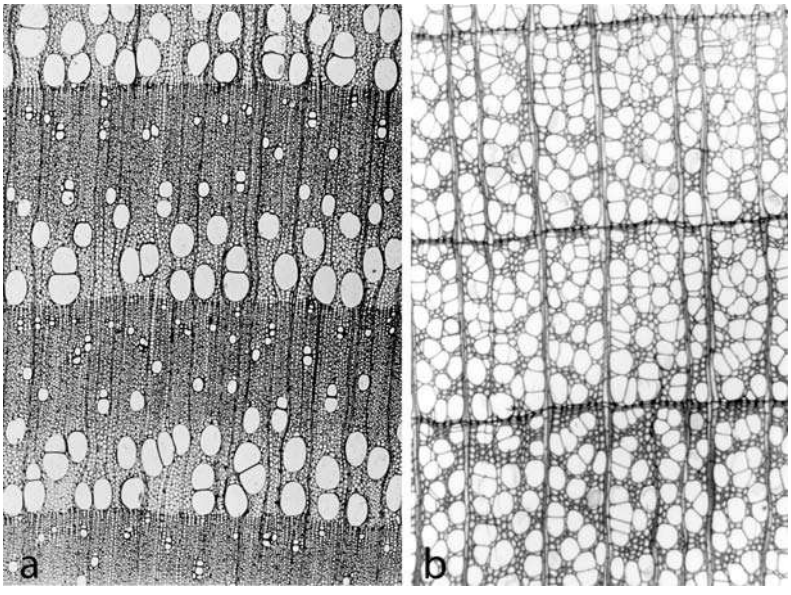

Figure 11.24 Distribution of vessels in secondary xylem as seen in transverse section. (a) Ring-porous secondary xylem in *Fraxinus* sp. (ash). (b) Diffuse-porous secondary xylem in *Tilia americana*. Magnification (a) and (b) × 58.

is the breakdown of the tonoplast (vacuolar membrane). This releases hydrolytic enzymes sequestered in the vacuole that cause the rapid degradation of all cytoplasmic organelles and the consequent death of the protoplast (Fukuda, 1996, 2000; Groover *et al*., 1997; Ito and Fukuda, 2002; Kuriyama and Fukuda, 2002; Turner *et al*., 2007).

Patterns of distribution of xylary elements and rays

The secondary xylem of different taxa of dicotyledons can be distinguished on the basis of the distribution in the xylem of vessels of different sizes and wall thickness, the distribution of axial parenchyma and its association with vessels, and the distribution of rays of various morphologies. For example, the secondary xylem can be characterized as ring-porous or diffuse-porous (Fig. 11.24a, b). If **ring-porous**, the early wood (that formed first during a growing season) contains one to several layers of very large, relatively thin-walled vessels and the late wood relatively uniformly distributed small, thicker-walled vessels (Fig. 11.24a). Well-known examples of taxa with ring-porous secondary xylem are *Quercus*, *Catalpa*, *Ulmus* (elm), and *Fraxinus* (ash). Among **diffuse-porous** taxa are *Betula* (birch), *Acer* (maple), and *Populus* (poplar). In these taxa, vessels of relatively uniform size are evenly distributed throughout the growth layers (Fig. 11.24b). In some other diffuse-porous taxa, such as *Juglans* (walnut) and *Malus* (apple), there is a gradual transition from larger to smaller vessels in the growth layers.

The distribution of axial parenchyma in the secondary xylem is relatively constant in genera and in some larger taxa. Axial parenchyma is classified as **paratracheal** when it is consistently associated with vessels, or **apotracheal** when it is not consistently associated with vessels.

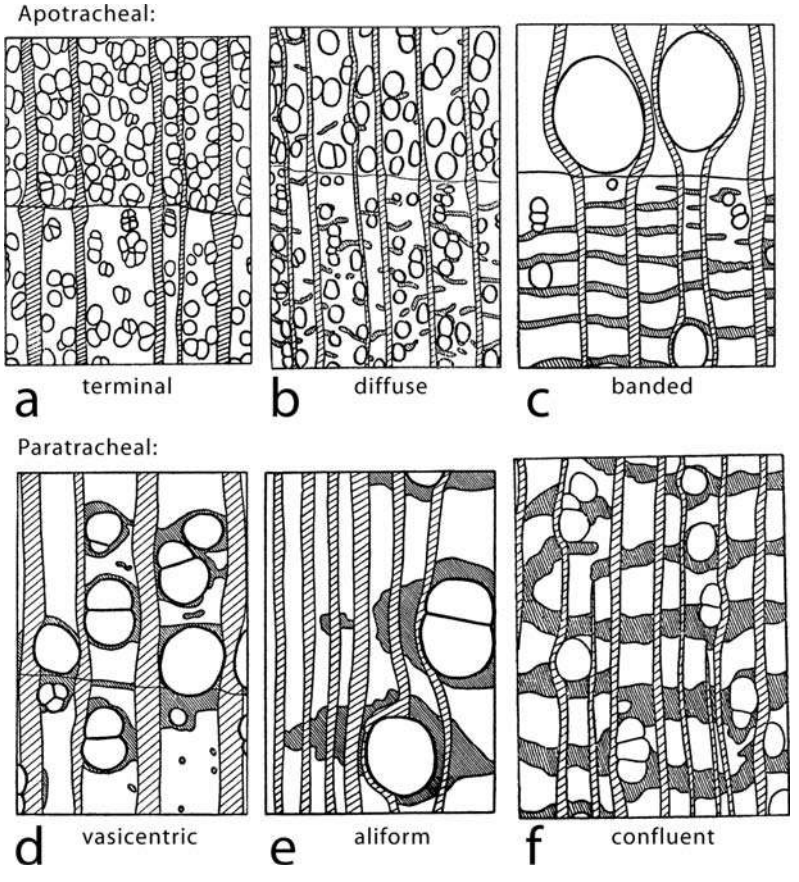

Figure 11.25 Distribution of axial parenchyma in secondary xylem as viewed in transverse section. Parenchyma is indicated by fine line shading; rays by coarse line shading. (a) *Liriodendron tulipifera*. (b) *Tilia cordata*. (c) *Carya tomentosa*. (d) *Grewia mollis*. (e) *Mangifera indica*. (f) *Celtis soyauxii*. From Metcalfe and Chalk (1950). Used by permission of Oxford University Press.

Three categories of apotracheal parenchyma are recognized: terminal (sometimes called boundary), diffuse, and banded (Fig. 11.25a–c). **Terminal parenchyma** occurs in the last-formed tissue, sometimes only in the last layer of cells, in a growth layer (Figs 11.25a, 11.26a). The term **boundary parenchyma** may appropriately be applied in instances in which parenchyma occurs on both sides of the boundary between growth layers. Examples of taxa with terminal parenchyma are *Liriodendron*, *Magnolia*, and *Salix* (willow). **Diffuse parenchyma** is scattered randomly throughout the growth layer (Figs 11.25b, 11.26b, c), as in *Malus*, *Diospyros* (persimmon), and *Quercus*, and **banded parenchyma** occurs in narrow bands interspersed between vessels or clusters of vessels (Fig. 11.25c). Examples are *Carya* (pecan) and *Calophylum wallichianum* (Guttiferae).

Three types of paratracheal axial parenchyma are also recognized: vasicentric, aliform, and confluent (Fig. 11.25d–f). In secondary xylem with **vasicentric parenchyma**, axial parenchyma surrounds or contacts vessels directly or indirectly (Figs 11.25d, 11.26d), and parenchyma cells may also occur in the last cell layers of the growth layer, i.e., in the position of terminal parenchyma. Examples of taxa with vasicentric parenchyma are *Fraxinus* and *Catalpa*. **Aliform parenchyma** surrounds

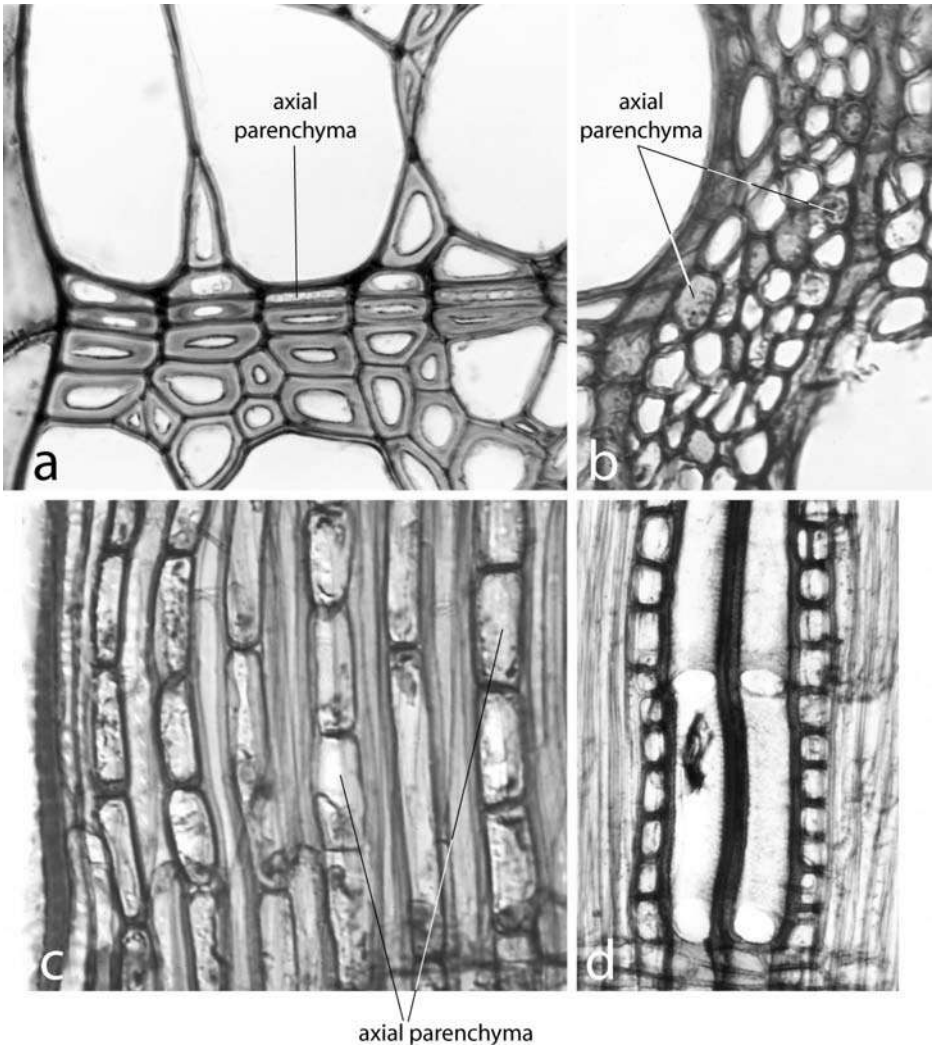

Figure 11.26 Distribution of axial parenchyma in secondary xylem. (a) Terminal parenchyma in *Liriodendron tulipifera* in transverse section. Magnification × 541. (b, c) Diffuse parenchyma in *Quercus rubra* in transverse section (b) and in radial section (c). Magnification (b) and (c) × 497. (d) Vasicentric parenchyma in *Fraxinus americana* (American ash) in radial section. Magnification × 181.

vessels and extends tangentially in wing-shaped masses (Fig. 11.25e) as in *Mangifera indica* (mango; Anacardiaceae) and *Acacia nilotica* (prickly acacia). **Confluent parenchyma** is banded, and the bands, which may branch, enclose or are in contact with vessels (Fig. 11.25f). The secondary xylem of *Celtis soyauxii* (Ulmaceae) and *Markhamia platycalyx* (Bignoniaceae) contain confluent parenchyma.

Secondary xylem is also characterized by the nature and distribution of rays. In woody dicotyledons most ray parenchyma cells are radially elongate although in some species some or all of the marginal ray cells

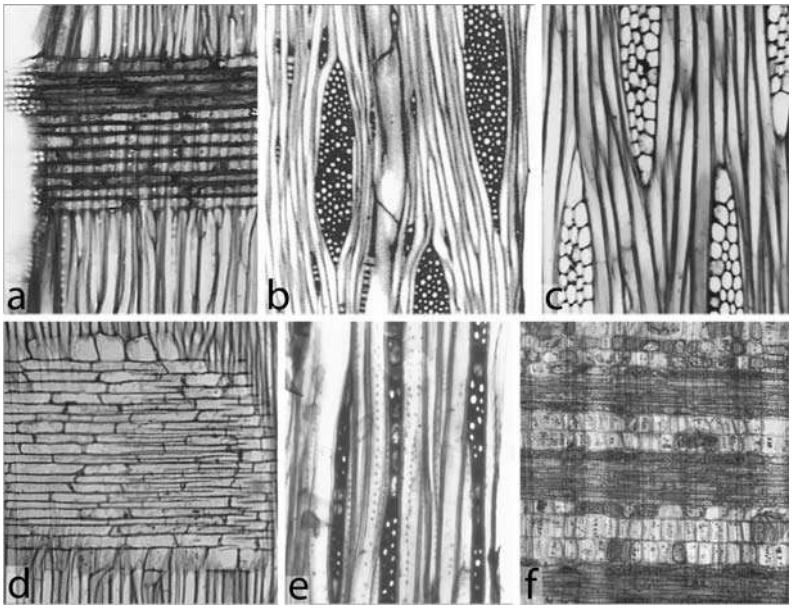

Figure 11.27 Vascular rays. (a, b) Homocellular rays from *Acer saccharum*. (a) Ray composed of radially elongate (procumbent) ray cells. Magnification × 156. (b) Tangential section containing a combination of uniseriate and multiseriate rays. Magnification × 96. (c–f) Heterocellular rays. (c) Tangential section showing multiseriate rays in *Swietenia mahogani* (mahogany) with upright marginal ray cells. Magnification × 122. (d) Radial section of the same wood. Magnification × 84. (e) Rays of *Cercidiphyllum japonicum* with marginal upright cells and internal bands of upright cells that alternate with bands of procumbent cells. Magnification × 115. (f) Radial section of the same wood. Magnification × 84.

may be longitudinally elongate. Rays in dicotyledons may be characterized as homocellular or heterocellular. **Homocellular rays** consist of ray parenchyma cells of similar size and shape which are commonly radially elongate (**procumbent**) as, for example, the rays of *Acer* (Fig. 11.27a, b). In some herbaceous plants, however, homocellular rays consist entirely of longitudinally elongate (**upright**) ray parenchyma cells. **Heterocellular rays**, in contrast, consist of cells of two shapes and sizes with the marginal cells usually differing from those of the remainder of the ray. Marginal cells may be longitudinally elongate (or sometimes with nearly equal longitudinal and radial dimensions) as in *Swietenia mahogani* (Fig. 11.27c, d) or may consist of a mixture of longitudinally and radially elongate cells. Heterocellular rays may also consist of alternating bands of marginal and internal upright cells as in *Cercidiphyllum japonicum* (Fig. 11.27e, f). The rays of conifers containing ray tracheids are also referred to as heterocellular as are those of at least two families of angiosperms, Proteaceae and Malvaceae, some species of which contain ray tracheids.

Rays vary in height from a fraction of a millimeter to 10 cm or more, and in width from one to several rows of cells. If rays are one cell

wide they are referred to as **uniseriate**, if two cells wide, as **biseriate**, and if three or more cells wide, as **multiseriate**. In some species, e.g., *Alnus* (alder) and *Carpinus* (ironwood), closely spaced, narrow rays occur in groups that simulate large rays. Such groups are called **aggregate rays**. Within the secondary xylem of a single species rays may be solely uniseriate or solely multiseriate (or biseriate). In some other species uniseriate and bi- or multiseriate rays may occur together in the xylem (Fig. 11.27b). In most woods, rays are arranged so that, as viewed in tangential section, their ends extend beyond those of others. In some taxa, however, in which all rays are of similar height as, for example, in *Diospyros virginiana*, they are arranged in rows. In such cases, the rays are said to be storied.

Rays in the secondary wood of both conifers and dicotyledons have long been known as sites of storage of photosynthate in the form of starch, and pathways of lateral transport of assimilates between the xylem and the phloem. Especially in the early spring, sugars are transported to the cambium, and through pits from ray cells into adjacent vessels through which they are delivered to developing buds (Esau, 1977). Axial parenchyma cells apparently play a similar role in providing carbohydrates to growing regions of the plant. Recently, Chaffey and Barlow (2001) have proposed that axial parenchyma and rays in the xylem, which are interconnected by plasmodesmata, comprise "a **three-dimensional symplasmic continuum**" which provides pathways of radial transport between the secondary xylem and the secondary phloem (see also Van Bel, 1990; Van Bel and Ehlers, 2000). They emphasize the role of the numerous plasmodesmata in the tangential walls which would facilitate radial transport and suggest, further, that the microfilament component of the cytoskeleton might also play a role in the intracellular movement of molecules. In this system, photosynthate is transported from both the xylem and the phloem to the highly active cambial zone and its developing xylary derivatives, and growth hormones could be transported to this region from sites of synthesis in the young leaves, as well as from root and shoot apices through the interconnected system of axial and ray parenchyma. As pathways of transport of proteins and nucleic acids as well as hormones and photosynthate to the cambial zone, this system apparently plays a significant role in the coordination of development.

Tyloses

Secondary xylem that functions in transport and contains living ray and axial parenchyma is called **sapwood**. Sapwood is peripherally located and encloses the **heartwood**, xylem that no longer functions in transport and contains no living cells. The volume of sapwood and heartwood varies greatly in different species, and in trees of different ages. The relative amounts may also be affected by environmental conditions. Generally, in young trees the quantity of sapwood is much greater than the quantity of heartwood whereas in old trees, heartwood typically

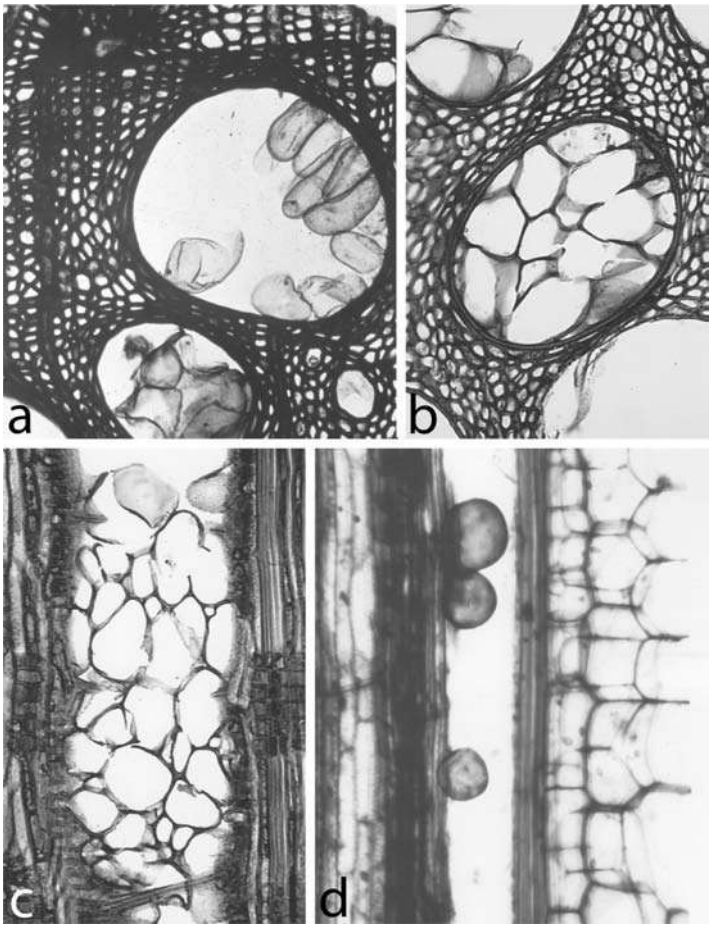

Figure 11.28 Tyloses. (a) Young tyloses in vessel members of *Quercus* sp. (b, c) Tyloses in *Quercus rubra* in transverse section (b) and radial section (c). Magnification (a), (b), and (c) × 139. (d) Tyloses in a vessel of *Pelargonium*. Magnification × 300.

comprises the greater volume. Not only does heartwood contain no living components, it is also characterized by the presence of large quantities of waste metabolites, primarily flavonoids and other phenolic compounds (Hillis, 1987). Plants, unlike animals, have no means of excreting waste products to the exterior. The central part of a tree trunk, therefore, becomes the repository for waste products. In some species the formation of **tyloses** (Fig. 11.28), extensions of adjacent parenchyma cells into vessel members, enhances the volume of metabolites that can be deposited in the heartwood.

