membrane to maintain a transverse orientation relative to the cell axis that results in the transverse orientation of cellulose microfibrils and polarized cell elongation. By contrast, the hormones ethylene and cytokinin cause a randomization of the microtubules that results in a randomization of the cellulose microfibrils and isodiametric growth (that is, growth having equal diameters or dimensions).

See also: **Plant hormones (/content/plant-hormones/523100)**

Other organelles and inclusions

Normal plant cells may contain other structures at specific stages, such as the blepharoplasts and centrioles that are characteristic of division stages in some lower plants and the basal bodies that are associated with cilia and flagella. Still other structures, such as the pyrenoid and the eyespot of cells of certain algae and the Woronin bodies of certain fungi, distinguish the cells of particular groups of plants.

Cytoplasmic streaming

Cytoplasmic streaming or cyclosis is one of the most easily observed and memorable process that can be seen under a microscope. As a consequence of the large size of most plant cells compared to most animal cells, diffusion is limiting. Cytoplasmic streaming facilitates the transport and mixing of substances in plant cells by causing convection, which is much faster than diffusion. Cytoplasmic streaming is an actomyosin-driven process that can be inhibited readily by drugs, including cytochalasin and latrunculin, which interfere with actin. The degree of organization and the rate of streaming in plant cells are correlated with the size of the cell. Small plant cells, including the epidermal cells of onion bulb scales, have circulation streaming where the organelles move at a rate of 5 micrometers per second, whereas larger cells, such as the intermodal cells of *Chara*, have rotational streaming where the organelles move at a rate of 100 μm per second. All movement in the cell is arrested if the cell is fixed for study under a microscope. Thus, the static picture of any cell fails to convey one of its most vital aspects. *See also:* **Cell motility (/content/cell-motility/116700)**

Cell wall

A distinctive feature of the plant cell is the rigid wall surrounding the cell outside the plasma membrane (**Fig. 13**). Indeed, it was the observation of the thick walls of cork that had been recently introduced to replace oil rags as bottle stoppers that allowed Robert Hooke to discover cells in 1665. While the wall may be variously thickened and sculptured in mature cells, it is only 100 nm thick in meri-stematic cells. The cell wall provides the mechanical strength that allows plant cells to build up turgor pressure without lysing when surrounded by dilute media. This turgor pressure makes it possible for herbaceous plants to stand erect.

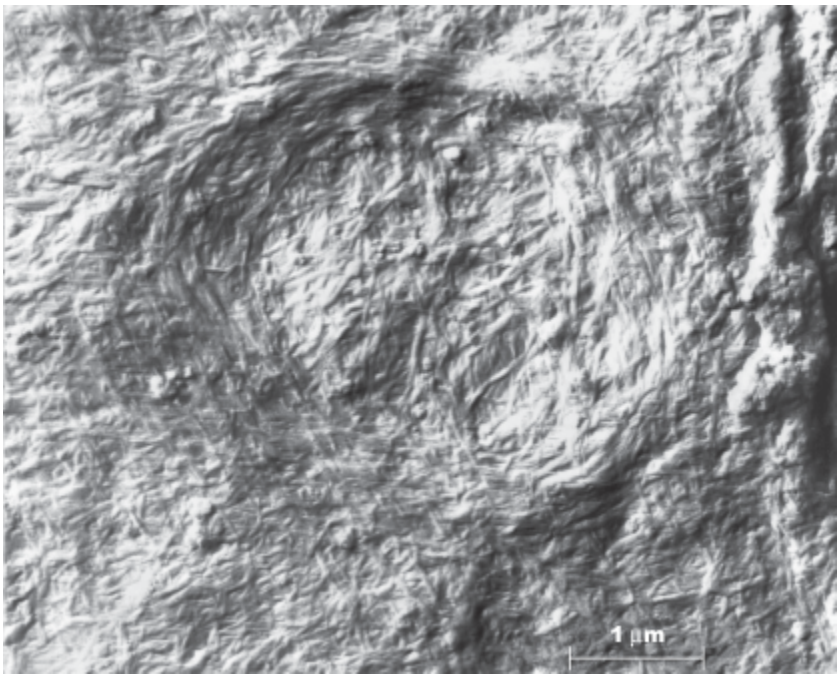

Fig. 13 Portion of a plant cell wall showing the fibrillar nature of cellulose. Microfibrils are oriented in a nearly circular arrangement surrounding intercellular connections (a pit field). (*Courtesy of J. A. S. Marshall*)

The cell wall or extracellular matrix is a network of polymers composed of cellulose microfibrils, hemicelluloses, pectins,

hydroxyproline-rich glycoproteins, and the enzymes used to build and modify the cell wall. The cell wall is formed in two stages, and because of this the botanist generally distinguishes between a primary and a secondary wall. The primary wall is laid down at the time of cell division and extended during cell growth. The secondary wall is laid down after the cell has ceased to grow and may vary greatly in structure and composition. The secondary cell wall has more cellulose than the primary wall and sometimes contains substantial amounts of lignin and other substances. In certain types of cells, the secondary wall is uniformly thickened; in others, it is thickened in bands or in spiral patterns; and in still others, the thickenings are only at the corners. The cellulose microfibrils are synthesized on the outer surface of the plasma membrane. The hemicelluloses and pectins are formed in the Golgi apparatus and secreted in exocytotic vesicles to the cell wall. The proteins are synthesized by ribosomes on the rough endoplasmic reticulum, transported to the Golgi apparatus, and secreted in exocytotic vesicles to the cell wall. The wall surrounding a given cell can differ in composition on different sides of the cell and a given pattern can change throughout development. How this occurs remains a mystery.

While the cell wall may be referred to as the extracellular matrix, it is intimately connected with the rest of the cell through proteins in the plasma membrane known as integrins that connect proteins in the extracellular matrix to proteins that make up the cytoskeleton. The extracellular matrix–plasma membrane–cytoskeletal continuum is used by plant cells to sense gravity and by fungal cells to sense the epidermal cell pattern on leaves that facilitates the directional growth of the mycelium and the formation of appressoria (penetrating structures).

The walls of plant cells with their loosely arranged microfibril structure constitute an intercellular continuum known as the apoplast through which ions, polar molecules, and even proteins, such as those involved in the incompatibility response that occurs during pollination, can move from one cell to another or even from the external environment of the plant to the plasma membrane of nonsurface cells. *See also:* **Cell walls (plant) (/content/cell-walls-plant/117510)**

Variations

Any generalized consideration of the plant necessarily must omit detailed attention to variations characteristic of particular cell types. These variations are myriad and it is possible to touch on only a few. At maturity, some cells, such as those of xylem vessels, lose all their cytoplasmic and nuclear contents. Others, such as the sieve-tube elements of the phloem, at maturity contain cytoplasm, but no nucleus. The extent of the endoplasmic reticulum, the number of ribosomes, mitochondria, and plastids, and the Golgi apparatus vary widely with the type and functional state of the cell, as does the degree of vacuolation and the relative thickness and character of the walls. All these variations reflect differences in the functioning and therefore the metabolic activities of the cells. *See also:* **Phloem (/content/phloem/507200)**; **Xylem (/content/xylem/752200)**

Cell growth

Sustained growth of the plant cell involves the participation of almost every organelle in the cell. Growth requires the simultaneous and coupled processes of cell wall loosening and water uptake. According to one model, the loosening of the polymers in the cell wall by protons pumped into the wall by the proton-translocating ATPase on the plasma membrane and enzymes activated by low pH reduces the turgor pressure of the cell. The reduced turgor pressure allows an increase in the rate of water uptake. The increased uptake of water into the vacuole stretches the loosened cell wall. While the loosened cell wall is stretched, additional wall polymers are added as a result of the secretion of hemicelluloses and pectins by the Golgi apparatus and the synthesis of cellulose by the plasma membrane. The newly added cellulose microfibrils are oriented transversely to the long axis of the cell to facilitate cell elongation or randomly to facilitate isodiametric growth. Sustained growth also requires the differential transcription of the DNA in the nucleus, the translation of proteins in the ribosomes of the endoplasmic reticulum, ATP produced by the mitochondria, and sugars produced by the chloroplast. The two sides of a cell may grow at different rates in response to light and gravity during processes known as phototropism and gravitropism, respectively. This is marvelously visible in the internodal cells of *Chara* and the sporangiophore of *Phycomyces*. The