Tyloses develop in a transition region between sapwood and heartwood in many angiosperms, and are common features in the heartwood of some hardwood species such as *Robinia*, *Quercus*, *Castanea* (chestnut), and *Juglans* (Fig. 11.28a–c). They are not known to occur under normal conditions in conifers although they can be stimulated to develop in response to wounding (Peters, 1974). They are uncommon in non-woody angiosperms, but do occur in some suffrutescent herbaceous taxa such as *Pelargonium* (Fig. 11.28d). In axial parenchyma and ray parenchyma cells in contact with vessel members in the region in which tyloses are forming, a thin, unlignified wall layer is deposited over the inner

surface of the entire wall, including the pit membranes, adjacent to vessel members. In response to an unknown stimulus, possibly the accumulation of flavonoids to a level of toxicity, the pit membranes are enzymatically degraded and the unlignified wall layer lying over the pit begins to grow, extending into the lumen of the vessel member (Fig. 11.28a, d). The nucleus of the parenchyma cell often migrates into the tylosis. This expansion of the cell provides a much greater volume for the accumulation of waste metabolites prior to the death of the cell, caused ultimately by the toxicity of these accumulations. A vessel member may be completely filled by the intrusion of many tyloses (Fig. 11.28b, c).

It is thought by some workers that vessels are no longer functional in transport at the time of tylosis development. If, on the other hand, the vessels are still functional, the formation of tyloses will greatly reduce the efficiency of transport of water and minerals, and ultimately eliminate their function in transport.

In addition to providing a site in which waste metabolites are stored, heartwood may have another adaptive value. The toxicity of the stored products in heartwood is thought to prevent or deter the invasion and decay by fungi of the central, non-living parts of tree trunks and large limbs. The presence of suberin in addition to lignin in the walls of tyloses in several tree species is believed to hinder the colonization of fungi in infected trees (Rioux *et al*., 1995). For a detailed discussion of heartwood, and an extensive bibliography, see Hillis (1987).

Evolution in secondary xylem of dicotyledons

Since the botanical studies of Carolus Linnaeus in the eighteenth century, plant systematists have used external morphological characteristics, especially characteristics of the flower, as the basis for classification. Not until the publication of a seminal paper by I.W. Bailey and W.W. Tupper in 1918, in which they compared the size of tracheary cells in seed plants and pteridophytes (including fossil taxa), did botanists begin to understand the taxonomic significance of anatomical characteristics of the xylem. Bailey and Tupper concluded that, as the terrestrial flora evolved through geologic time, tracheids evolved along two pathways, one that led to fibers, the primary function of which was support, and a second that led to vessel members, the primary function of which was transport of water and minerals. In a series of papers by Bailey, his students, and other comparative anatomists during the 1920s through the 1950s, cell types as well as cell and tissue patterns in secondary xylem were characterized, and their levels of evolutionary specialization proposed. The secondary xylem of both fossil and living gymnosperms as well as that of the most primitive dicotyledons (members of the Magnoliales) is composed of tracheids with scalariform or circular bordered pits, and vascular rays. Since there is evidence that circular bordered pits evolved from scalariform bordered pits, it was

concluded that fibers, characteristic of the secondary xylem of dicotyledons, evolved from tracheids with circular bordered pits followed by fiber-tracheids and, ultimately, libriform fibers. Fiber-tracheids, longer than tracheids in the same wood, are characterized also by reduced transverse diameters and smaller lateral wall pits. Libriform fibers, the most highly specialized, are usually longer, have thicker walls, and on average, smaller transverse diameters than fiber-tracheids. The lateral wall pits are highly reduced, lacking borders in many taxa, and considered by some anatomists to be simple pits.

Vessels are thought to have evolved from tracheids with scalariform lateral pitting similar to those of several of the primitive vesselless dicotyledons. The primitive vessel member is characterized as being long, narrow, and multifaceted (angular in transverse section) with very oblique, scalariformly perforate ends. During evolution, through a series of stages, vessel members became shorter and broader and the perforation plates became less oblique with fewer perforation bars, and in the most derived state, transverse with simple, open perforation plates without bars (see Frost, 1930a, 1930b, 1931).

Bailey and Tupper (1918) demonstrated that shorter and broader vessel members occur in specialized taxa that also are characterized by specialized floral features. On the assumption that cell types and tissue patterns in secondary xylem of dicotyledons evolved at similar rates, correlation with the primitive vessel member, especially vessel member length, became the primary basis for determining their evolutionary level and led to a large series of hypotheses of trends of specialization, which with other evidence is used by plant systematists in suggesting phylogenetic relationships. Among these trends are the following: vascular rays in the secondary xylem comprise systems that are either **heterogeneous**, the primitive state, or **homogeneous**, the derived state. Heterogeneous systems consist of rays that are heterocellular, i.e., comprised of both upright and procumbent ray cells, and that may be either uniseriate or multiseriate. Some systems contain both uniseriate and multiseriate rays. Systems of homogeneous rays consist of **homocellular** rays comprised entirely of procumbent ray cells and which may also be uniseriate or multiseriate. Homogeneous systems may also contain both uniseriate and multiseriate rays. For more detail please see Kribs (1935). Other patterns in secondary xylem considered to be useful in determining relationships among taxa of dicotyledons are the distribution of vessels and axial parenchyma. Diffuse porous xylem, with vessels of similar size distributed evenly throughout the growth layer, is considered the primitive state; ring porous xylem, with the largest vessels in the early wood, is considered derived. Diffuse and apotracheal distributions of axial parenchyma are considered primitive; paratracheal distributions are considered derived.

During the period in which I. W. Bailey, F. H. Frost, D. A. Kribs, and many other comparative anatomists were active, there was little consideration of factors such as the age of the plant, the part of the plant from which samples were obtained (for example, whether from the trunk or a lateral branch), and the environmental conditions in which the plant

was growing, among others. Although I. W. Bailey realized that adaptation to environmental conditions was a factor in plant evolution, the importance of ecology in the evolution in secondary xylem was not fully recognized until the work of Sherwin Carlquist (1975, 1988, and many research papers). Carlquist demonstrated that ecology has a profound influence on the structure of secondary xylem in many diverse taxa. He warned of the pitfalls of using solely the methods of comparative anatomy (i.e., without regard for the effects of environment) in drawing conclusions about xylem evolution. For example, in his paper on wood anatomy of the Compositae Carlquist (1966) provided evidence of a correlation of vessel member characteristics with habitat (i.e., whether xerophytic or mesophytic). Correlations of this type led to his viewpoint that the characteristics of vessel members and vessels are adaptations to water economy, i.e., the efficiency of vessels in water conduction. He concluded that this would explain better than level of evolutionary specialization, the characteristics of vessel members of certain taxa of Compositae growing in very dry habitats (short, narrow vessel members with helical thickenings, and occurring in large groups). Carlquist has emphasized, also, that in addition to habitat, one must know the age and size of the plant, and the part of the plant from which samples are taken in order to determine the significance of differences in tracheary cells. Tracheary cells, for example, tend to be longer in large, old plants than in young, small plants, and longer in the trunk than in lateral branches. For many more examples, detailed discussions of ecological plant anatomy, and for references to the work of others in this area, please see Carlquist (1975, 1988) and the extensive bibliographies in his works.

Mechanism of water transport

Since the proposal of Dixon and Joly in 1894, the **Cohesion Theory** has been the most widely accepted explanation for the transport of water and minerals in the xylem. According to this theory, water loss from leaves through transpiration results in the development of tension in the water column in the tracheids and vessels that is transmitted throughout the column to the roots. As transpiration continues, water is pulled from the soil into the roots and upward through the system. Thus, as water is being lost from the plant, it is constantly being replaced. For such a mechanism to work there must be "sufficient tension to lift the water to the top of the tallest trees, and sufficient cohesive strength in the columns of water to withstand this tension" (Canny, 1995). Canny notes that for a tree 100 m tall, there must be established "a gradient in the xylem of 2 bar $(10\ m)^{-1}$ and a cohesive strength of xylem sap in excess of 20 bar."

Over the years experiments using pressure chambers have led many plant physiologists to conclude that these conditions are met in nature. Some doubt was expressed very early, however, and recently has been elaborated upon by Zimmermann *et al*. (1995) who concluded, on the

basis of measurements with the xylem pressure probe, that "xylem tension in the leaves of intact, transpiring plants is often much smaller than that predicted for transpiration-driven water ascent through continuous water columns." Canny (1995) states that "no one has devised a system with a known tension generated in a water column which can be put into the pressure chamber to check its reliability." Canny's experiments with the xylem pressure probe, supported in part by those of Zimmermann *et al*. (1995), suggest that "(1) The necessary high tensions in the xylem are not present; i.e., the operating tension in the xylem (both from direct measurement and from the determined thresholds or cavitation of water) is around 2 bar not 20+ bar. (2) The necessary gradient of tension with height is not present. (3) The measurements of tension with the pressure-chamber (believed to verify the Cohesion Theory) conflict with those made with the xylem-pressure probe." Consequently, he concludes that "the resolution of these conflicts demands some source of compensating pressure in the xylem to reduce the operating tension from 20 bar to <2 bar." The source of this compensating pressure, as presented in his **compensating pressure theory (**Canny, 1995), is the xylem parenchyma and ray cells. He suggests that positive pressures in these cells in contact with tracheary elements "squeeze them" by "pressing onto the closed fluid spaces of the tracheary elements." He notes that under his theory, "the driving force and the transmission of the force [required in the ascent of water in tall trees] are the same as in the Cohesion Theory, but the operating pressure of the xylem is raised into a stable range by compensating tissue pressures pressing upon the tracheary elements." Thus, he concludes that whereas "the tissue pressure does not propel the transpiration stream, which is still driven by evaporation . . . it protects the stream from cavitation."

Important new concepts and hypotheses such as those described above, need to be carefully analyzed and corroborated by many researchers before they are universally accepted or rejected. In this case, results obtained by use of the xylem pressure probe have been criticized by Milburn (1996), Comstock (1999) and Stiller and Sperry (1999). Canny (1998) provides additional support for his theory, and Canny (2001) presents a rebuttal of these criticisms.

At present, the cohesion theory remains the most widely accepted explanation for the transport of water through the secondary xylem. Students interested in learning in more detail about the evidence in support of the several theories of water transport in plants, the techniques used in research in this area of plant physiology, and the controversy surrounding these theories should read the papers cited above and others cited therein.

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Chapter 12

The phloem

Perspective: evolution of the phloem

With increase in the size of plants over geologic time, efficient systems for the transport of water and minerals (primary and secondary xylem) as well as for photosynthates, hormones and other substances (primary and secondary phloem) evolved (see Chapter 1). The protoplasts of differentiating conducting cells of the xylem (tracheids and vessel members) were eliminated through autolysis, thus providing at functional maturity open, but non-living, passageways through which water could be pulled upward and out through the leaves by the force of transpiration (see Chapter 11). Evolution in the phloem took a different course. An open, but living, system of interconnected tubes, formed by overlapping sieve cells in gymnosperms (and more primitive vascular plants), and superposed sieve tube members forming sieve tubes in angiosperms evolved. The protoplasts of sieve elements became degraded, losing the nucleus, tonoplast (vacuolar membrane), and all other organelles except some mitochondria, plastids, and endoplasmic reticulum. In conifers and dicotyledons, distinctive plastids and P-proteins (phloem proteins) evolved and, with the mitochondria and ER, became located peripherally in the cells. Concurrently, plasmodesmata which connected contiguous sieve tube members were replaced by open pores, thus forming a symplastic system of essentially unimpeded passageways (Ehlers *et al*., 2000) through which photosynthate and other molecular substances were transported throughout the plant. Although living, but because of the loss of the nucleus, the sieve elements were no longer able to control their genetic and metabolic activities. Associated, specialized parenchyma cells (companion cells in angiosperms and cells of similar function in conifers called Strasburger cells) evolved which took over these functions, and which also facilitated the transfer of photoassimilates from mesophyll cells into and out of the sieve cells and sieve tube members. In angiosperms the sieve element–companion cell complex became a structural and functional unit, often symplastically isolated, in large part, from surrounding living cells (Van Bel and Kempers, 1990; Robinson-Beers and Evert, 1991; Wimmers and Turgeon, 1991; Botha and Van Bel, 1992; Van Bel and

Van Rijen, 1994) with each component of the sieve element–companion cell complex playing an integral role in the movement of photoassimilates and other compounds throughout the plant. Because during their evolution the sieve elements retained a functional plasma membrane, the evolution of a mechanism of transport through the phloem utilizing the force of osmosis, controlled by solute concentration, was possible.

Gross structure and development of the phloem

The phloem is, thus, a distinctive, important and highly complex tissue through which photosynthate is transported throughout the plant. **Primary phloem** differentiates from provascular tissue and, with primary xylem, is a major component of stem vascular bundles, leaf traces, and the vascular systems of leaves, flower parts, fruits, and seeds (see Chapter 6). In roots of seed plants it usually occurs in discrete bundles that alternate with ribs or bundles of primary xylem. In pteridophytes primary phloem usually encloses either a central column or a cylinder of primary xylem. In axes with a pith, the primary xylem may be bounded on both the inside and the outside by primary phloem.

The primary phloem consists of protophloem and metaphloem. **Protophloem** differentiates earlier and nearer the apical meristem than protoxylem, and in regions that are actively elongating. Consequently (especially in stems) the conducting elements are stretched and often obliterated. **Metaphloem** differentiates later than protophloem, in regions in which growth in length has ceased (for more detail, see Chapter 6). In both structure and function the conducting elements and associated cells of the primary phloem are remarkably similar to those of the secondary phloem.

Secondary phloem, like secondary xylem, is derived from the vascular cambium, and is composed of axial and radial systems of cells (Figs 12.1a–d, 12.2a, b). The axial system is made up of conducting cells, associated parenchyma cells, companion cells (in angiosperms), and phloem fibers. The radial system consists of phloem rays that are continuous with rays in the secondary xylem.

The conducting cells, longitudinally elongate, are collectively called **sieve elements**. There are two types of sieve elements: sieve cells characteristic of gymnosperms, pteridophytes, and other lower vascular plants, and sieve tube members, characteristic of angiosperms. These cells develop from **sieve element mother cells** which are direct descendants of fusiform cambial initials. Following periclinal, longitudinal divisions, the mother cells in gymnosperms differentiate into functional **sieve cells** (Figs 12.1b, 12.2a), generally with little or no longitudinal (intrusive) growth. The mature sieve cells, like the fusiform cambial initials from which they are derived, are very long with overlapping ends. By contrast, in dicotyledons, transverse, anticlinal, and/or oblique divisions in the sieve element mother cells lead to columns of superposed **sieve tube members** (Fig. 12.3b). Among the distinctive

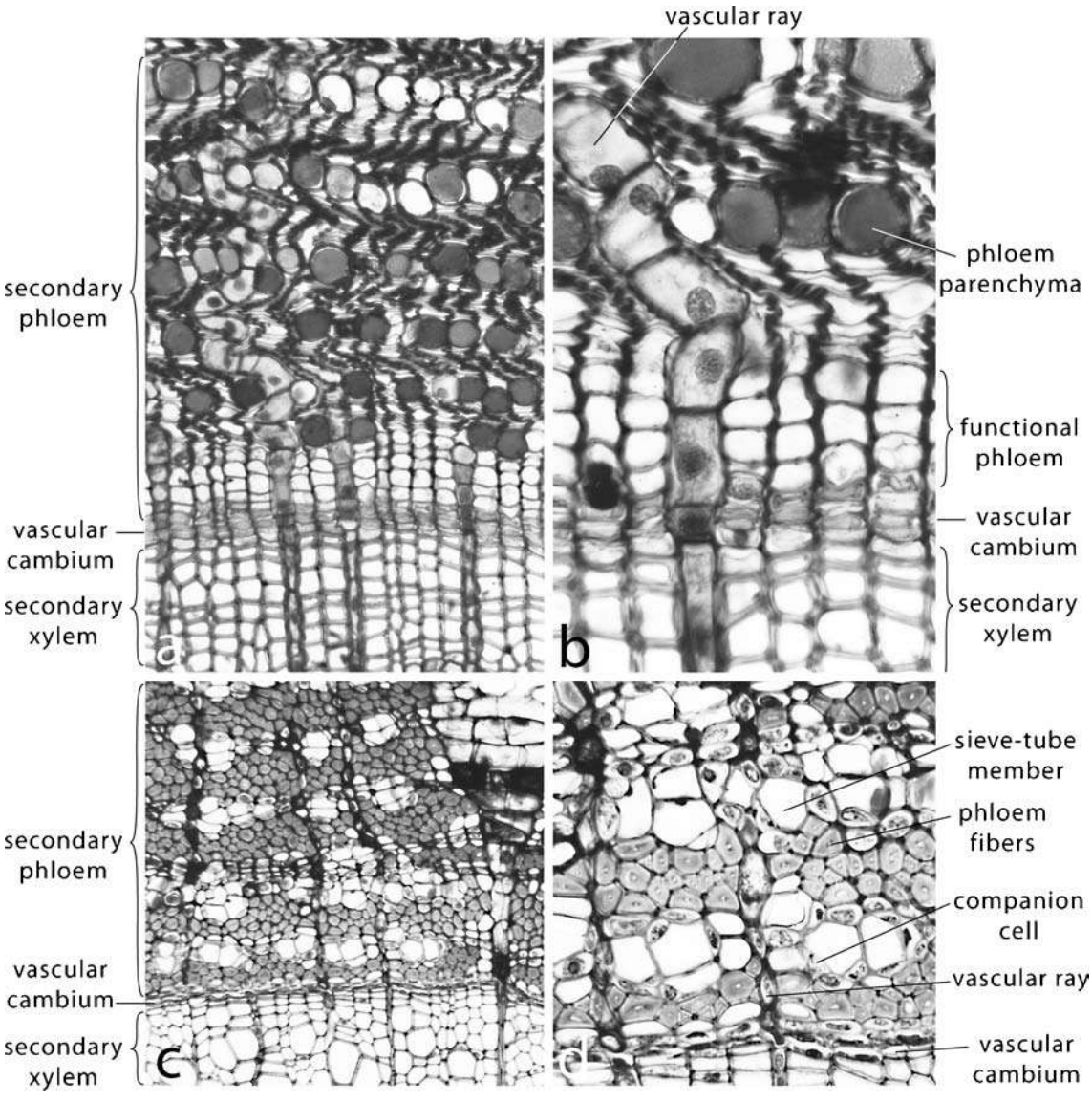

Figure 12.1 (a, b) Transverse sections of secondary phloem of *Pinus strobus*, a conifer, and (c, d) *Tilia americana*, a woody dicotyledon. The secondary phloem is derived from the vascular cambium and, like the secondary xylem, consists of axial and radial systems. Magnification (a) × 206, (b) × 520, (c) × 60, (d) × 160.

features of sieve elements is the fact that they comprise longitudinal, open, but living, systems through which photosynthate is transported. At maturity, the sieve element protoplast is highly modified, lacking a nucleus and vacuolar membrane, but it retains a functional plasma membrane, and some parietal endoplasmic reticulum, mitochondria, and plastids.