mechanism of differential growth within a cell remains unknown. *See also:* **Plant growth (/content/plant-growth/523000)**

Differentiation

The remarkable range of specializations in plant cells is often unappreciated, and each specialized cell type is valuable for understanding a given aspect of life. For example, the large internodal cells of the characean algae, with their dramatic cytoplasmic streaming, serve as a splendid material to study actomyosin-driven motility. The leviathan chromosomes in the stamen hair cells of *Tradescantia* or the endosperm cells of many lilies are fabulous for the study of mitosis. The guard cells that compose the stomatal complexes that regulate the exchange of carbon dioxide and water between the plant and the environment are excellent cells to study the mechanism and regulation of ion movements. Pollen tubes and the zygotes of *Fucus* and *Pelvetia* are fantastic cells to study the causes of polarity. Pollen grains and tracheary elements are extraordinary cells for studying the causes of the fascinating architecture of the cell wall. The cells of the aleurone layer of cereals or the gorgeous glandular trichomes found in leaves and flowers are wonderful for the study of secretion. The tip cell of the protonema of a fern gametophyte is outstanding for studying the generation of geometric form. The readily synchronized tobacco BY-2 cells are stupendous for studying a given aspect of the cell cycle. The cells of the spadix of *Arum* are unparalleled for the study of heat generation by the mitochondria. There is also a vast number of plant cells in the treasure house of nature that specifically produce valuable products, including quinine, salicylic acid, taxol, colchicine, vinblastine, vincristine, serotonin, histamine, acetylcholine, morphine, tetrahydrocannabinol, latex, caffeine, nicotine, vitamins, and antioxidants. How these cells differentiate both structurally and metabolically in order to produce a given end product remains a mystery. *See also:* **Plant anatomy (/content/plant-anatomy/522500)**; **Plant development (/content/plant-development/900115)**

Dividing Cell

Plant cells arise only by division of preexisting cells. This observation also pertains to some of the compartments of cells—the nucleus, the mitochondria, and the plastids. The manner in which other organelles such as the endoplasmic reticulum, Golgi apparatus, microbodies, and vacuoles behave in cell division is less clear.

Mitosis begins with the condensation of the chromatin in the nucleus into the chromosomes. As the chromosomes are resolved during prophase, the nucleoli either disappear or are substantially reduced. There follows a breakdown of the nuclear envelope and the development of what is called a mitotic figure. *See also:* **Cell division (/content/cell-division/116300)**; **Chromosome (/content/chromosome/134900)**

The mitotic figure includes the spindle fibers, some of which are attached to the chromosomes and some of which pass between the chromosomes through the equator of the spindle (**Fig. 14**). While microtubules make up the majority of the spindle fibers, they only contribute to a small percentage of the volume of the spindle and consequently many other proteins may participate in mitosis. In mitosis, the most conspicuous difference between plant and animal cells is the absence of centrioles in all but a few types of lower plant cells. In the animal cell, two centrioles, one located at each end of the spindle, appear to represent “anchor points” because the spindle fibers seem to radiate from the centrioles. The spindle figure of plant cells appears to be firmly anchored without any demonstrable centrioles, indicating that centrioles are not required for mitosis. *See also:* **Mitosis (/content/mitosis/428300)**

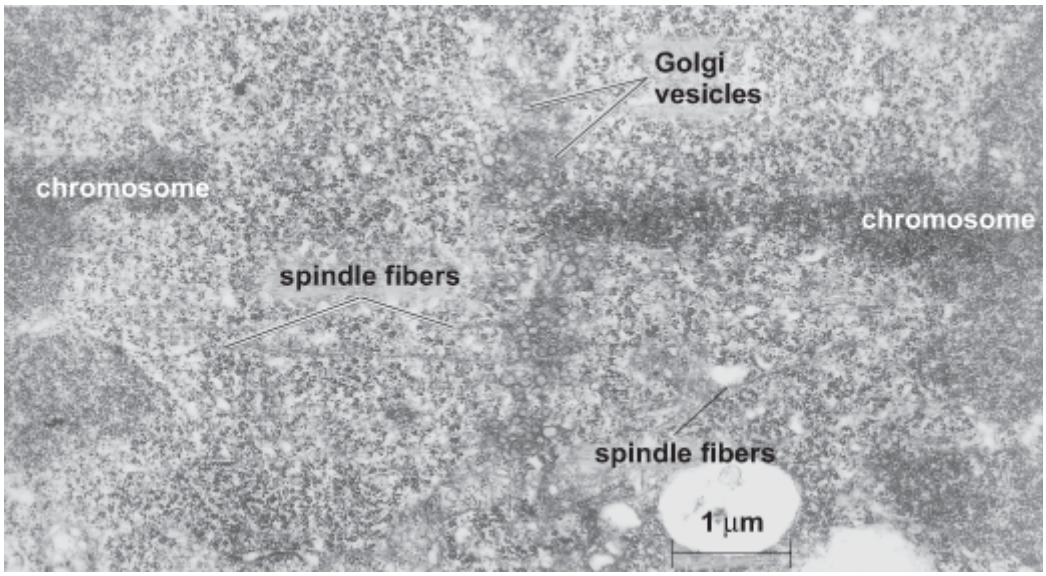

Fig. 14 Dividing cell showing aggregation of small Golgi vesicles in the equatorial region and spindle fibers. Chromosomes have moved toward the poles. In the right part of the cell, a chromosome still extends as far as the forming plate. (*Courtesy of H. J. Arnott*)

During metaphase, the chromosomes first move to a region midway between the two poles. After the chromosomes split, each member of the pair moves toward a different pole of the spindle and sometimes the poles themselves move apart too. The latter two types of movements are known as anaphase A and anaphase B, respectively. During telophase, a new nucleus is organized at each pole along with reconstitution of the nuclear envelope and redevelopment of the nucleoli in association with specific chromosome sites, known as nucleolar organizer regions. During mitosis, the segmented nuclear envelope appears to surround the spindle figure. The manner in which the nuclear envelope is reconstituted is not known.

The partition of the cytoplasm into two masses, one surrounding each new nucleus, is a vastly different process in most plant cells from that in most animal cells. With few exceptions, this cytoplasmic division (cytokinesis) takes place in plants by a process known as cell-plate formation; a plate-shaped structure consisting of cell-wall material bounded by new plasma membrane appears in the mass of cytoplasm in the center of the cell and extends outward, ultimately connecting with the original walls. The initial stage of cell-plate formation is the movement of small vesicles produced by the Golgi apparatus along the microtubules that make up the phragmoplast (a thin barrier formed across the spindle equator in late cytokinesis in plant cells and within which the cell wall is laid down). These small vesicles appear to form a group of islands so aligned as to determine the plane of cell division. The vesicles form tubular, irregularly branched, or starlike bodies with fuzzy arms as they fuse to form the cell plate. The endoplasmic reticulum entrapped during this process becomes part of the plasmodesmata. The Golgi apparatus produces the new plasma membranes and the initial wall components, which consist primarily of callose and hemicelluloses. Autoradiographic experiments have shown that glucose purposely incorporated into the cell during cell-plate formation collects in the Golgi apparatus, where it becomes part of one or more of these wall substances and from where it moves directly into the new wall (**Fig. 15**). Golgi apparatuses are frequently seen clustered around the edges of the cell plate (**Fig. 16**). When the plate is fully extended to the existing walls of the cell, cytokinesis is complete, with the two new cells being separated by both plasma membrane and wall.