Another distinctive feature of sieve elements is the presence of **sieve areas** in the lateral walls of sieve cells (Fig. 12.2a) and on the end walls and, in some taxa, on lateral walls of sieve tube members (Figs 12.2b, 12.3). Sieve areas which are highly specialized and evolutionarily modified primary pit fields consist of groups of **pores** through which the protoplasts of contiguous conducting cells are connected

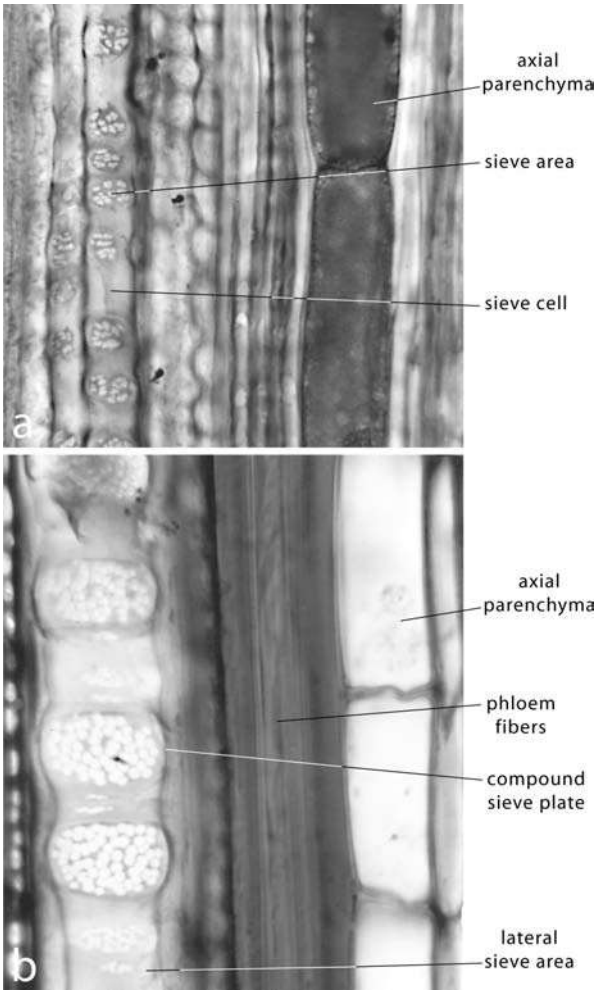

Figure 12.2 (a) A longitudinal section of secondary phloem of *Pinus strobus* showing functional sieve cells characterized by lateral sieve areas. Note the columns of superposed, axial parenchyma cells in a region of the phloem in which sieve cells are no longer functional. Magnification × 555. (b) A longitudinal section of secondary phloem of *Tilia americana*, illustrating part of a sieve tube member with an oblique, compound sieve plate. Note also the lateral sieve areas, a strand of thick-walled fibers, and a column of axial parenchyma cells. Magnification × 944.

(Fig. 12.4a, b, d, e). Pores in dicotyledons are often lined with cylinders of **callose** (the carbohydrate, β-1,3-glucan) (Fig. 12.4a, b) that enclose the plasma membrane, endoplasmic reticulum, and other cytoplasmic components that traverse the pores. Callose-lined pores have been reported in the Gnetales, but only rarely have been observed in other gymnosperms. It is unclear whether or not the callose cylinders are a normal feature of the sieve areas of living, functioning sieve cells and sieve tube members. It is known that wounding stimulates rapid synthesis of callose, and some evidence indicates that callose cylinders in sieve areas are the result of the stimulation that results from the cutting of a segment of stem to be sectioned. As a sieve element approaches the end of its functional life, callose accumulates in large quantities, occluding the pores, and may even completely cover the surfaces of sieve areas. Callose in this state is referred to as **definitive callose** (Fig. 12.4c).

In sieve tube members sieve areas occur on end walls called **sieve plates**. A sieve plate containing a single sieve area is called a **simple sieve plate** (Figs 12.3a, 12.4a, b) whereas one with several sieve areas is

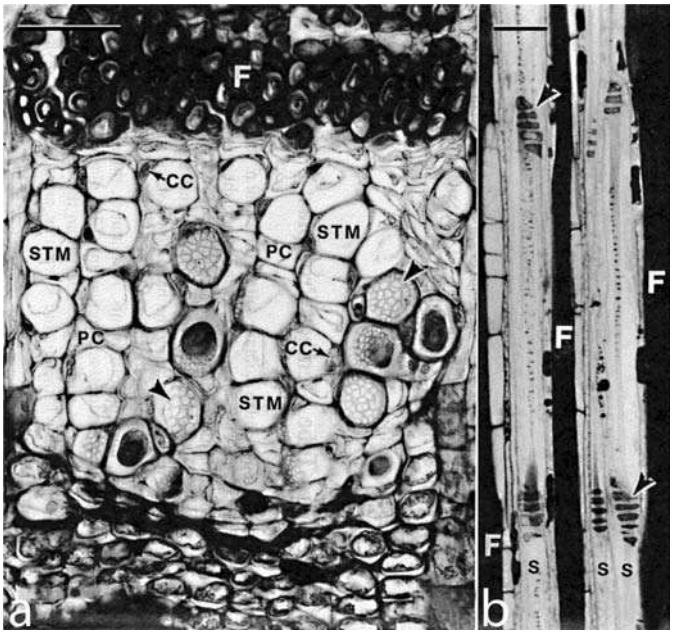

Figure 12.3 (a) Transverse section of the secondary phloem of *Robinia pseudoacacia* (black locust) illustrating sieve tube members (STM) with transversely oriented, simple sieve plates (arrowheads). Note also companion cells (CC), phloem parenchyma cells (PC) and phloem fibers (F). Bar = 50 μm. (b) Radial section of secondary phloem of *Tilia americana* showing sieve tubes consisting of sieve tube members (S) with oblique, compound sieve plates (arrowheads). Also note the small lateral sieve areas. F, fibers. Bar = 50 μm. From Evert (1990b). Used by permission of Springer-Verlag GmbH and Co. KG. © Springer-Verlag Berlin Heidelberg.

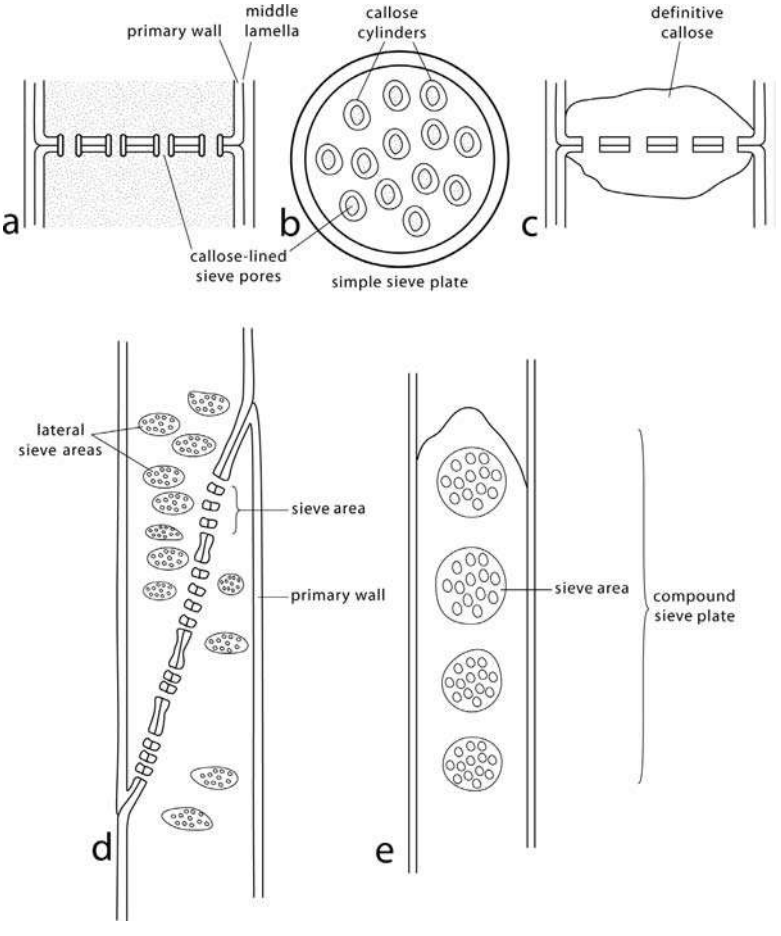

Figure 12.4 (a–c) Diagrams of simple sieve plates, each consisting of a single sieve area. (a) Sectional view of a sieve area. (b) Face view of a sieve area. (c) A sieve area enclosed in definitive callose and, consequently, non-functional. Stippling represents cytoplasmic contents continuous through sieve pores between contiguous sieve tube members. (d, e) Compound sieve plates. To simplify the diagrams callose and cytoplasmic contents are not shown. (d) Sectional view. (e) Face view.

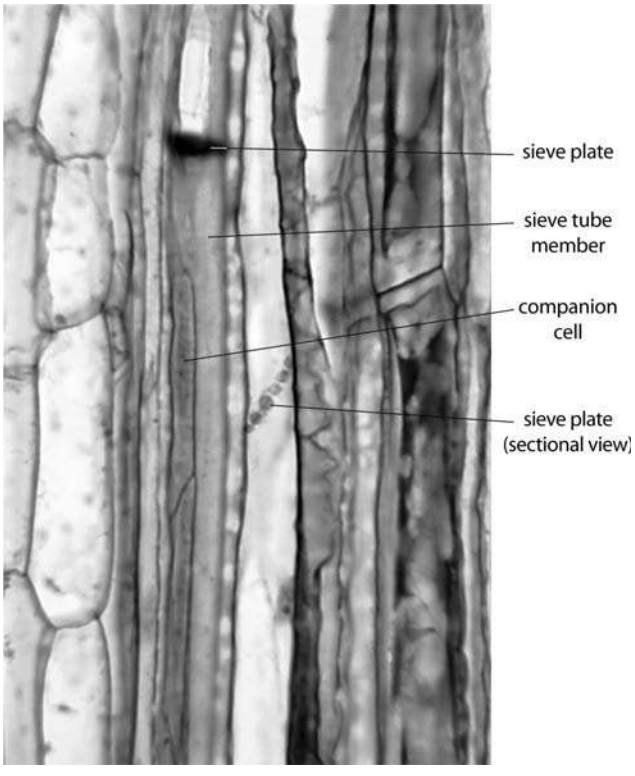

Figure 12.5 Longitudinal section of the primary phloem of *Cucurbita*. Note the companion cells associated with the sieve tube member on the left, and the sectional view of a simple sieve plate between two adjacent sieve tube members on the right. Magnification × 400.

a **compound sieve plate** (Figs 12.2.b, 12.3b, 12.4d, e). Simple sieve plates usually occur on transverse end walls, and compound sieve plates on oblique end walls. The sieve tube members of some taxa also contain scattered, somewhat indistinct sieve areas in their lateral walls (Figs 12.2b, 12.3b, 12.4d). The sieve cells of gymnosperms and lower vascular plants do not have end walls. Sieve areas occur over the entire lateral walls (Fig. 12.2a), but often occur in greater frequency in the walls of the overlapping ends of the cells.

Associated with the sieve tube members in the phloem of angiosperms are **companion cells** (Figs 12.1d, 12.3a, 12.5), many of which, in the small veins of leaves, are transfer cells that facilitate the loading of photosynthate into sieve tube members (for more detail, see a later section in this chapter on companion cells and Strasburger cells). Although several companion cells may be associated with a sieve tube member (Fig. 12.6), each companion cell is derived from the same cambial initial as the sieve tube member with which it is in contact. Companion cells also accompany sieve tube members in the metaphloem of angiosperms, as well as the protophloem of some but not all species.

In conifers (possibly other gymnosperms; see Behnke, 1990), cells similar in function to the companion cells of angiosperms differ both in origin and morphology. These cells (Fig. 12.7), called **albuminous cells** in the older literature, have in recent years been widely labeled **Strasburger cells** after the German botanist who first described them.

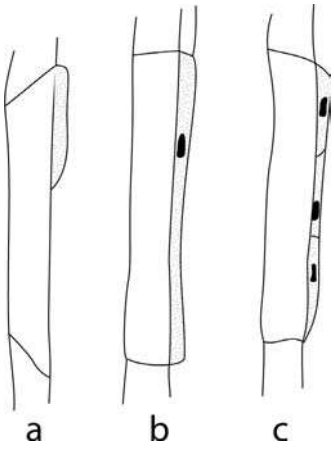

Figure 12.6 Diagrams of sieve tube members (details of sieve plates omitted) with associated companion cells (stippled).

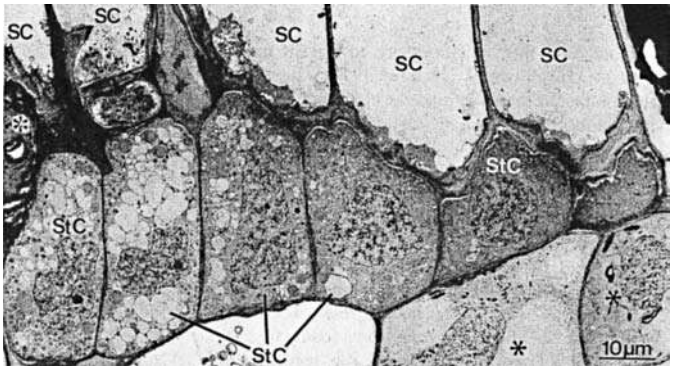

Figure 12.7 Marginal ray cells of *Abies* that have developed as Strasburger cells (StC) in contact with sieve cells (SC). Note the lobed nuclei in several Strasburger cells. Asterisks designate starch-containing cells. From Schulz (1990). Used by permission of Springer-Verlag GmbH and Co. KG. © Springer-Verlag Berlin Heidelberg.

They are derived largely from marginal ray cell initials as well as from some short fusiform initials (Srivastava, 1963) and generally are shorter than companion cells.

Axial parenchyma cells are usually associated with strands of conducting cells (Figs 12.1a, b, 12.2a) and in angiosperms are often difficult to distinguish from companion cells (Fig. 12.3a). **Phloem fibers** (Figs 12.1a, b, 12.2b) occur in longitudinal strands and appear, in transverse sections, as tangential and/or radial bands in dicotyledons. Because during cambial activity the secondary phloem is pushed outward and compressed, only the most recently formed annual increments are functional in transport. In these increments, the living conducting cells and the associated parenchyma cells are protected from compression by the surrounding masses of phloem fibers. In increments formed earlier, however, the forces resulting from the production of secondary xylem are so great that the sieve tube members, companion cells, and phloem parenchyma cells become severely compressed and non-functional in dicotyledons. Although in some conifers (e.g., *Abies* and *Pinus*) the sieve cells become non-functional, the axial parenchyma cells (Figs 12.1b, 12.2a) resist the forces of compression, becoming repositories of phenolic compounds which provide a defense against invading insects and pathogens (see Franceschi *et al*., 1998). This compression of the phloem explains, in part, why the annual increments (growth layers) of secondary phloem are so much less conspicuous than the growth layers of secondary xylem. Equally important is the fact that the cambium produces fewer phloem cells than xylem cells.

The nature and development of the cell wall of sieve elements

In both angiosperms and gymnosperms, with the exception of some members of the Pinaceae, the sieve elements have only primary walls although the walls may be lamellate. Consisting of cellulose and pectic compounds, the sieve element wall is of variable thickness, often much thicker than that of associated parenchyma cells. Because of

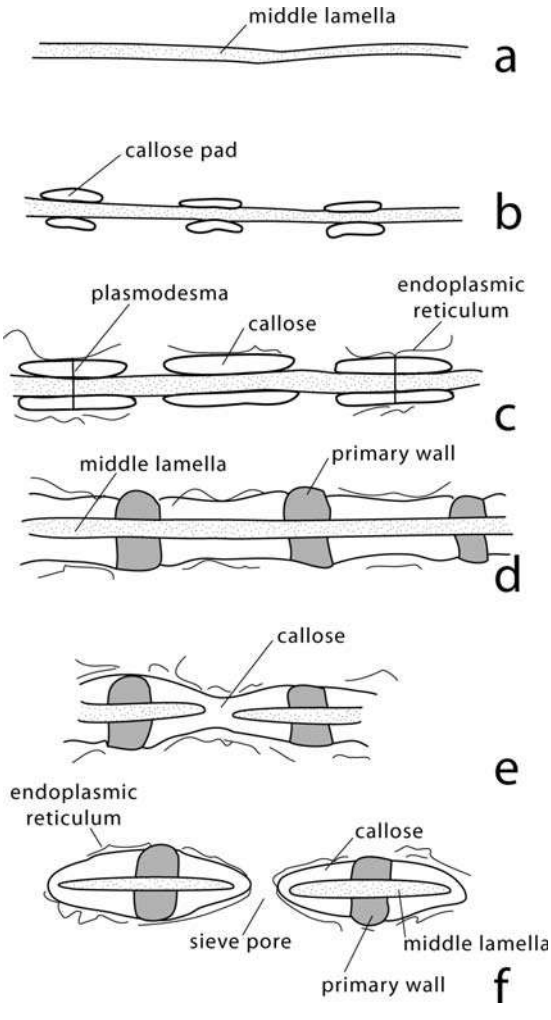

Figure 12.8 (a–f) Diagrams of stages in the development of sieve pores in a sieve plate as seen in sectional view. See the text for descriptions. Based on photographs and text descriptions in Esau *et al.* (1962) and Esau and Thorsch (1985).

their glistening, pearly appearance in unkilled tissue, the term **nacreous wall** has been applied to walls of sieve elements.

The development of sieve areas in the walls of superposed sieve tube members has been studied extensively, and has been described in detail. For example, following mitosis of a sieve element mother cell in *Cucurbita maxima* (Esau *et al.*, 1962; Esau and Cheadle, 1965; Esau and Thorsch, 1985), the protoplasts of the incipient sieve tube members are initially separated only by the middle lamella (Fig. 12.8a). On either side of the middle lamella in the region that will develop into a sieve area, pairs of **callose platelets** (Fig. 12.8b) are synthesized synchronously. Endoplasmic reticulum, associated with the callose platelets on either side of a developing pore, is connected by the desmotubule of a single plasmodesma (Figs 12.8c, 12.9a, b). As development of the sieve area continues, the callose platelets increase in area and thickness as primary wall material is synthesized between them (Figs 12.8d, 12.9a). Then each pair begins to decrease in thickness

centrally, presumably the result of hydrolysis of the callose under influence of the plasmodesma, and the middle lamella also begins to disappear around the plasmodesma (Fig. 12.8e). Upon completion of hydrolysis a cylindrical **pore** results (Figs 12.8f, 12.9d). The pore may be lined with callose or, if hydrolysis has been complete, no callose will remain (Esau and Thorsch, 1985). The plasma membranes of the two contiguous sieve elements are continuous through the pore (Figs 12.9d, 12.10). ER cisternae which may traverse the pores are located parietally, and any P-protein in the pores is either parietally located or in a filamentous network (Figs 12.9d, 12.10), thus the pores are unoccluded (Evert, 1990a; see also Ehlers *et al*., 2000). The development of sieve area pores in gymnosperms is similar to that in angiosperms (see later section for details of differences), but no callose platelets have been observed in association with the developing pores. Furthermore, sieve pores in the mature sieve areas may or may not be lined with callose (see Schulz, 1990). Because it is known that callose synthesis is stimulated by injury, many researchers have suspected that the association of callose with the developing sieve pores in angiosperms is not a normal feature in the living plant, but an artifact resulting from the sectioning of the material to be studied. To test this hypothesis, Walsh and Melaragno (1976) immersed an entire specimen of the diminutive, aquatic plant *Lemna minor* in chemical fixative before sectioning. They found no callose deposition on the developing sieve areas in this specimen. In a similar specimen sectioned prior to fixation, callose was found to be associated with the sieve areas, indicating that callose formation during sieve area development in *Lemna* is an artifact. In a recent study (Ehlers *et al*., 2000), however, in which the exposed, presumably undamaged midribs of leaves of *Vicia faba* (broad bean) were fixed while attached to the living plant, callose was deposited on the developing sieve areas. Similarly, in *Lycopersicon esculentum* (tomato) vascular bundles were exposed in the stem and fixed on the living plant. Callose was also observed

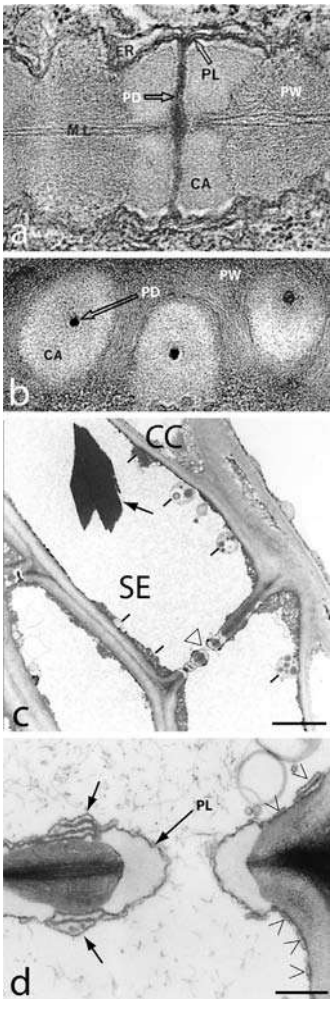

Figure 12.9 (a, b) Views of developing sieve areas in *Gossypium hirsutum* (cotton). (a) Sectional view of a developing sieve pore, showing the single plasmodesma (PD) connecting the protoplasts of the superposed sieve tube members. Note that the plasmodesma is enclosed by callose (CA). ER, endoplasmic reticulum; ML, middle lamella; PL, plasma membrane; PW, primary wall. (b) Face view of developing sieve pores. CA, callose; PD, plasmodesma; PW, primary wall. Magnification (a, b) × 32 250. (c) Part of a sieve tube member of *Vicia faba* (broad bean) illustrating a simple sieve plate in sectional view with open pores (only one shown) between superposed sieve tube members (SE). Note the peripheral position of cytoplasmic organelles. Bar = 3 μm. (d) Sectional view of an open sieve pore, lined with callose, in a mature sieve area of *Lycopersicon esculentum* (tomato). Note that the plasma membrane (PL) is continuous between the two protoplasts, covering the surface of the callose. The walls of the sieve area are covered by stacked ER cisternae (arrows). Endoplasmic reticulum also covers regions of the lateral walls of the sieve tube members (arrowheads). Bar = 0.4 μm. (a, b) From Esau and Thorsch (1985). Used by permission of the Botanical Society of America. (c, d) From Ehlers *et al.* (2000). Used by permission of Springer-Verlag Wien.

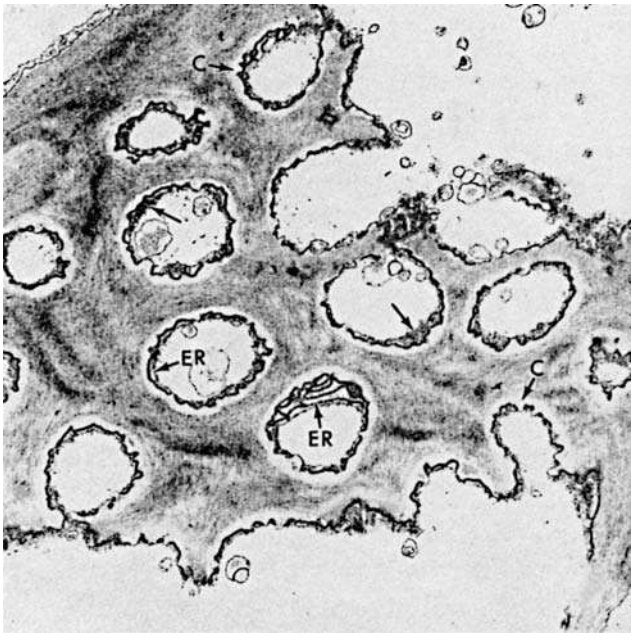

Figure 12.10 Face view of part of a simple sieve plate of *Cucurbita maxima*. The open sieve pores are lined with callose (C) which, in turn, is lined with the plasma membrane covered in some regions by endoplasmic reticulum (ER) and P-protein (unlabeled arrows). Magnification × 16 760. From Evert (1984). Used by permission of copyright-holder Ray F. Evert.

on the sieve areas in this plant (Fig. 12.9d). These results provide some support for the viewpoint of Esau and Thorsch (1985) that (the results of Walsh and Melaragno notwithstanding) "the phenomenon [production of callose during sieve area development] may be a unique feature of sieve element development in higher plants."

Role of the cytoskeleton in wall development

In the past, phloem development has been studied primarily utilizing electron microscopy. Although techniques of molecular biology such as immunolocalization of the cytoskeleton have been utilized extensively in studies of secondary xylem development, such approaches have only recently been applied to the problem of differentiation of phloem cells. Chaffey *et al*. (2000) studied the role of microtubules in the differentiation of phloem cells in the roots of *Aesculus hippocastanum*. They observed that microtubules are transversely oriented in the cambial initials and become arranged in a steep helix in all types of phloem cell derivatives as differentiation progresses. They believe that the change in orientation is correlated with an increase in synthesis and deposition of wall material. As wall thickening occurred they observed a parallel orientation of the cortical (i.e., peripheral) microtubules and the putative cellulose microfibrils in the developing wall, supporting the view of others that there is a functional relationship between microtubules and the synthesis of new microfibrils (e.g., Giddings and Staehelin, 1991; Hable *et al*., 1998). Chaffey *et al*. (2000) observed, further, that as the walls of the developing phloem cells increased in thickness,

they became laminate, but they were unable to detect any significant differences between them and the primary walls of the cambial cells from which they were derived (see also Evert, 1990b). In some phloem parenchyma cells Chaffey *et al*. (2000) observed microtubules and cellulose microfibrils arranged in rings around developing primary pit fields, a condition similar to the arrangement of these structures associated with developing bordered pits in tracheary elements described by many workers (see Chapter 11). They suggest, however, that unlike the possible function of microtubules in tracheary elements in which wall thickening occurs during the development of pit borders, the rings of microtubules in phloem parenchyma cells enclose domains in which wall thickening is restricted in the region of the developing primary pit fields. As in late stages of the development of vessel members, the peripheral microtubules in developing sieve tube members lose their helical orientation, becoming more or less transverse as the cells increase in diameter. This indicates that the microtubules are probably attached to the plasma membrane, but it is not clear what, if any, role change in microtubule arrangement plays in an increase in cell circumference (Chaffey *et al*., 2000). Although it has been assumed that microtubules disappear prior to maturity of sieve tube members (see Evert, 1990b), they were observed in possibly mature and functional sieve tube members in the secondary phloem of *Aesculus* roots. However, no evidence of any role for microtubules in sieve plate formation was found which might be related to the fact that callose rather than cellulose is synthesized during the development of sieve area pores (Chaffey *et al*., 2000).

The nature and development of the protoplast of sieve elements

Following division of a sieve element mother cell, the protoplast of an incipient sieve element is essentially identical to that of any other immature living cell. It contains a nucleus, rough endoplasmic reticulum dispersed throughout the protoplast, mitochondria, Golgi bodies, microtubules, microfilaments, and many small vacuoles, and is enclosed by a plasma membrane. During development profound changes occur in the protoplast. With increase in size of the cell, small vacuoles fuse forming a conspicuous central vacuole, enclosed by a single vacuolar membrane, the **tonoplast**. In angiosperms, highly chromatic P-protein bodies form, and small plastids that contain starch and/or protein granules appear (Fig. 12.9c). Prior to functional maturity, the nucleus disintegrates. By the time of nuclear disintegration, Golgi bodies, microtubules, and microfilaments, associated with cell wall formation, will also usually have disappeared. However, peripherally located plastids and mitochondria persist and, with endoplasmic reticulum which has become smooth by having lost its ribosomes, are the only organelles remaining in the functional sieve element

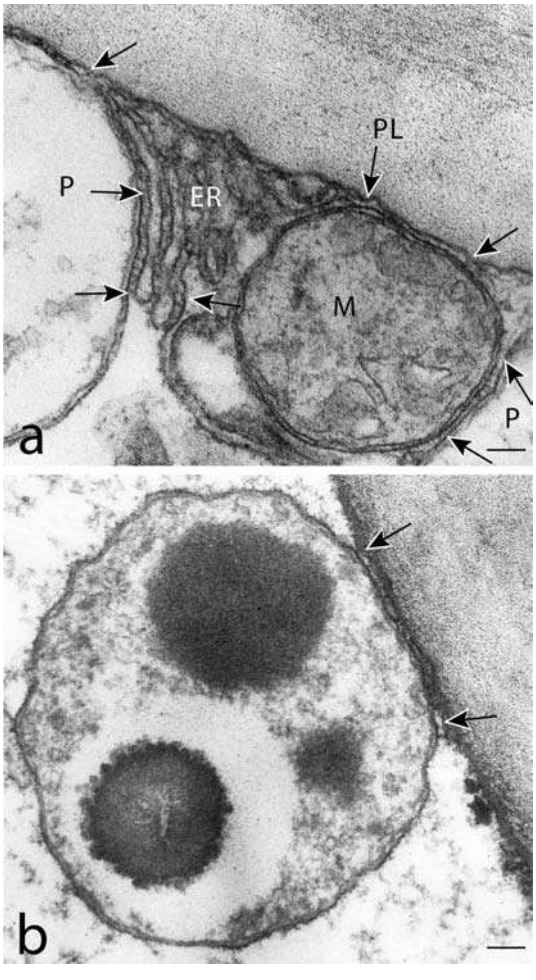

Figure 12.11 Parietal cytoplasmic organelles of sieve tube members attached to each other and to the plasma membrane by "clamp-like" structures (at arrows). (a) Attachment of the outer membrane of a plastid (P), a mitochondrion (M), and cisternae of endoplasmic reticulum (ER) to the plasma membrane of a sieve tube member of *Lycopersicon esculentum*. A region of endoplasmic reticulum (between arrows) is also attached to the plastid. (b) A plastid of *Vicia faba* attached to the plasma membrane. Bars (a, b) = 100 nm. From Ehlers *et al.* (2000). Used by permission of Springer-Verlag Wien.

(Fig. 12.9c). Late in development the tonoplast disintegrates, and P-protein bodies disaggregate, with P-protein becoming dispersed throughout the periphery of the protoplast.

Recently, Ehlers *et al.* (2000) have provided evidence indicating that in *Vicia faba* and *Lycopersicon esculentum* the peripherally located sieve element organelles seem to be connected to each other and to the plasma membrane by minute "clamps" that prevent them from being moved along in the assimilate stream (Figs 12.11, 12.12). P-protein also maintains a parietal position, but is thought to be more loosely attached than the sieve element organelles (Fig. 12.12). Since at this stage of development the sieve pores are open and any P-protein and/or ER in the pores are located parietally in the pore lumina (Fig. 12.10) the sieve elements comprise open passageways through which pressure flow of assimilates can take place with minimal impedance.

Although it is clear that, at functional maturity, sieve tube members and sieve cells are characterized by highly modified, some would say denatured, protoplasts, it has been clearly demonstrated that they possess normal properties of differential permeability and thus can exert

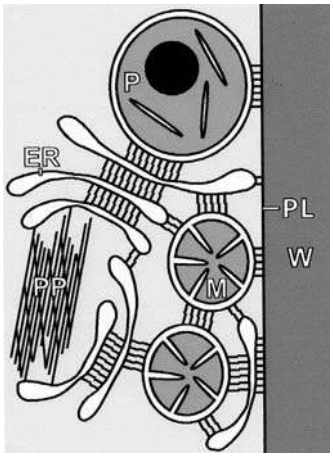

Figure 12.12 Diagram illustrating the attachment of cytoplasmic organelles in a sieve element to each other and to the plasma membrane. ER, endoplasmic reticulum; M, mitochondrion; P, plastid; PL, plasma membrane; PP, P-protein; W, cell wall. From Ehlers *et al.* (2000). Used by permission of Springer-Verlag Wien.

an active influence on the movement of assimilates into and out of themselves. It is now well established, also, that the accumulation of P-protein on the surface of sieve plates commonly observed in section is not a feature of the functional cell but, rather, the result of displacement of cell contents upon the release of pressure in the cells when sections are cut. The more normal state of the protoplasts has been determined by osmotically reducing the pressure within the cells prior to preparing tissue for sectioning (e.g., Evert *et al*., 1973) and by the use of other "gentle preparation" methods (Ehlers *et al*., 2000). Recently, however, Knoblauch *et al*. (2001) have concluded that in the Fabaceae (= Leguminosae), at least, the dispersal of P-protein and its accumulation on the sieve plates may be a mechanism to control sieve tube conductivity. As sieve elements approach the end of their functional lives, callose is synthesized in large quantities (definitive callose) and deposited on the surface of sieve areas, sometimes completely covering them (in angiosperms often covering entire sieve plates), effectively restricting further transport in the system (Fig. 12.4c). Just prior to death of the protoplasts, the callose is hydrolyzed, and the open pores in the sieve areas become conspicuous.

Nature and function of P-protein

P-proteins (Figs 12.9c, 12.12, 12.13) occur in both dicotyledons and monocotyledons but are absent from gymnosperms and lower vascular plants (see Cronshaw and Sabnis, 1990, Evert, 1990b). As observed with the electron microscope, P-protein, called slime in the older literature, occurs in several forms (Fig. 12.13): tubular, granular, filamentous, and crystalline. Aggregation of P-protein into ellipsoidal or spheroidal **P-protein bodies** (Fig. 12.13a) occurs early in the differentiation of sieve cells. These bodies increase in size during differentiation of the cell and may fuse. Polyribosomes are associated with P-protein filaments or tubules during aggregation and are thought to have a functional role in the process. Conspicuous crystals of P-protein, commonly associated with tubular, filamentous or granular P-protein, are characteristic of many members of the Fabaceae. The small, spheroidal bodies, previously thought to be extruded nucleoli, are now considered to be a type of P-protein body.

At about the time that the nucleus begins its disintegration, components of the P-protein bodies begin to separate and to disperse within the protoplast (Fig. 12.13b). Some researchers conclude that the individual filaments or tubules form a peripheral network of P-protein whereas evidence provided by others indicates that the network extends throughout the protoplast. Cronshaw (1975) suggested that P-protein, no matter what the distribution, is relatively stationary in the mature sieve element protoplast and does not move in the assimilate stream. This viewpoint is supported by the work of Ehlers *et al*. (2000), described above, who have demonstrated that peripherally located P-protein, plastids, ER, and mitochondria are attached to each other and to the

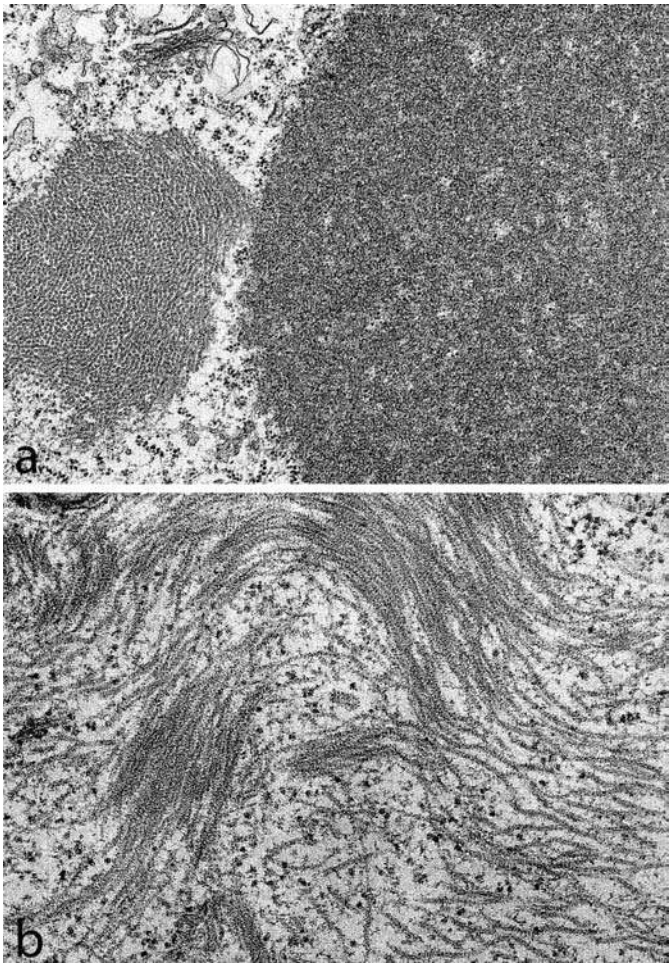

Figure 12.13 P-protein in differentiating sieve tube members. (a) A large P-protein body consisting of filamentous P-protein and a smaller body comprised of tubular P-protein in *Cucurbita maxima*. Magnification × 20 300. (b) Tubular and striated filaments in a dispersing P-protein body in *Nicotiana tabacum*. Magnification × 32 154. From Cronshaw and Sabnis (1990). Used by permission of Springer-Verlag GmbH and Co. KG. © Springer-Verlag Berlin Heidelberg.

plasma membrane by minute "clamps" (Figs 12.11, 12.12). They emphasize further, however, that the parietal P-proteins are probably loosely attached at the cell periphery and, in the event of injury, would be quickly released in order to plug the sieve pores, thus preventing the release of assimilates. Although the function of P-protein in sieve elements is not fully understood, it has been long observed that upon the release of internal pressure, the P-protein moves suddenly in the direction of the pressure release to the ends of the cells and plugs the sieve pores. It has been shown, recently, that P-protein crystalloids in legumes can undergo rapid, reversible changes from the globular to the dispersed state in which they occlude the sieve pores (Knoblauch *et al*., 2001). Experimentally, dispersal can be triggered by leakage of the plasma membrane caused by mechanical injury, by substances such as Ca^{2+} that increase its permeability, or by abrupt turgor changes. Reversion to the globular state can be induced by chelators, indicating that the P-protein crystalloids of legumes represent a unique class of proteinaceous structures by which conduction through sieve tubes can be controlled (Knoblauch *et al*., 2001).

Distinctive features of the phloem of gymnosperms

Since angiosperms are believed to have diverged from gymnosperms during their evolution, it is perhaps not surprising that the sieve elements in these two groups of seed plants are similar, especially in the differentiation of the sieve element protoplast and even in the nature of the mature sieve element. One distinctive feature of angiosperms that is lacking in gymnosperms, however, is the presence of P-protein. This suggests that this substance first evolved in the sieve tube members of primitive angiosperms or the sieve elements of their immediate, extinct ancestors. It is, in fact, interesting to note that P-protein is present in primitive extant angiosperms such as *Austrobaileya*, *Degeneria*, *Drimys*, *Liriodendron*, *Magnolia*, and *Trochodendron* (see Evert, 1990b).

As noted above, the sieve cells of gymnosperms are relatively very long and have overlapping ends. Sieve areas (Fig. 12.2a) occur on the lateral walls but in greater frequency near the ends of the cells. Sieve pores tend to be smaller than those of angiosperms, but more phloem in relation to xylem is produced in conifers (possibly in other gymnosperms) than in angiosperms. This might be a compensation for the smaller sieve pores which result in a slower translocation of metabolites through overlapping sieve cells than through pores of sieve tubes of comparable transverse area (Romberger *et al*., 1993). In the Pinaceae, unlike other gymnosperms, the sieve cells have thick secondary walls.

In conifers as in angiosperms, endoplasmic reticulum is associated with sieve areas during their differentiation (Schulz, 1992). Tubules of ER and/or plasmodesmata mark the site of future pores, but unlike sieve area differentiation in angiosperms, no callose platelets are associated with pore formation. Pores in the walls of contiguous cells begin their differentiation by the formation opposite each other of incipient pore canals. As the differentiating canals extend toward the middle lamella, a central cavity develops with which they merge. Upon completion of development, endoplasmic reticulum extends from one cell to the adjacent cell through the pores, connecting the protoplasts (Schulz, 1992).

As in the sieve tube members of angiosperms, the only organelles that persist in the functional sieve cells of gymnosperms are endoplasmic reticulum, mitochondria, and plastids. The plastids of all conifers contain starch grains, but plastids in most members of the Pinaceae contain, in addition, protein crystals and protein filaments. The only known exceptions are *Tsuga canadensis* (hemlock) and *Larix decidua* (larch) which contain only protein filaments.

A distinctive feature of many conifers is the presence of large, axial parenchyma cells in the secondary phloem (Figs 12.1a, b, 12.2a). These cells remain alive in the non-conducting part of the secondary phloem until they are incorporated into the bark (Esau, 1977). They are characterized by a dark-staining substance, recently identified in *Picea abies* (Norway spruce) as composed of phenolic compounds, and demonstrated to play an important role in defending the plant against invasive

organisms such as fungi (Franceschi *et al*., 1998). Another distinctive feature of gymnosperms is the presence of Strasburger cells (Fig. 12.7) which in these groups serve the same function as companion cells in angiosperms.