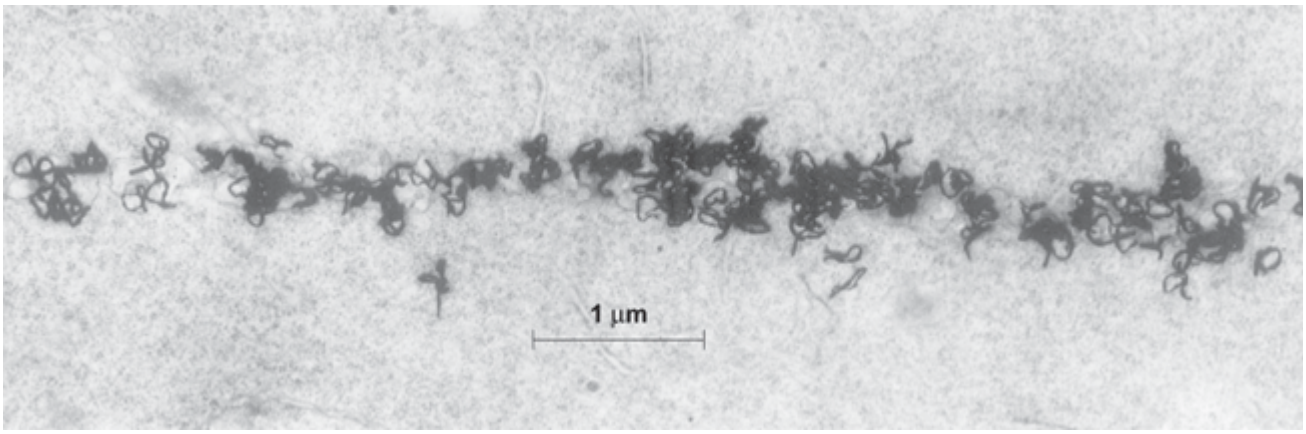

Fig. 15 Autoradiograph of an early stage in cell-plate formation in a maize root cell treated with tritiated glucose. Silver grains at the plate area result from glucose, transported via Golgi apparatus to the forming wall. (*Courtesy of T. P. Leffingwell*)