The nature and function of companion cells and Strasburger cells

The phloem accumulates photosynthate from the mesophyll of leaves, transports it throughout the plant, and releases it at sites where it is utilized in the growth and development of the plant. These functions are implied by the terms "source," "transport," and "sink" commonly used in the literature. Recently, Van Bel (1996) has proposed the terms **collection phloem**, **transport phloem**, and **release phloem** to indicate more clearly these important functions of the phloem, but these terms are not as yet widely used. In this book we shall use these terms as well as source and sink where each seems most appropriate. Each of these functions (i.e., collection, transport, and release of photosynthate) is intimately related to the structure and activity of **companion cells** associated with the sieve elements. Companion cells are derived from the same mother cells as the sieve tube members with which they are in contact. In contrast to the mature sieve tube member, the companion cell is characterized by a dense protoplast (Figs 12.14, 12.15) containing a prominent nucleus, many mitochondria, extensive rough ER and abundant ribosomes, and plastids which in a few species have been observed to contain starch grains. The density of the protoplast increases throughout the differentiation of the cell which also may become vacuolated. Companion cells in the collection phloem and transport phloem are relatively large in comparison with the sieve tube members (Fig. 12.14). By contrast, they are small or entirely lacking in the release phloem (Van Bel, 1996).

Companion cells and contiguous sieve tube members form **sieve tube–companion cell complexes** (see, e.g., Van Bel and Kempers, 1990). In collection phloem (sources), companion cells in the veins of leaves function in the transfer of assimilates from photosynthetic tissues and bundle sheaths into the sieve tubes. Abundant, often branched, plasmodesmata that extend through the companion cell wall are connected to tubules of endoplasmic reticulum in the pores of sieve areas in the wall of the sieve tube member (Fig. 12.14b) (Fisher, 1986). These symplastic connections have been designated **plasmodesmata–pore connections** by Fisher (1986; see also Van Bel and Kempers, 1997). Because of their intimate association with sieve tube members, the companion cells also play an important role in maintaining the viability and long-distance translocation system of the enucleate sieve tube members by providing them with proteins, including informational (signaling) molecules, and ribonuclear protein complexes as well as ATP (e.g., Schobert *et al*., 2000; Ruiz-Medrano *et al*., 2001).

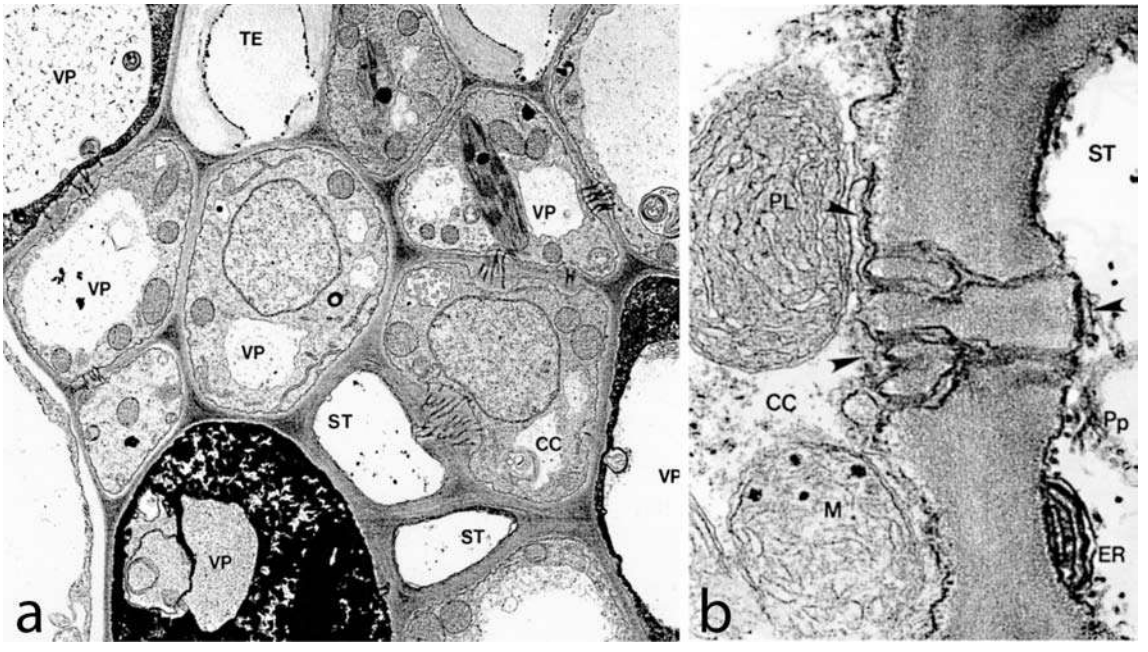

Figure 12.14 (a) A transverse section of part of a minor vein in the leaf of *Populus deltoides* (poplar). Note the large companion cell (CC) associated with smaller sieve tube members (ST); also the plasmodesmatal connections between a vascular parenchyma cell (VP) and the companion cell and between the companion cell and a sieve tube member. TE, tracheary element. Magnification × 42 330. (b) Sectional view of a plasmodesmata-pore connection between a companion cell and a sieve tube member in *P. deltoides*. CC, companion cell; ER, endoplasmic reticulum (stacked cisternae); M, mitochondrion; PL, plastid; Pp, P-protein; ST, sieve tube member. Arrowheads indicate fragments of parietal endoplasmic reticulum. Magnification × 50 300. From Russin and Evert (1985). Used by permission of the Botanical Society of America.

The structure of companion cells is directly related to the mode of **phloem-loading**, that is, the method of movement of photosynthate from the companion cell into the sieve tube member. If **symplastic**, the companion cell wall will be traversed by numerous plasmodesmata (Fig. 12.14a, b) (see Turgeon, 2000). On the other hand, if phloem-loading is **apoplastic**, the companion cell will have the structure of a transfer cell.

In some symplastic loaders (e.g., members of the squash family, among other taxa), the companion cells in the primary phloem are called **vascular parenchyma cells** or **intermediary cells**. Vascular parenchyma cells are specialized companion cells that function either as intermediate providers to other cells (including other companion cells (Fisher, 1986)) or by transferring photosynthate directly into contiguous sieve tube members (see Robinson-Beers and Evert, 1991; Van Bel *et al.*, 1992; Turgeon *et al.*, 1993; Haritatos *et al.*, 2000). In squash, photosynthate enters the vascular parenchyma cells from the bundle sheaths of veins through plasmodesmata (Turgeon, 1996). Sucrose in the vascular parenchyma cells is polymerized into oligosaccharides such as raffinose and stachyose. The oligosaccharides accumulate in high concentration because they are characterized by a molecular size too large to diffuse back into the bundle sheaths. Sieve tube loading then occurs through plasmodesmata with larger size exclusion limits than those that connect the vascular parenchyma cells and the bundle sheaths (see Oparka and Turgeon, 1999; Turgeon, 2006).

Apoplastic loading, a process utilizing energy, is facilitated by carrier proteins called **sucrose transporters** which are located in the plasma membranes of companion cells and/or sieve tube members. Most herbaceous and many crop plants are apoplastic loaders. In some plants photosynthate loading occurs directly from the apoplast of

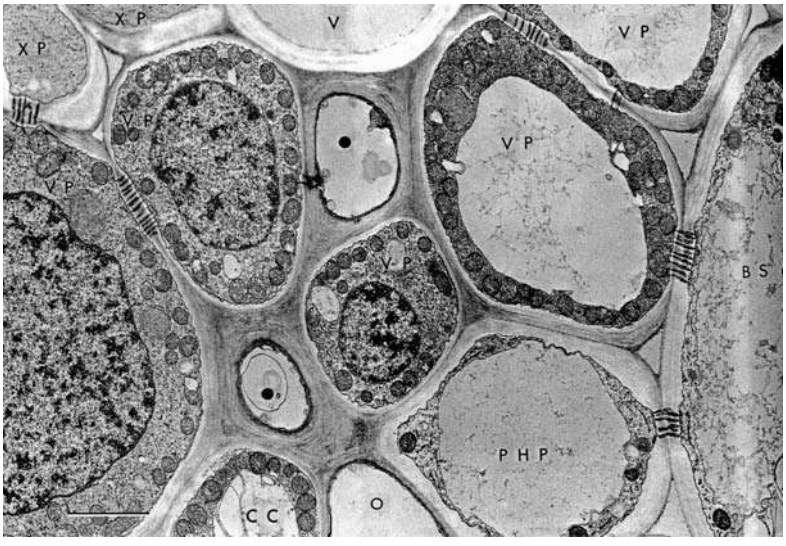

Figure 12.15 Transverse section of part of a vascular bundle in a sugar cane leaf containing two thick-walled sieve tubes (solid dots) and one thin-walled sieve tube (small circle) with associated parenchyma cells. Note the clusters of plasmodesmata connecting adjacent vascular parenchyma cells (VP), a bundle sheath cell (BS) and a vascular parenchyma cell, a bundle sheath cell and a phloem parenchyma cell (PHP), a xylem parenchyma cell (XP) and a vascular parenchyma cell, and a vascular parenchyma cell and a thick-walled sieve tube. CC, companion cell; V, vessel. Bar = 2 μm. From Robinson-Beers and Evert (1991). Used by permission of Springer-Verlag GmbH and Co. KG. © Springer-Verlag Berlin Heidelberg.

surrounding parenchyma cells into the sieve tube members as, for example, in maize (*Zea mays*) and taxa characterized by thick-walled sieve tubes which lack companion cells. In others, however, (e.g., morning glory and soy beans) in which the companion cells are transfer cells, apoplastic loading occurs through the companion cell walls into the sieve tube members (Oparka and Turgeon, 1999). Companion cells that function as transfer cells are characterized by extensive wall ingrowths that vastly increase the surface area of the plasma membrane. Developmentally, this formation of wall ingrowths occurs at about the same time as the leaf ceases utilization of assimilates in its own development and becomes a source of photosynthate. For a detailed and comprehensive discussion of modes of photoassimilate loading in leaves, please see Turgeon (2006).

The phloem of some, perhaps most, grasses contains sieve tube–companion cell complexes as well as **thick-walled sieve tubes** which lack companion cells (Eleftheriou, 1990; Robinson-Beers and Evert, 1991; Botha, 1992; Evert *et al.*, 1996) (Fig. 12.15). Recent evidence indicates that phloem loading in grasses can follow several different pathways. For example, in sugar cane, photosynthate is transferred from the mesophyll into bundle sheath cells by way of plasmodesmata. In small and intermediate-sized veins, loading of assimilates in the thick-walled sieve tubes seems also to be largely symplastic since there are numerous

plasmodesmata between the bundle sheath cells, vascular parenchyma cells, and the thick-walled sieve tube members (Fig. 12.15). However, in the sieve tube–companion cell complexes which are largely isolated symplastically (i.e., they are connected to surrounding parenchyma cells by very few or no plasmodesmata), sieve tube loading is probably apoplastic (Robinson-Beers and Evert, 1991). In two South African grasses, characterized by predominantly apoplastic assimilate loading of thick-walled sieve tubes, loading in sieve tube–companion cell complexes is possibly symplastic (Botha, 1992). On the other hand, in the *Hordeum* (barley) leaf in which both sieve tube–companion cell complexes and thick-walled sieve tubes are symplastically isolated from surrounding parenchyma tissue, Evert *et al*. (1996) concluded that both phloem loading and unloading were apoplastic.

It is now clear that sieve tube–companion cell complexes can be symplastically isolated from surrounding parenchyma cells by virtue of the absence or restriction of plasmodesmatal connections between them (Fisher, 1986; Van Bel and Kempers, 1990; Wimmers and Turgeon, 1991; Botha, 1992; Botha and Van Bel, 1992; Van Bel and Van Rijen, 1994; Van Bel, 1996; Botha *et al*., 2000). The degree of isolation can vary, depending on the frequency of plasmodesmatal connections, from incomplete to almost total. Autonomy of sieve element–companion cell complexes is especially important in the transport phloem in stems where many plasmodesmata between the complexes and adjacent parenchyma cells appear to be closed (Kempers *et al*., 1998). This presumably prevents leakage from the sieve tube–companion cell complexes into surrounding tissue, thus maintaining solute concentration sufficient to ensure pressure flow through the system and ensuring nutrition to terminal and axial sinks along the stem such as the cambial zone (Van Bel, 1996; Van Bel *et al*., 2002). In the release phloem (sinks), where there may be no companion cells, there is a symplastic transfer of assimilates directly from the sieve tubes into the adjacent parenchyma (Van Bel *et al*., 2002).

As in grasses and some other monocotyledons, diverse pathways also characterize photosynthate transport in dicotyledons. A method of presenting graphically the differences in phloem loading involves the use of plasmodesmograms (Botha and Van Bel, 1992), diagrams that indicate the frequency of symplastic connections (plasmodesmata) between cells in phloem-loading pathways (Fig. 12.16). Because it is difficult to determine accurately the area of interface contact and the number of plasmodesmata between different types of cells, the accuracy of the assessment of plasmodesmatal frequency is fraught with uncertainty. Nevertheless, in such diagrams one can visualize the pathway of photosynthate movement from mesophyll cells to the sieve tube members, and predict the mode of phloem-loading, whether symplastic or apoplastic (Botha and Van Bel, 1992). A low frequency of plasmodesmata between cells that contact sieve tube members will indicate an apoplastic mode of phloem-loading whereas a high frequency will indicate a symplastic mode.

An interesting phylogenetic analysis by Turgeon *et al*. (2001) indicates that extensive connection by plasmodesmata between minor

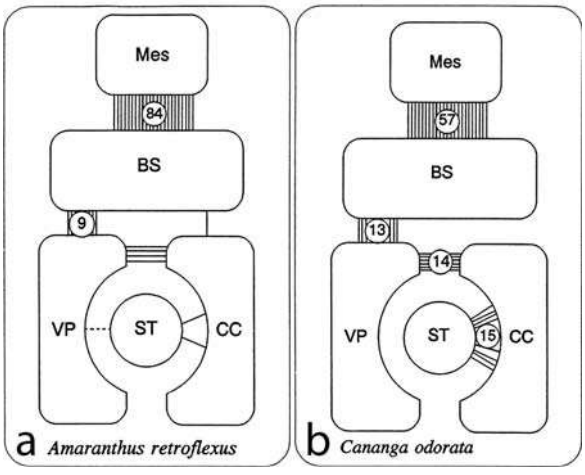

Figure 12.16 Plasmodesmograms illustrating the presumed pathways of photosynthate transport in (a) *Amaranthus retroflexus* and (b) *Cananga odorata*. Numbers in circles indicate percent plasmodesmatal frequency. Solid lines indicate plasmodesmatal frequency of greater than 1%, whereas dotted lines indicate plasmodesmatal frequency of less than 1%. BS, bundle sheath; CC, companion cell; Mes, mesophyll cell; ST, sieve tube member; VP, vascular parenchyma cell. From Botha and Van Bel (1992). Used by permission of Springer-Verlag GmbH and Co. KG. © Springer-Verlag Berlin Heidelberg.

vein phloem and surrounding cells is a primitive character whereas limited connectivity is derived in angiosperms. This may explain the highly reduced frequency of plasmodesmata in minor vein phloem in crop plants.

Although of similar function, the Strasburger cells of gymnosperms (Fig. 12.7) differ in origin and structure from the companion cells of angiosperms. Most are highly specialized marginal ray cells in contact with sieve cells. Like the protoplast of the companion cells, that of Strasburger cells has very dense protoplasm containing abundant ribosomes, extensive rough ER, numerous mitochondria, plastids which may contain starch grains, and a prominent nucleus which may be lobed; also a large vacuole may develop. The protoplasts of Strasburger cells and adjacent sieve cells, like those of companion cells and sieve tube members, are connected through sieve area pores in the walls of the sieve cells and extensive plasmodesmata in the contiguous walls of the Strasburger cells. The Strasburger cells are also connected to ray parenchyma cells by numerous plasmodesmata, presumably facilitating the translocation of solutes from the rays into the sieve cells by way of the Strasburger cells.

The mechanism of transport in the phloem

According to the widely accepted **pressure flow hypothesis**, proposed by the German botanist Ernst Münch in 1927, the movement of solutes within the sieve tubes is essentially passive, the result of hydrostatic

pressure developed osmotically along gradients established by the presence of high concentrations of sugar near the sources of photosynthate and lower concentrations in the vicinity of sinks, i.e., areas of use or storage. The loading and unloading of sugars is essential for the establishment of a high solute concentration and a pressure gradient and, ultimately, for the transport of photosynthate and other substances throughout the plant. Photosynthate is produced largely in the leaves, and transported predominantly downward to sites of utilization and/or storage in the stems and roots, but photosynthate and growth hormones are also transported to regions of active primary growth in buds and the tips of stems distal to the sites of photosynthate production.

This hypothesis envisages an essentially open system whereby photosynthate is moved from cell to cell through the sieve pores. Because of the presence of large quantities of P-protein on the sieve plates as seen by electron microscopy, the concept of a passive flow through the sieve area pores has been severely criticized. As noted above, however, recent evidence utilizing techniques that reduce the deleterious effect on the protoplast of cutting indicate that the slime plugs are artifacts resulting from a sudden change in pressure within the system. Furthermore, utilizing confocal laser scanning microscopy, van Bel and Knoblauch (2000) report *visual* evidence of mass flow in intact plants. One might assume that if pressure flow were the only, or primary, means whereby photosynthate was transported through sieve tubes there would be relatively few, large sieve pores that were free of any cell components that might tend to restrict movement of substances through them. In fact, the velocity of transport through sieve areas with many very small pores is quite efficient, reaching as high as 100 cm per hour (Romberger *et al*., 1993).

Peterson (Peterson and Currier, 1969) demonstrated that translocation in the phloem is bidirectional although she found no evidence of bidirectional translocation within individual sieve tubes. Her research made an important contribution to the knowledge that, in major axes of the plant, photosynthate moves, predominantly, toward the base of the plant from sugar sources, but also in the direction of developing tissues and organs just below the apical meristem. Translocation in the phloem is also bidirectional in developing leaves which, when very young, import (receive) photosynthate from the more mature regions of the plant. Commonly, however, when a leaf has achieved about 50% of its mature size (about 80% in *Festuca arundinacea* (Brégard and Allard, 1999)), it ceases to import photosynthate from more basal mature leaves, and becomes a source, that is, an exporter of photosynthate (Turgeon, 2006). Thus, movement of photosynthate in the developing leaf is bidirectional, at an early developmental stage moving toward the leaf tip, and later moving toward the leaf base.

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Chapter 13

Periderm, rhytidome, and the nature of bark

Perspective

Except in the very youngest regions, the stems and roots of woody plants (specifically, gymnosperms and dicotyledons) are covered by bark consisting of the functional secondary phloem and rhytidome, a complex tissue comprised of successively formed periderms, often of overlapping shell-like morphology, between which are enclosed dead cortical and/or phloem tissues. The outer covering of stems of large monocotyledons differs from that of woody dicotyledons and will be discussed later. The outer bark of woody dicotyledons, consisting primarily of rhytidome, is a protective layer which restricts entrance of both insects and microorganisms and also protects the inner living tissues from temperature extremes. It also inhibits water loss through evaporation, but at the same time allows gaseous exchange through specialized regions in the periderm called lenticels. In addition it supplements the secondary xylem in stiffening young stems (Niklas, 1999), thus contributing to their ability to withstand the bending forces exerted by excessive wind and/or the weight of ice.

Periderm: structure and development

Periderm consists of phellem and phelloderm, both derived from a single-layered secondary meristem, the **phellogen** (Fig. 13.1a, b). Cells of the phellogen are tabular, radially thin, somewhat elongate, and polygonal as viewed tangentially. In many plants the phellogen forms at about the same level in the stem and at about the same time as the vascular cambium. The site of its initiation is highly variable but often is an outer layer of cortical parenchyma one or two layers beneath the epidermis (Fig. 13.1b). In some other plants, however, it may form deep within the cortex, or even in the outer secondary phloem. The phellogen may become a complete cylinder relatively quickly, or it may be initiated in segmental sheets that ultimately connect, forming a cylinder.

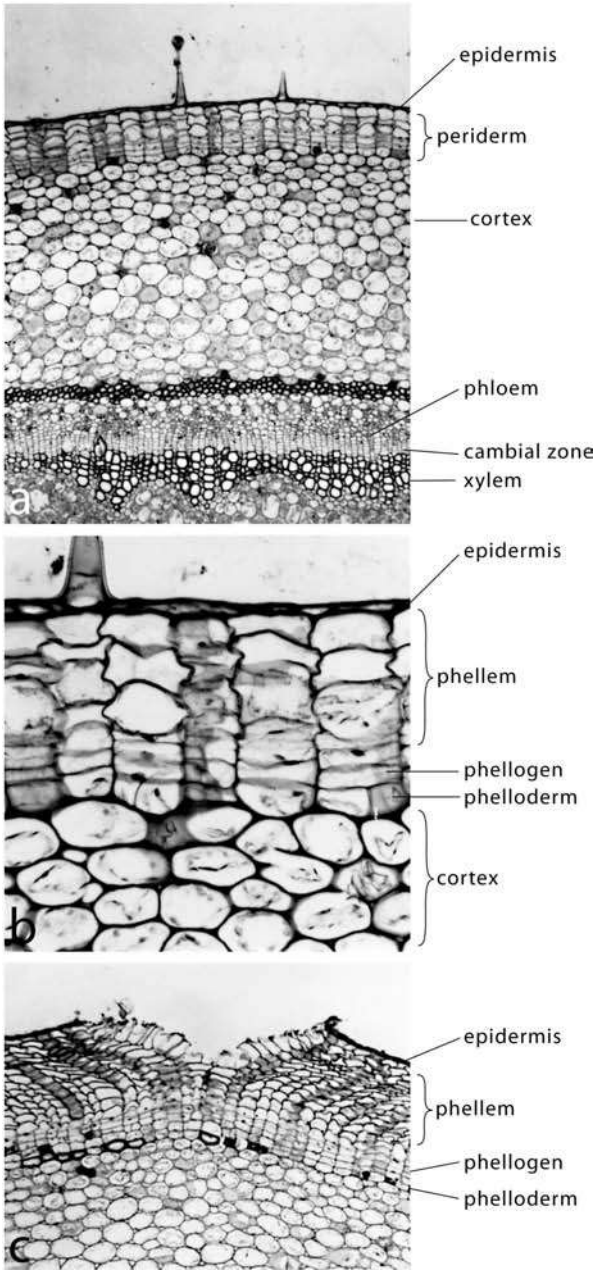

Figure 13.1 Transverse section of a young stem of *Pelargonium* illustrating the periderm and its relationship to other tissue regions. Magnification × 48. (b) Enlargement of the periderm shown in (a). Note the phellogen and the proportion of phellem to phelloderm. Magnification × 113. (c) Older stem of *Pelargonium* in which diametric growth has resulted in splitting of the periderm. Note also that some cells of the phelloderm have differentiated into sclereids. Magnification × 48.

Phellogen initials arise through **dedifferentiation** (i.e., the reversion to a meristematic state) of mature parenchyma cells followed by periclinal cell divisions. Following a division, the smaller of the two daughter cells usually becomes a phellogen initial, whereas the larger differentiates into either a phellem or a phelloderm cell. During its cell divisional activity, the phellogen typically produces larger quantities of phellem cells than phelloderm cells (Fig. 13.1b, c). In many woody plants of temperate regions, the phelloderm may consist of only one

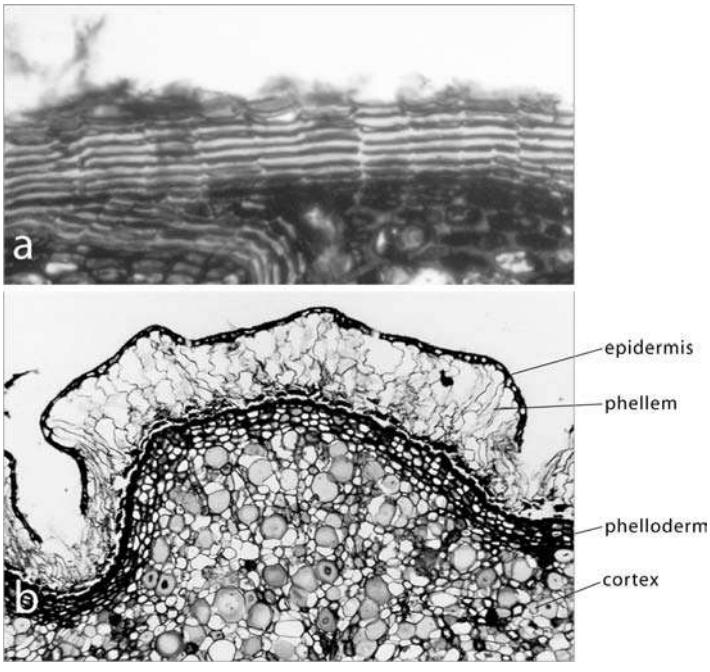

Figure 13.2 Transverse sections illustrating types of phellem. (a) Thick-walled phellem cells from a stem of *Quercus* sp. Magnification × 291. (b) Thin-walled phellem cells from a stem of *Abies* sp. Note also the several-layered phelloderm. Magnification × 47.

to several layers of cells (Figs 13.1b, 13.2) although in some tropical plants thick layers of phelloderm are produced. Since both phellem and phelloderm cells are direct descendants of phellogen initials that divide periclinally, they occur in well-defined radial files (Fig. 13.1), especially in the first-formed periderm(s). With increase in stem diameter and resulting anticlinal divisions of phellogen initials, new radial files, often of lenticular shape, are formed between the earlier formed files.

Phellem, formed to the exterior of the phellogen, is a compact tissue, consisting of cells similar in shape to the initials from which they are derived, non-living at functional maturity, and with no intercellular spaces except in lenticels. The secondary walls of phellem cells are heavily suberized, and thus relatively water impermeable. Consequently, tissues to the exterior of the phellem are destined to die.

Two distinct types of phellem cells, thick-walled and thin-walled, are recognized on the basis of their morphology and cell wall structure. A single type may characterize a species, or the two types may occur in alternate layers. This latter condition characterizes some species of *Picea*, *Tsuga*, and *Abies*. **Thick-walled phellem cells** (Fig. 13.2a) are radially narrower than the thin-walled type and are characterized by a three-layered wall, an outer primary wall that is frequently lignified, a middle secondary wall layer that is usually heavily suberized, and an inner layer, sometimes called a tertiary wall, that often becomes impregnated with waxes. Some evidence suggests that the phellem cells are not completely impermeable to water upon suberization of the secondary wall and that at least some of the plasmodesmata are still functional. Upon impregnation of the inner, tertiary wall with waxes,

the cell protoplast dies and the cell becomes fully impermeable. The lumina of thick-walled phellem cells commonly contain dark-staining resins and tannins that were translocated into the protoplasts prior to cell autolysis.

Thin-walled phellem cells (Fig. 13.2) typically have much greater radial dimensions than the thick-walled cells, usually have a thinner secondary wall, and lack the inner secondary (or tertiary) wall layer. The protoplast is transparent in slide preparations. Phellem of this type is desirable for use in making bottle corks. At functional maturity phellem cells in some species are known to have gas-filled lumina which, with the suberized and wax-impregnated walls, contribute to their impermeability to water. Whereas typical phellem cells have suberized walls, in some species layers of cells lacking suberized walls, called **phelloid cells**, alternate with layers of suberized cells.

Phelloderm, formed to the interior of the phellogen, consists of cells that retain living protoplasts, and that resemble cortical parenchyma cells. Like the latter, phelloderm cells in the first-formed periderm(s) are photosynthetic and contain chloroplasts and starch grains. As the phelloderm ages, some of its component cells may differentiate into sclereids (Fig. 13.1c).

In many non-woody plants, following loss of the epidermis, the periderm becomes the bounding tissue and functions both in restricting the entrance of pathogens and other small organisms as well as in reducing water loss. It serves these same functions in the young stems of woody plants prior to the formation of rhytidome. Following abscission of plant parts such as branches (in some plants such as *Populus*), leaves, and flower parts, periderm usually forms just beneath the abscission site (for more detail see Chapter 17 on the leaf). Wound sites are also underlain by periderm which develops following initiation of a phellogen through dedifferentiation in parenchyma cells below the wound.

Formation of rhytidome

In most woody species in temperate climates, the initial cylindrical periderm persists for only a few years, and is followed by the formation of a succession of **internal periderm** layers. These periderms, like the initial one, may be cylindrical, completely encircling the stem, and may be formed by phellogens that differentiate in the cortex immediately below the initial cylinder of periderm, or even in a layer of phelloderm of the initial periderm. If this is the pattern, a smooth bark will result, common in many tropical trees and some temperate zone trees such as *Fagus* (beech) and *Prunus* (cherry) (Fig. 13.3a). In many trees, however, the internal periderms are lens-shaped or shell-like, partially overlapping each other (Figs 13.4, 13.5). The internal phellogens from which they develop differentiate from parenchyma of the cortex to the interior of the initial periderm (Fig. 13.5), and ultimately in secondary phloem parenchyma. Whether internal periderms are cylindrical or shell-like,

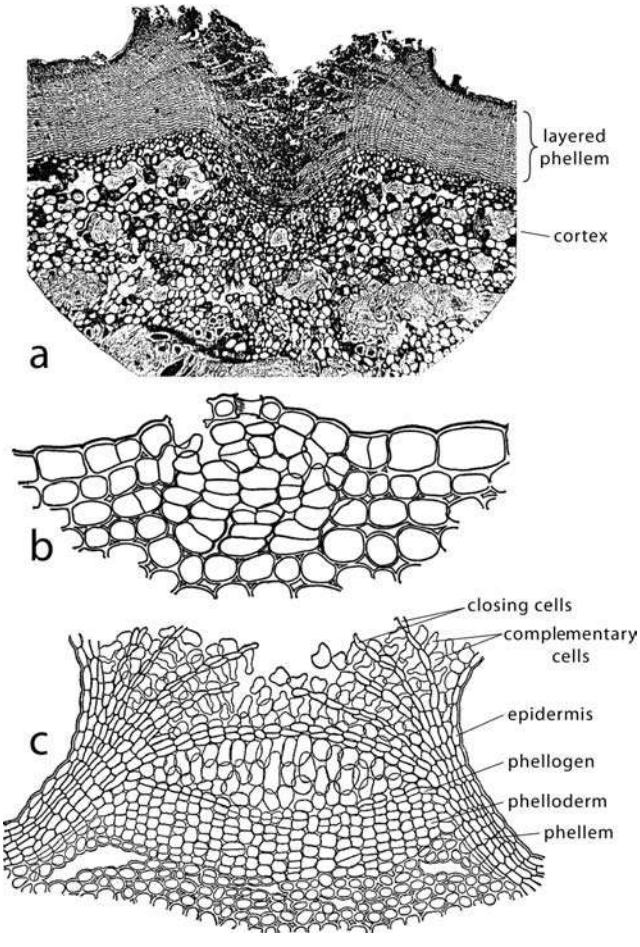

Figure 13.3 Lenticels.
(a) Transverse section showing a lenticel in sectional view from a stem of *Prunus serotina*.
(b) Drawing of an early stage in the development of a lenticel.
(c) Sectional view of a lenticel of *Prunus avium*. From Eames and MacDaniels (1925).

they initially enclose regions of cortical parenchyma. Ultimately, as they progress toward the inner tissues, they enclose primary and secondary phloem which, cut off from water and solutes, will die. This complex tissue region of periderms and enclosed non-living tissue is called **rhytidome**, and in most trees comprises the bulk of the bark (Fig. 13.4e).

At the same time that rhytidome is forming the vascular cambium is producing large quantities of secondary vascular tissues that result in an outward, diametric expansion of the stem. This results not only in the compression of the outer functional phloem, but also the splitting and furrowing in the surface layers of the rhytidome (Fig. 13.4e). The structure of the rhytidome and the abundance and arrangement of fibers in the enclosed secondary phloem directly influence the surface morphology of the bark, and provide the unique features of particular species such as the depth and direction of furrowing and the type of exfoliation. In some species, for example, *Betula* (birch), non-suberized layers of phelloid cells in the periderm function as **excision layers** that result in exfoliation of the bark. In some other species,

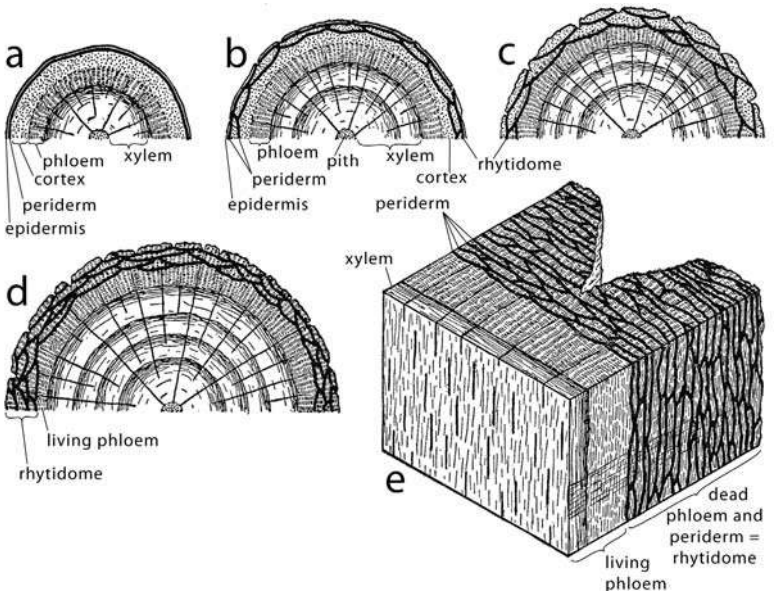

Figure 13.4 Diagrams illustrating the development and structure of rhytidome. See the text for a detailed description. From Eames and MacDaniels (1925).

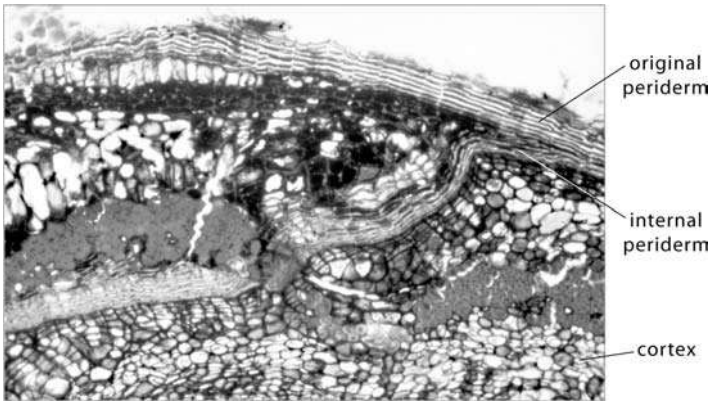

Figure 13.5 Early development of rhytidome in *Quercus* sp. oak as seen in transverse section. Magnification × 99.

e.g., *Platanus* (sycamore) specialized excision layers develop below layers of rhytidome. For more detail on the structure of bark, see Chattaway (1953, 1955), Chang (1954), Schneider (1955), Tomlinson (1961), Howard (1971, 1977), Borger and Kozlowski (1972), Patel (1975), Godkin *et al*. (1983), and Patel and Shand (1985).

Lenticels

Specialized regions of the periderm, called lenticels, allow for gaseous exchange between the outside atmosphere and the interior living tissues of the plant. A **lenticel** (Figs 13.1c, 13.3a, c) is a region consisting of loosely arranged cells, derived from the phellogen. As viewed on the surface of the bark, this structure, consisting of a tissue containing

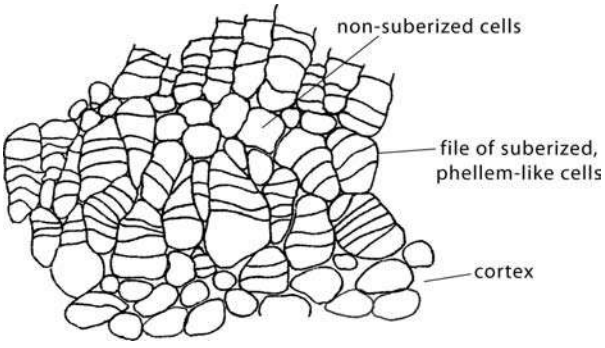

Figure 13.6 Drawing of the outer protective tissue of the monocotyledon *Curcuma longa* (Zingiberaceae) consisting of short, radial files of phellem-like cells. Each file is formed by a series of periclinal divisions originating in a cortical parenchyma cell. From Philipp (1923). Used by permission of E. Schweitzerbart'sche Verlagsbuchhandlung. http://www.schweizerbart.de.

many large intercellular spaces, is usually lenticular in shape (thus its name) with its long axis parallel to the long axis of the stem. As the stem enlarges through diametric growth, the lenticels expand laterally, and their long axes may become oriented at right angles to the long axis of the stem. The form and distribution of lenticels on the exterior of the bark and in the internal periderms is highly variable among diverse species.

Lenticels usually originate beneath large cauline stomata (Fig. 13.3b). In the region of the developing lenticels in woody plants, the phellogen functions differently than it does in other areas, producing parenchyma cells of two types, loosely arranged **complementary cells** and **closing cells** in tangential files interspersed among the complementary cells (Fig. 13.3a, c). As mentioned above, lenticels develop in the internal periderms as well as in the initial periderm. As a result, the system of intercellular spaces in the lenticels and the cortical parenchyma and/or phloem in the rhytidome provide conduits for essential gaseous exchange.

The outer protective layer of monocotyledons

Monocotyledons typically do not produce periderm. In the smaller, more herbaceous taxa, the epidermis may persist for the life of the plant, and the walls of outer cortical parenchyma cells may become suberized or thickened and sclerified, thus forming an outer protective covering. In a few taxa characterized by secondary growth, however, a more specialized outer protective tissue develops. Within the outer cortex, parenchyma cells become meristematic, and through their periclinal divisions as well as the divisions of their daughter cells, a tissue of radial files of cells is produced (Fig. 13.6). The cells of this tissue, like phellem cells, are non-living at maturity and have heavily suberized walls. In very large taxa, successive zones develop in a similar manner to the interior of the initial zone. In some taxa, non-suberized cells become trapped between zones of suberized cells (Philipp, 1923).

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Chapter 14

Unusual features of structure and development in stems and roots

Perspective

A large part of this book, thus far, has dealt with the typical condition in stems of gymnosperms and dicotyledons. This chapter will present interesting and important information about stem growth in monocotyledons as well as development and patterns of organization in lianas (vines) and other plants usually characterized as having "anomalous" structure. Unlike gymnosperms and dicotyledons, monocotyledons, even the largest taxa among the palms, do not produce a typical vascular cambium. Although most are characterized solely by primary growth, some palms, some members of the Liliaceae and Agavaceae, and a few other monocotyledons increase in size by secondary growth. The tissues derived from the secondary meristem are strikingly different from the secondary xylem and phloem of the gymnosperms and other angiosperms.