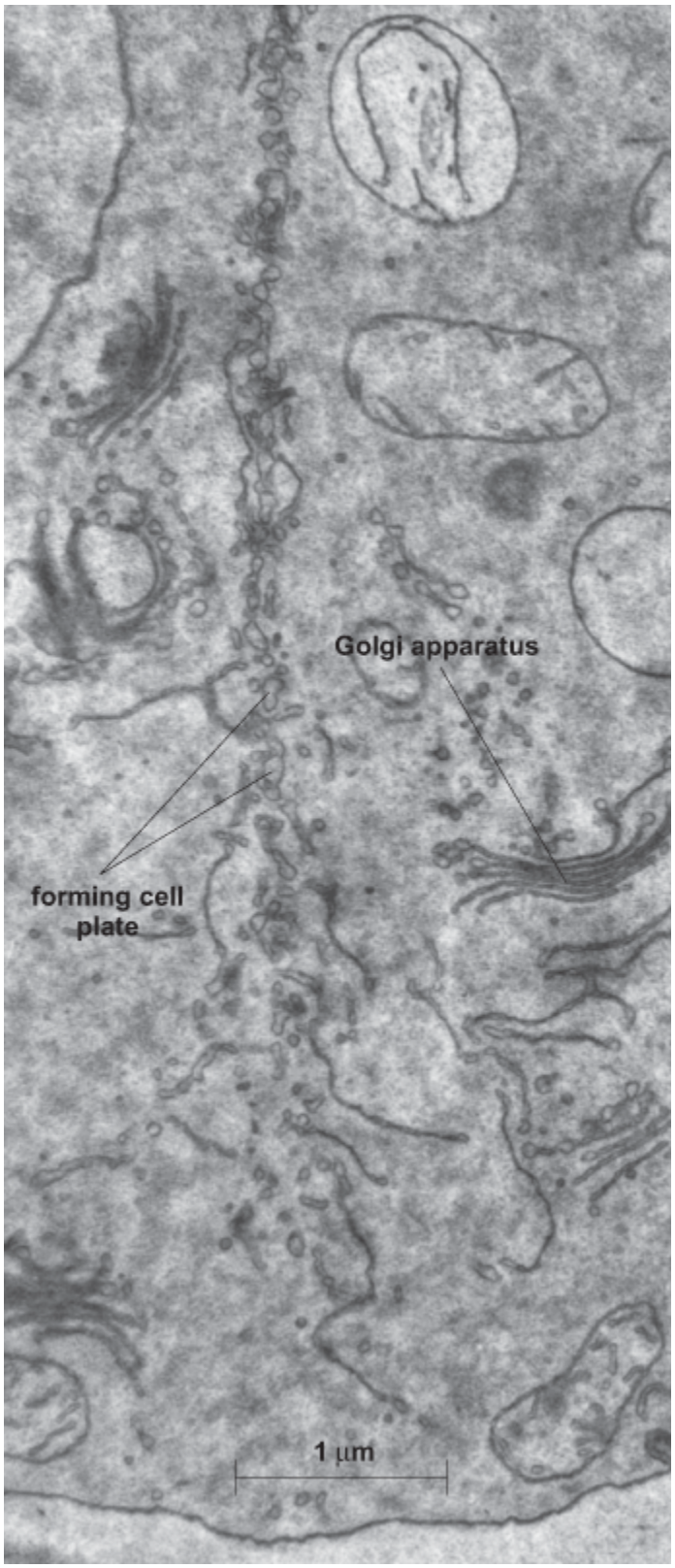

Fig. 16 A stage of cell-plate development showing the close association of the Golgi apparatus with the forming cell plate. (*Courtesy of H. H. Mollenhauer*)

In most cases, the mitochondria and plastids appear to increase in number more or less concurrently with the division of the cell. Each is apparently also capable of increasing without cell division because cell differentiation following the period of cell growth is often characterized by increases in the number of one or more of these organelles. The asymmetrical segregation of these organelles, which may exclude them from particular sex cells, plays a role in maternal or paternal inheritance in plants.

The endoplasmic reticulum, the Golgi apparatus, and the various small organelles seem to be randomly distributed between the daughter cells, but not enough is known about developmental activities of these components to make any conclusive statements about the pattern of their distribution in cell division. There is substantial evidence that certain classes of plant hormones exert control over cell division, but the mechanism by which this control is exerted has not been clarified. There is little evidence concerning the means by which certain cells are caused to divide, while others do not. It is clear that cell reproduction involves not only the structural developments treated here, but also significant metabolic changes, including changes in the concentration of cytoplasmic calcium (Ca^{2+}).

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Plant Protoplasts

Although the plant cell is the basic unit of structure and function in nearly all plants, the term protoplast has been used to describe the organized entity of the living components of the plant cell that lie inside of the cell wall. The protoplast includes the differentially permeable plasma membrane as well as the cytoplasm and the organelles that are within it. The definition of the protoplast differs from the definition of the cell in that the protoplast does not include the highly permeable extracellular matrix. Plasmolysis studies on plant cells have established that a functional plasma membrane surrounds the protoplast.

For many years, plant protoplasts remained largely cytological curiosities of little interest to physiologists, biochemists, and geneticists. However, the introduction of enzymatic methods for the isolation of protoplasts in 1960 stimulated renewed interest. Cell wall–degrading enzymes, including cellulases, hemicellulases, and pectinases, which were isolated from fungi, were employed, and large numbers of protoplasts could be isolated from various plant organs and also from plant tissue cultures. A typical preparation of protoplasts isolated enzymatically from leaves of *Coleus* is shown in **Fig. 17**.