Primary peripheral thickening meristem

As in other plants, the activity of apical meristems of monocotyledons results primarily in an increase in length of the stems. The diameter of a palm stem does not vary greatly from the base to the most distal leaf-bearing region; thus considerable diametric growth must occur in the internodes just beneath the apical meristem, and this is accomplished by activity of the **primary peripheral thickening meristem**. This meristem is a rather diffuse region located in the periphery of the broad region of the stem immediately below the apical meristem. Its longitudinal extent varies in different species. Periclinal divisions in this meristem result in anticlinal files of cells that comprise cup-shaped regions of new ground tissue nearest the apical meristem and bowl-shaped to plate-shaped regions more basally, which result in the lateral expansion of the stem. Traversing this tissue are numerous provascular strands that will differentiate into axial bundles and leaf traces. The differentiation of cells in these tissues results in internodal expansion

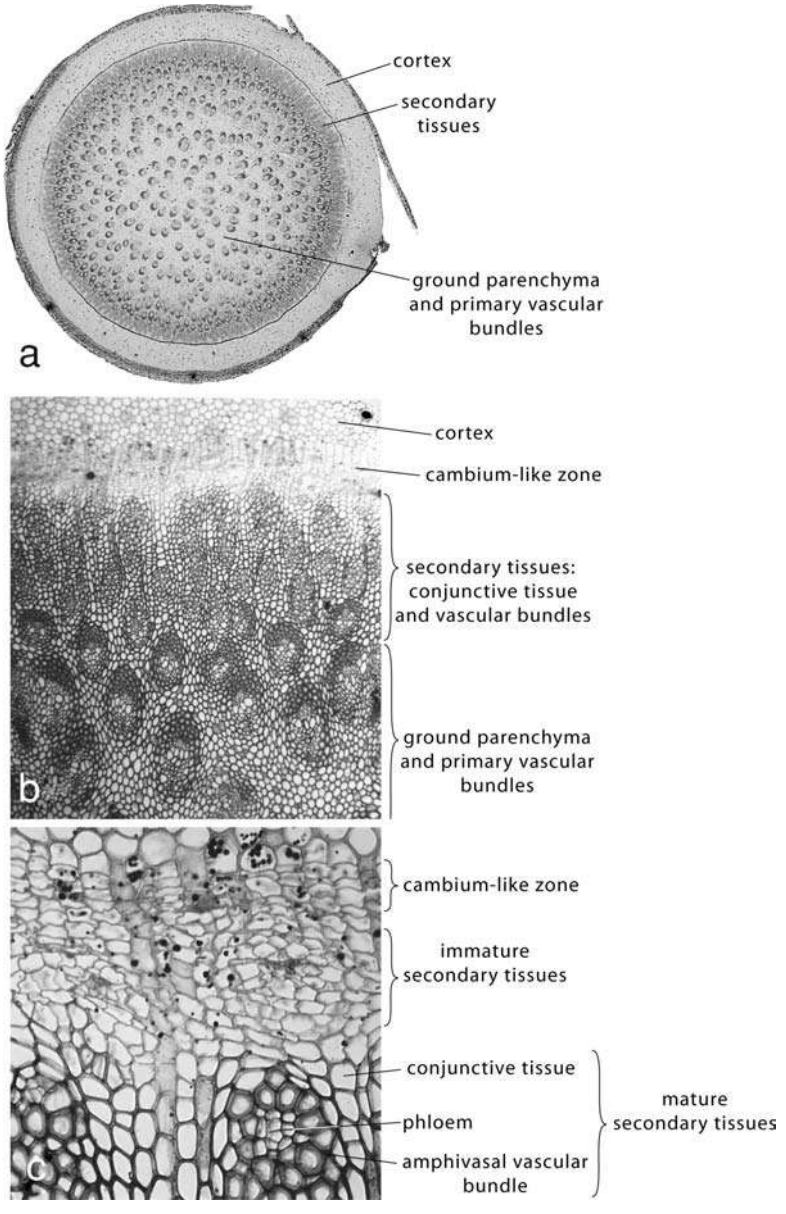

Figure 14.1 *Dracaena.* (a) Transverse section of a stem. Magnification × 3.8. (b) Transverse section showing secondary tissue to the exterior of primary tissues. Note also the cambial zone. Magnification × 41. (c) Englargement showing detail of the cambial zone, and immature and mature secondary tissues. Magnification × 165.

and elongation. (For more detail and illustrations, see Chapter 5 on meristems of the shoot.)

Secondary growth in monocotyledons

In some monocotyledons, especially in some members of the Liliaceae, the primary peripheral thickening meristem extends downward into a narrow cambium-like meristem, to the exterior of the primary vascular bundles. Activity of this meristem results in the formation of an unusual secondary tissue (Fig. 14.1b, c). As in gymnosperms and dicotyledons, secondary tissues in monocotyledons are produced only in regions that

have completed their longitudinal growth. Periclinal divisions in the cambium-like meristem result largely in secondary tissues being produced toward the inside of the stem. Only a very small amount of tissue, which will differentiate solely into parenchyma, is produced toward the outside. The cells produced to the interior of the meristem, arranged in radial files, differentiate into a ground parenchyma, often called **conjunctive tissue**. Embedded in this tissue are numerous collateral or amphivasal vascular bundles composed of tissues similar to those of primary vascular bundles. Usually these bundles contain only a very small quantity of phloem (Fig. 14.1c). The xylem contains no annular or helical tracheids, consisting primarily of scalariform and pitted tracheids. Whereas there seems to be no recent, definitive supporting evidence, several workers suggest that these bundles connect with axial bundles and leaf traces of the primary body.

In taxa that feature such secondary growth (for example, *Cordyline*, *Dracaena*, *Yucca*) the primary body is obconical, and without additional support from secondary tissues the stem would be unstable. Secondary tissues are thickest at the base of such stems and thinnest near the apex. Consequently, the two tissues result in a stem of similar diameter from base to apex (Fig. 14.2). Another strategy that results in the stabilization of obconical stems is the development of prop roots as in *Pandanus* (screw pine).

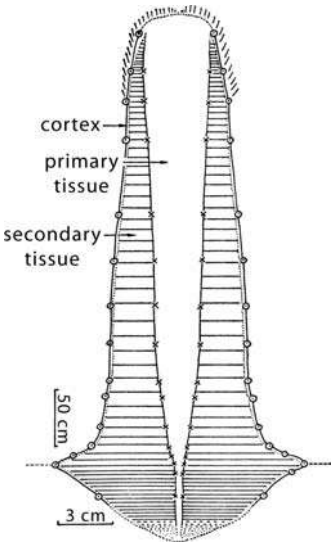

Figure 14.2 *Cordyline australis* (cabbage palm). Diagrammatic representation of a young stem in median longitudinal view showing distribution of primary and secondary tissues. Note the obconical form of the primary body. Secondary tissues are formed in quantities that result in a stem of approximately equal diameter throughout its length. Plotted from measurements on a specimen 4 m high. The longitudinal axis is foreshortened 16 times. The thickness of the cortex is arbitrary. From Tomlinson and Esler (1973). Used by permission of the Royal Society of New Zealand.

Anomalous stem and root structure

An unusual distribution of primary vascular bundles, especially the occurrence of cortical bundles in dicotyledons, irregularity in the activity of the vascular cambium, and the activity of several successively formed cambia in the same stem result in unusual stem structure, often referred to as being anomalous. Although these unusual patterns of development characterize some taxa in temperate regions, they are most common in lianas (vines) of tropical forests.

Whereas dicotyledons are typically characterized by a single cylinder of stem vascular bundles, in several taxa the bundles occur in more than one cylinder, or appear somewhat scattered as seen in transverse section. *Cucurbita*, for example, is characterized by an inner cylinder of large vascular bundles and an outer cylinder of smaller cortical bundles (Fig. 14.3a). The bundles in both cylinders are bicollateral with primary phloem occupying both outer and inner parts. The genus *Piper* of the Piperaceae also has an unusual arrangement of vascular bundles. In *Piper betle*, for example, there is a somewhat irregular cylinder of vascular bundles enclosing the pith and a system of much smaller cortical bundles to the exterior of an undulating cylinder of sclerenchyma (Fig. 14.4a). In some taxa, cortical bundles are leaf traces that extend over great longitudinal distances in the stem prior to entering the leaves. *Piper excelsum* (Fig. 14.4b, c) is also characterized by two cylinders of vascular bundles. Two primary vascular bundles, often referred to as **medullary bundles**, occupy the very center of the stem. These are enclosed by an irregular inner cylinder of similar bundles. Enclosing

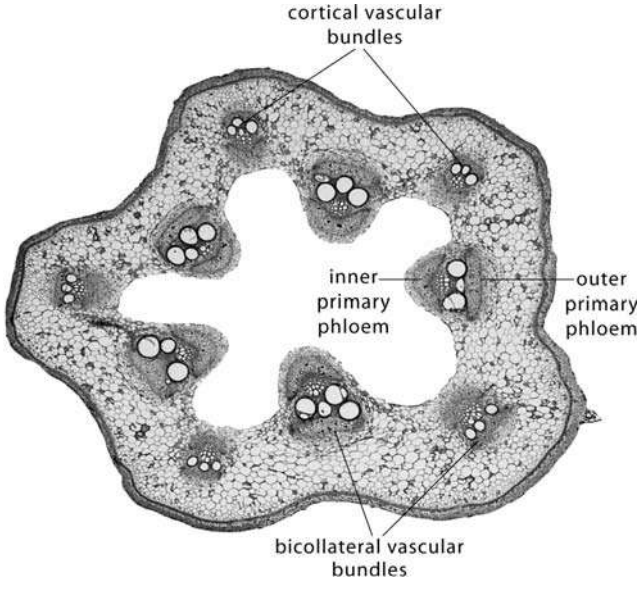

Figure 14.3 Transverse section of *Cucurbita*, a vine with inner and outer cylinders of primary bicollateral vascular bundles. Magnification × 6.

this cylinder is an outer cylinder of vascular bundles in which cambium develops (Fig. 14.4c). Cambial activity results in large, radially extended regions of secondary vascular tissues that are separated from each other by wide ray-like regions of primary parenchyma (often called **medullary rays**).

The structure of stems in several families (e.g., Amaranthaceae, Chenopodiaceae, Menispermaceae) results from the presence and activity of **accessory cambia**. Upon cessation of activity of an initial vascular cambium, additional cambia differentiate successively to the exterior in cortical tissue. Their activity results in a series of cylinders of secondary vascular tissues, separated by narrow cylinders of parenchyma. In *Chenopodium album* (lamb's quarters) (Fig. 14.5) a vascular cambium initially differentiates in individual vascular bundles arranged in a cylinder. Cambial activity results in the production of some secondary xylem and phloem and the consequent increase in their size. Upon cessation of cambial activity in these bundles a new vascular cambium, forming a continuous cylinder (Fig. 14.5a), differentiates to the exterior in cortical tissue. The activity of this cambium results in formation of a cylinder of secondary vascular tissues of unusual characteristics consisting of alternating bands of xylem, phloem, and secondary parenchyma (conjunctive tissue) (Fig. 14.5b).

Variation in the activity of the vascular cambium, either by the nature and quantity of the tissues produced by particular segments, or by variation in the frequency of cell division in different regions of the cambium, results in unusual distribution patterns of xylem and phloem, or even differently shaped stems, the exterior of which conform largely to the shape of the secondary xylem. Many tropical vines are characterized by anomalous stem structure, but such structure is not confined to them. A few examples will suffice.

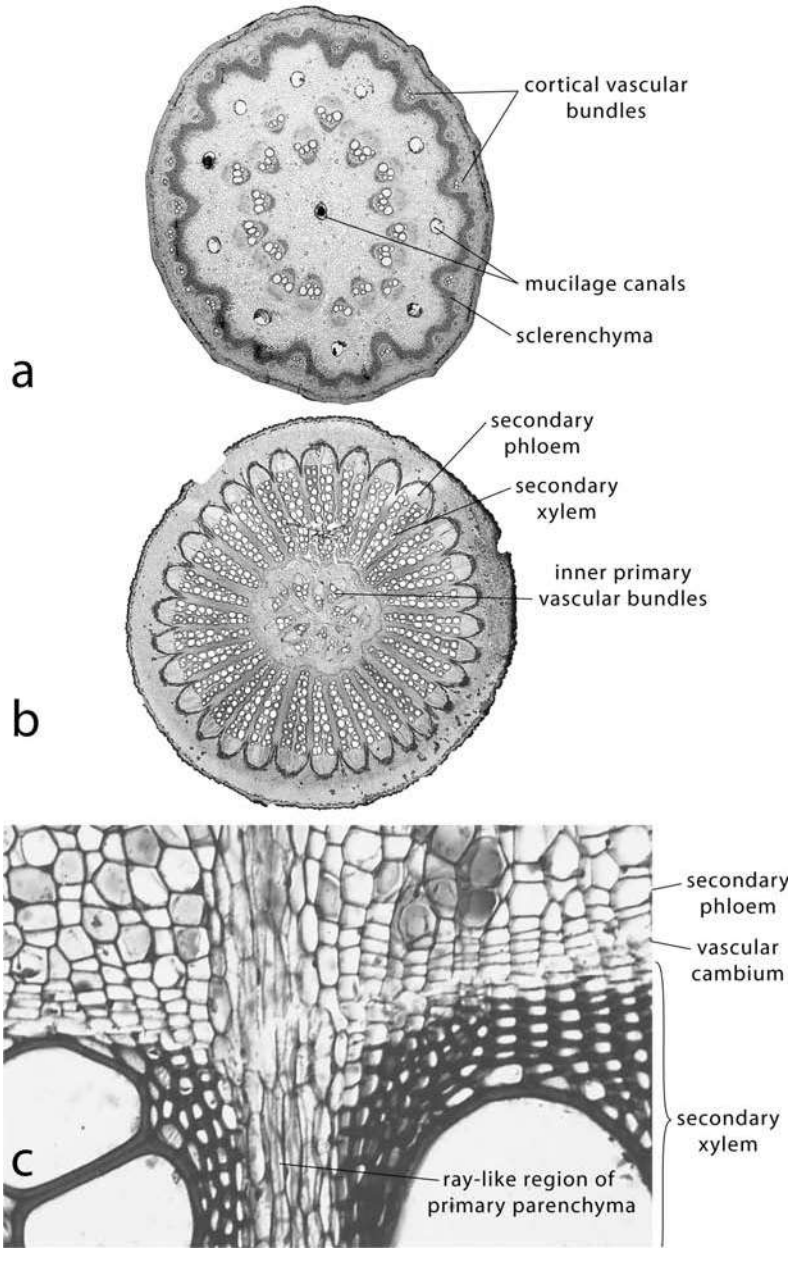

Figure 14.4 Variation in stem structure in two species of *Piper* (Piperaceae, pepper family). (a) Transverse section of a stem of *Piper betle*. The stem has an inner, irregular cylinder of primary vascular bundles, and an outer cylinder of smaller bundles to the exterior of an undulating wall of sclerenchyma. Note also the large mucilage ducts in the pith and inner cortex. Magnification × 8. (b) The stem of *Piper* sp. characterized by a central, irregularly arranged group of primary vascular bundles enclosed by a thick cylinder of secondary tissues consisting of regions of tracheary tissues capped by phloem. The secondary tracheary tissues are separated by ray-like regions of secondary parenchyma. Magnification × 3.3. (c) Detail of the vascular cambium and its derivative tissues from the stem shown in (b). Magnification × 180.

In some taxa, the vascular cambium produces, to the inside of itself, clusters or bundles of phloem which become embedded within the secondary xylem. This **intraxylary secondary phloem** is characteristic of several families, including the Apocynaceae and Asclepiadaceae. In several members of the tropical family Bignoniaceae, the vascular cambium produces, in different regions, largely secondary xylem or largely secondary phloem. Consequently the xylem cylinder becomes fluted (Fig. 14.6a). By contrast, in *Aristolochia*, a vine of temperate regions, certain segments of the vascular cambium produce only secondary

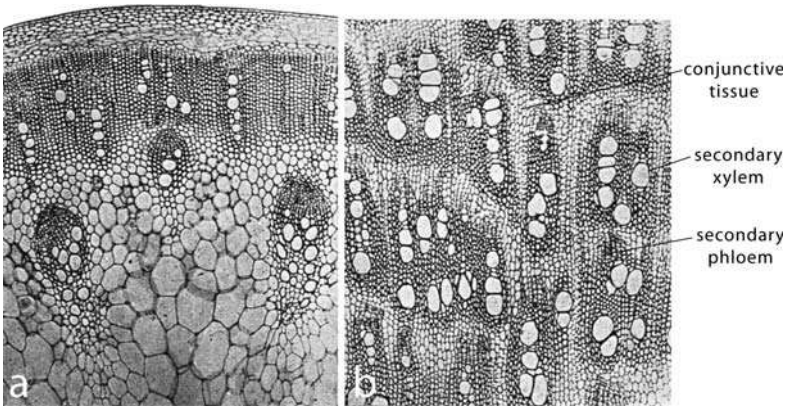

Figure 14.5 Transverse sections of *Chenopodium album*. (a) Part of a stem showing inner vascular bundles, consisting of both primary and secondary tissues, enclosed by a cylinder of secondary vascular tissues. (b) Part of the secondary cylinder in an older stem showing secondary xylem, conjunctive tissue, and patches of phloem. From Eames and MacDaniels (1925).

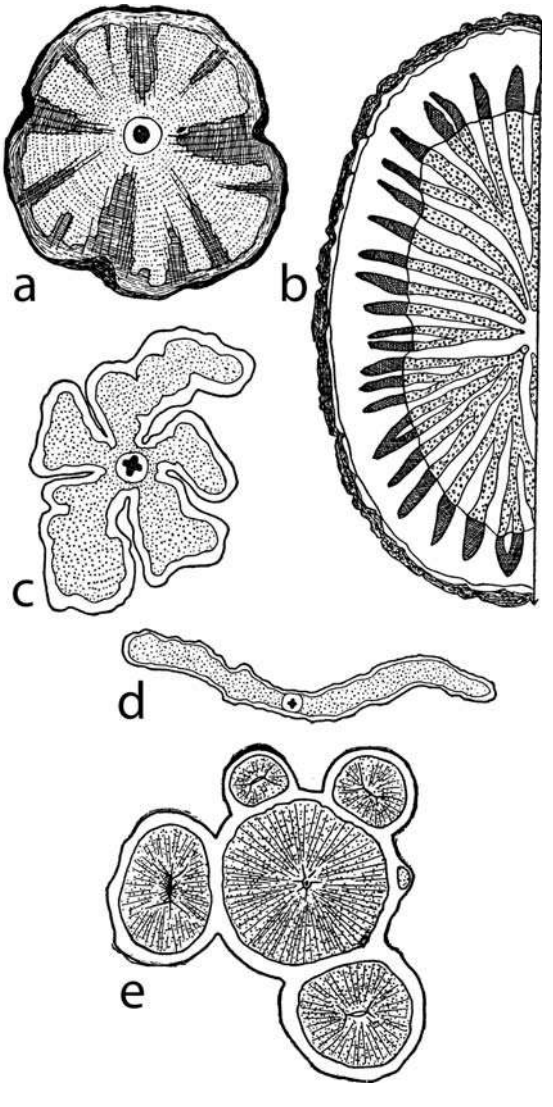

Figure 14.6 Diagrammatic representation of unusual ("anomalous") stem structure in several vines as viewed in transverse section. (a) A bignoniaceous species. (b) *Aristolochia triangularis*. (c) *Bauhinia rubiginosa*. (d) *Bauhinia* sp. (e) *Thinouia* (Sapindaceae). Please see the text for descriptions. From Schenk (1892–3).

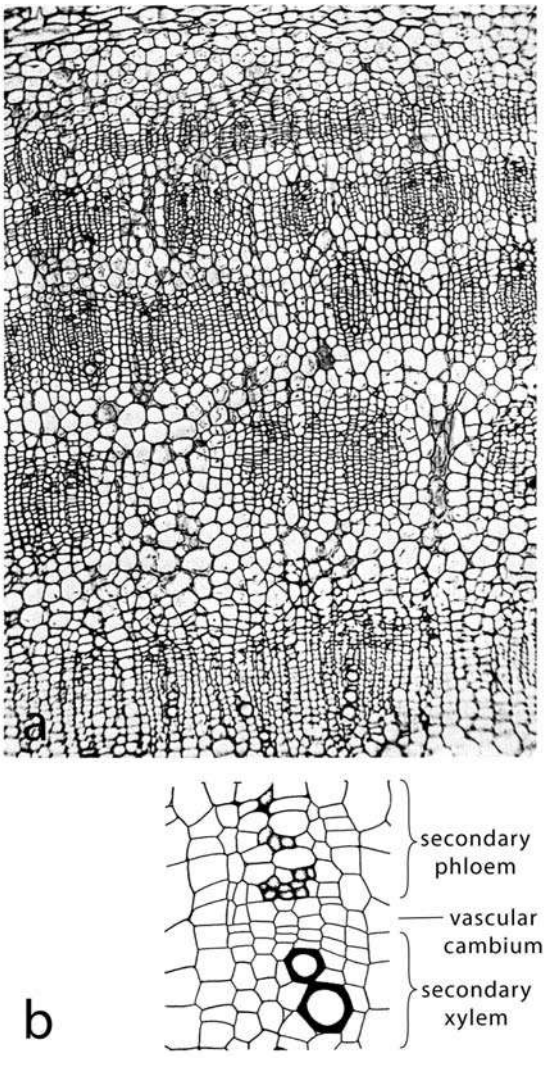

Figure 14.7 Transverse sections of *Beta* (sugar beet) root. (a) Cylinders of secondary vascular tissues, produced by a succession of accessory cambia, are separated by secondary storage parenchyma. Secondary xylem and secondary phloem are composed largely of parenchyma. Magnification × 58. (b) Drawing illustrating the sparse occurrence of vessels and sieve tubes in the xylem and phloem. (a, b) From Artschwager (1926).

parenchyma whereas others produce typical proportions of xylem and phloem. Thus, the vascular cylinder consists of alternating, radially extended regions of these tissue types (Fig. 14.6b). In *Bauhinia* of the Leguminosae (sometimes included in the Caesalpiniaceae), normal cambial activity in certain areas and the restriction of activity in others results in fluted or flattened stems (Fig. 14.6c, d). In *Thinouia* (Sapindaceae) in early stages of cambial development, some regions of the cambium become convoluted, pinch off, and produce separate cylinders of secondary vascular tissue resulting in a stem of **polystelic structure** (Fig. 14.6e).