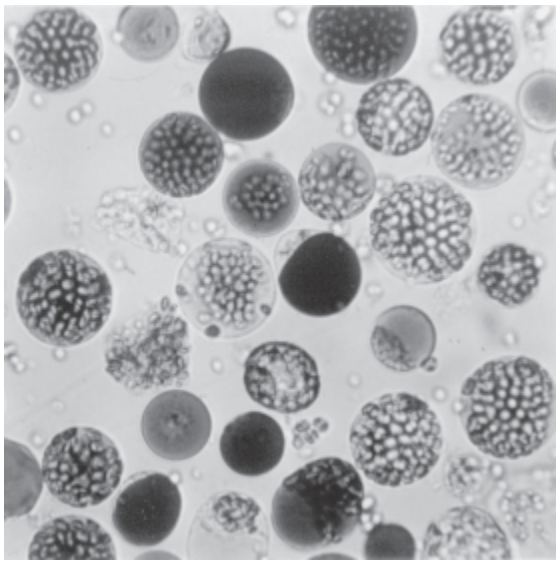

Fig. 17 Protoplasts isolated from *Coleus* leaves.

Experimental value

Protoplasts provide an exceptional experimental system for the study of the plasma membrane and cell wall regeneration. The conductance, selectivity, and regulation of single ion channels on the plasma membrane can be studied in protoplasts using patch-clamp techniques, and studies on cell wall regeneration by protoplasts have provided a wealth of new information on the early stages of wall synthesis and the early organization of the wall. Protoplasts offer an important biological entity for

many other physiological and biochemical studies. For instance, chloroplasts isolated from protoplasts possess excellent structural and biochemical integrity, and fractionation of protoplasts has supplied large quantities of mature plant vacuoles. Plant protoplasts have also provided a system for plant virus research via laboratory culture. Once cell wall regeneration has become initiated, protoplasts cultured in suitable media under sterile conditions exhibit mitosis and cytokinesis similar to that normally found in cultured cells undergoing division.

Genetic manipulation

The use of protoplasts for genetic manipulations centers on two major areas: (1) the use of protoplasts in transformation studies and (2) obtaining new genetic variability by protoplast fusion.

Transformation

Protoplasts provide an ideal single-cell system for basic studies in plant cell biology as well as for the generation of genetically modified plants. Both the nuclear and the plastid genome can be transformed. Transformation can be stimulated using either chemical or physical techniques. Incubation of *Petunia* protoplasts in a solution of poly-l-ornithine (a known stimulator of virus uptake by protoplasts) promotes the uptake of isolated *Agrobacterium* plasmids into the protoplast. DNA can also be incorporated into protoplasts through microinjection and electroporation. The transformed protoplast regenerates a cell wall and begins to divide, forming undifferentiated callus tissue. When the callus tissue is transferred to a medium containing auxin and cytokinin, shoots and roots develop and the resulting plantlets can be transferred to pots. Subsequently, the genetically modified plants can be used for food or for the production of pharmaceuticals.

Fusion

Fusion of protoplasts appears to be initiated when the plasma membranes are able to come sufficiently close to one another to enable membrane adhesion to take place. Most protoplasts are negatively charged, and the addition of the fusion-inducing agent (or fusogen) probably eliminates this charge. They no longer repel each other, and apposition at molecular distances can take place with resultant fusion of the plasma membranes. Calcium ions at high pH (9.5–10.5) and polyethylene glycol are the most commonly used fusogens for protoplasts. Large electric fields are also used to fuse protoplasts. Within the *Petunia* genus, sexually incompatible species can be crossed by this process of protoplast fusion and, coupled with the selective culture of somatic hybrid cells, grown into whole flowering hybrid plants. Horticulturally, this new somatic amphidiploid hybrid between *P. parodii* and *P. parviflora* is of interest because it is suitable for the introduction of the hanging-basket habit of the sexually isolated *P. parviflora* species into the cultivated *Petunia*. Intergeneric hybrids have also been made using protoplast fusion. *See also:* **Breeding (plant) (/content/breeding-plant/095100)**; **Somatic cell genetics (/content/somatic-cell-genetics/636300)**

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