Roots as well as stems may exhibit unusual patterns of structure and development. The common root vegetable *Beta vulgaris* (beet) provides an excellent example of the formation of accessory cambia in a root (Fig. 14.7a). Following cessation of activity of the initial cambium, a succession of cambia differentiate toward the exterior in pericyclic

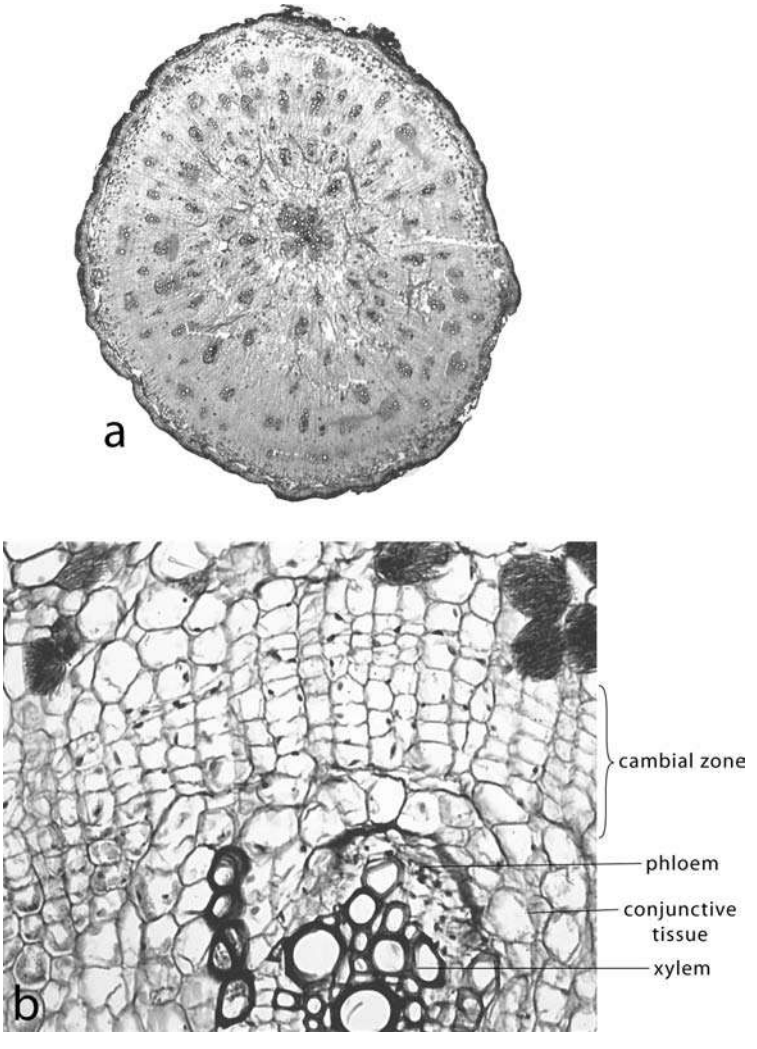

Figure 14.8 (a) A transverse section of *Boerhaavia* sp. root. The central actinostelic primary xylem column is enclosed in secondary tissue consisting of conjunctive parenchyma in which are embedded numerous vascular bundles. Magnification × 8. (b) Enlargement showing the cambial zone and part of a vascular bundle. Magnification × 216.

tissue. Each of these cambia produces, for a limited period, secondary xylem and phloem in bands of variable width, and intervening secondary parenchyma. Sieve tubes in the phloem occur in small clusters embedded in secondary phloem parenchyma. Sparsely scattered vessels occur singly or in small clusters, also enclosed in extensive secondary xylem parenchyma (Fig. 14.7b). Additional tissue is produced by cytokinesis within the pericycle to the exterior of each cylinder of secondary tissue. Consequently the beet root is composed of cylinders of highly parenchymatous secondary vascular tissues which alternate with cylinders of pericyclic parenchyma with the result that the predominant tissue of the beet root is **storage parenchyma**.

Accessory cambia characterize both stems and roots of *Boerhaavia* of the Nyctaginaceae. Following cessation of activity in the initial cambium in roots of *Boerhaavia diffusa* (Fig. 14.8a), additional cambia differentiate to the exterior, producing small vascular bundles and

intervening conjunctive tissue to the inside and secondary parenchyma to the outside. Each new cambium (Fig. 14.8b) differentiates in the secondary parenchyma produced by the previously active cambium.

For additional information about other interesting and often bizarre stem and root structure, see sections on Bignoniaceae, Apocynaceae, Amaranthaceae, Chenopodiaceae, Asclepiadaceae, Loganiaceae, Menispermaceae, Nyctaginaceae, Caesalpiniaceae, Acanthaceae, and Sapindaceae in Metcalfe and Chalk (1950).

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Chapter 15

Secretion in plants

Perspective

Waste products in animals are excreted to the exterior through the digestive system, the urinary system, and, to a lesser extent, through sweat glands. By contrast, in the plant, waste products of metabolism as well as substances that will be further utilized are stored within individual cells or transferred to regions of living or non-living tissues or into cavities and ducts within the organism. A good example is the transfer of waste metabolites into the secondary wood (with the consequent formation of heartwood) where they are isolated from the functional regions of the plant body. The transfer of metabolites from one site to another is referred to as secretion rather than excretion although some substances are transferred to the plant surface, such as precursor compounds of cutin and waxes and a variety of substances that exit the plant through glands and glandular hairs. This concept of secretion also includes the transfer of substances within single cells such as, for example, the movement of enzymes to chloroplasts, sites of photosynthesis, and the transport in vesicles of precursors of cellulose to sites of wall synthesis. We can, thus, define **secretion in plants** as the transfer of certain intermediate or end products of metabolism from one region to another within the cell or out of the protoplast to another part of the plant body.

Substances secreted by plants

Both metabolic and non-metabolic substances are transferred within or to the exterior of the plant body. **Metabolic compounds** are those that will have a continuing function in the plant such as RNA that is transferred from the nucleus to the ribosomes, enzymes as well as precursor compounds of cellulose and/or lignin that are transferred to the region of the developing cell wall, hormones that are transferred from meristematic parenchyma into sieve tubes and through them to various parts of the organ or organism, and photosynthates transferred from

mesophyll parenchyma to more interior storage parenchyma cells, or by way of companion cells into sieve tube members, among others. Although fitting the concept of secretion as defined, the transfer of photosynthates into and out of the phloem is more commonly referred to as assimilate loading and unloading.

Whereas **non-metabolic compounds** may not be further functional in the plant, they may have important adaptive value to the species. Such compounds are the essential oils, including terpenes, which provide flower fragrance and attract pollinators, alkaloids that are highly poisonous which prevent predation by herbivores (ironically *Homo sapiens* is attracted by certain alkaloids such as nicotine, caffeine, cocaine, etc.), glycosides which, on being acted upon by enzymes, release pungent odors (as in cabbage and other Cruciferae) that repel many insects, tannins and resins that may impede fungal invasion of wood, calcium oxalate crystals that make plants unpalatable to grazers, certain alcohols that accumulate in glandular hairs such as those of stinging nettle which also inhibit predation, some flavonoid pigments which, in leaves, block ultraviolet radiation that destroys nucleic acids and proteins but which admit blue-green and red light utilized in photosynthesis, and others (e.g., Thomas, 1991; Duke, 1994; Fahn, 2000).

Mechanisms of secretion

Two primary mechanisms of secretion have been recognized (Esau, 1977). **Granulocrinous** (or **granulocrine**) **secretion** is effected by the fusion of Golgi or ER vesicles with the plasma membrane or tonoplast resulting in the transfer of substances in the vesicles to the exterior of the plasma membrane or from them into the vacuole. A good example is the granulocrinous transfer of precursor compounds of cellulose into the region of cell wall formation. In many glands, compounds that have passed through the plasma membrane of cells continue to the exterior through the tangential walls. They are prevented from diffusing back into the plant through the wall apoplast by the presence, in radial and transverse walls, of cutinized regions resembling the Casparian bands of endodermal cells. If the compounds accumulate in subepidermal or subcuticular chambers, they usually reach the exterior through epidermal pores (sometimes, modified stomata), or by disintegration of the cuticle.

Passage of small molecules directly through the plasma membrane and wall is called **eccrinous** (or **eccrine**) **secretion**. This movement of substances can be either passive, along concentration gradients, or active, utilizing energy in the process. Examples of eccrinous secretion are the transport of water-soluble compounds such as salts and sugars from the symplast through the cell wall apoplast, sometimes directly to the exterior as in salt glands and nectaries. In such cases the cells from which these compounds enter the cell wall are transfer cells. **Transfer cells** are widely distributed in the plant at sites of rapid flux of solutes such as between the mesophyll in leaves and sieve tube members, at

transfer interfaces such as that between embryo and endosperm in seeds, and in secretory structures, especially in glands of various types. The secondary wall of transfer cells is characterized by extensive, complex ingrowths that greatly increase the wall surface area. Such wall structure is often called a **wall labyrinth**. Since the plasma membrane covers the inner surface of the wall, the area for transfer, that is, secretion through it, is greatly increased, sometimes by as much as 20 times that of cells in which there are no wall ingrowths. Substances may also be released to the exterior from glandular trichomes or other secretory structures by disintegration of the gland or secretory tissue, or its destruction by insects. Such release of compounds is called **holocrine secretion**.

Internal secretory structures

Within the plant, various substances are transported into individual cells as well as into cavities and ducts of several types. **Idioblasts** are single, isolated, and specialized secretory cells that are common within parenchyma tissue and contain distinctive substances such as mucilage, tannin (Fig. 15.1a), oils (Fig. 15.1b), and calcium oxylate (usually in crystalline form). **Mucilage cells** that occur in the secondary phloem of some plants often also contain a bundle of **raphides**, needle-like crystals composed of calcium oxylate, as in *Hydrangea paniculata*. Single large crystals (Fig. 15.1c) as well as spherical aggregates of crystals of calcium oxylate, called **druses** (Fig. 15.1d), are also common components of idioblasts in many taxa. **Lithocysts** characterize the epidermis of several genera of the Moraceae. The lithocysts of *Ficus elastica* (Fig. 15.1e) are cells that occur in the upper, multiple epidermis of the leaves. Each contains a large calcium carbonate crystalline structure called a **cystolith** attached to the cell wall by a cellulose stalk which originated as a wall ingrowth. Although lithocysts are most common in the upper epidermis of leaves they also occur in both the upper and lower epidermis in some members of the family.

Many plants contain **schizogenous ducts** or **cavities** (e.g., Curtis and Lersten, 1990; Turner *et al*., 1998), formed by the separation of cells from each other during development (Fig. 15.2). The resultant cavity becomes bounded by a layer of **secretory cells** (sometimes called **epithelial cells**). These cells secrete various substances (either eccrinously or granulocrinously) into the cavities formed, such as mucilage in certain members of Malvaceae, Tiliaceae, and Sterculiaceae; oils as in Hypericaceae (Fig. 15.2a–c) in which the secretory cavities occur in the leaves of all genera, appearing, macroscopically, as opaque or translucent dots; and resins or gums as in many conifers as well as in several families of angiosperms (e.g., Anacardiaceae). Whereas in some species a single substance may characterize the contents in ducts and cavities, in others there may be a mixture of substances as, for example, in the Umbelliferae in which secretory canals (sometimes called resin canals) contain oils, resins, and mucilage.

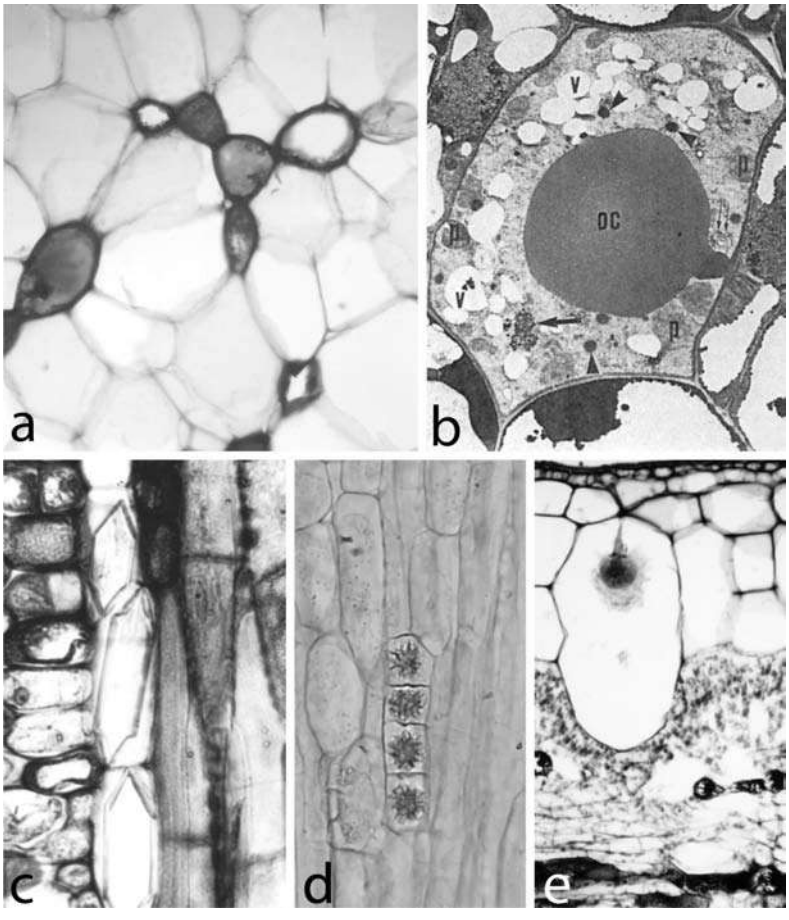

Figure 15.1 Internal secretory cells (idioblasts). (a) Cells containing tannin in the pith of *Tilia americana*. Magnification × 300. (b) An oil idioblast in a leaf of *Annona muricata*. Magnification × 1950. (c) Axial parenchyma cells in the secondary phloem of *Tilia americana* containing large, prismatic crystals of calcium oxylate. Magnification × 482. (d) Druses, spherical aggregates of small crystals of calcium oxylate. Magnification × 165. (e) A lithocyst containing a cystolith in the multiple epidermis of *Ficus elastica* (rubber plant). The cystolith consists of a crystalline structure of calcium carbonate attached to the cell wall by a cellulose stalk that originated as an ingrowth of the wall. Magnification × 174. (b) From Bakker and Gerritsen (1990). Used by permission of Oxford University Press.

Resin ducts of conifers (Fig. 15.2d) are by far the best known schizogenous secretory ducts. They form an extensive system in the secondary xylem, extending longitudinally as well as radially (through vascular rays). (For more detail and illustrations, see Chapter 11 on secondary xylem.)

In contrast to schizogenous ducts and cavities, **lysigenous ducts and cavities** (Fig. 15.2e) are thought to develop by the lysis of cell protoplasts and dissolution of the cell walls. Consequently, the contents of the cavities and ducts thus formed are derived directly from the lysed cells. The lysigenous cavities of citrus fruits, which contain essential oils among other substances, provide a good example. Although the concept of lysigeny has been widely accepted since early in the last century, Turner *et al*. (1998) have recently concluded that supposed lysigeny in the development of oil glands in *Citrus limon* (lemon) results from an artifact of fixation. They believe that the swelling of epithelial cells in hypotonic fixatives has led workers to interpret this as an indication of "early senescence" and, thus, lysigeny in *Citrus* glands.

Laticifers, which contain latex, differ greatly in development from both schizogenous and lysigenous ducts. Two types, articulated and

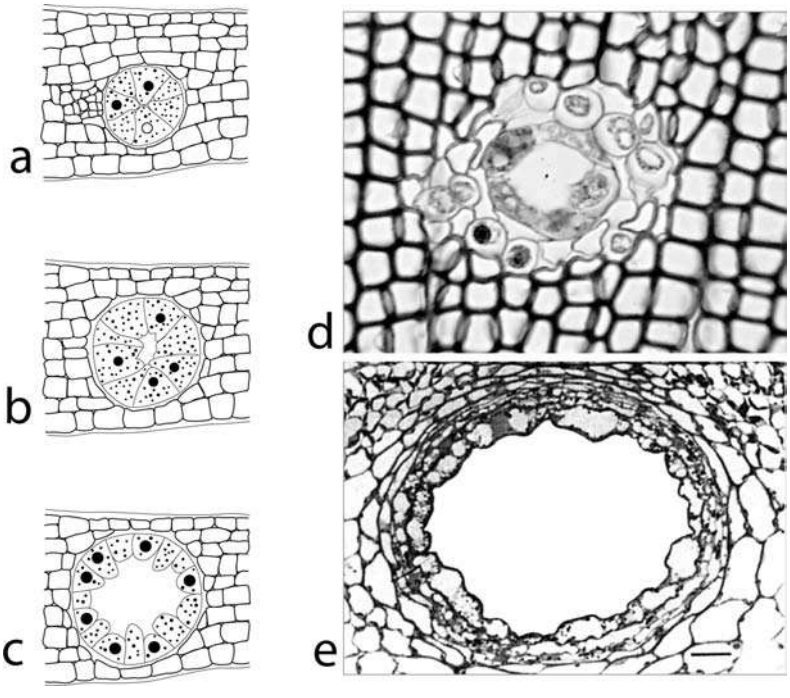

Figure 15.2 Schizogenous ducts and cavities. (a–c) Three stages in the development of a schizogenous oil cavity in the leaf of *Hypericum* sp. Note the beginning of separation of cells in (b). Cell divisions in the incipient secretory cells in (b) resulted in a more extensive single-layered epithelium in the nearly mature cavity in (c). (d) Transverse section of a schizogenous resin duct in the secondary xylem of *Pinus strobus*. Note the single, inner layer of epithelial cells and the thicker-walled parenchyma cells enclosing the duct. Magnification × 246. (e) An oil cavity in *Citrus limon* (lemon) often considered to have lysigenous development, i.e., to be formed by autolysis of the secretory cells which, as a result, release their contents into the cavity that forms. Recent research (Turner *et al.*, 1998) indicates that development of the oil cavities of *Citrus* as well as those of other taxa may actually be schizogenous having been incorrectly interpreted in the past. See the text for more detail. Bar = 20 μm. (e) From Turner *et al.* (1998). Used by permission of the University of Chicago Press.

non-articulated laticifers, are recognized on the basis of their development. **Non-articulated laticifers** (Fig. 15.3a, b) are found in many members of the Euphorbiaceae, Asclepiadaceae, and Apocynaceae among other families. They originate in the embryo from single-celled laticifer primordia and, as development of the plant proceeds, the primordia grow longitudinally and symplastically with some apical intrusion and, often, extensive branching (Mahlberg, 1961). Nuclei divide repeatedly but without accompanying cytokinesis and cell wall formation (Mahlberg and Sabharwal, 1967). The result is a coenocytic system that extends throughout the primary body of the plant, and in some cases into the secondary body as well.

Articulated laticifers (Fig. 15.3c, d) characterize members of the Euphorbiaceae (e.g., *Hevea*, rubber tree); Compositae (e.g., dandelion); Papaveraceae (e.g., poppy), etc. They originate in the apical meristem as

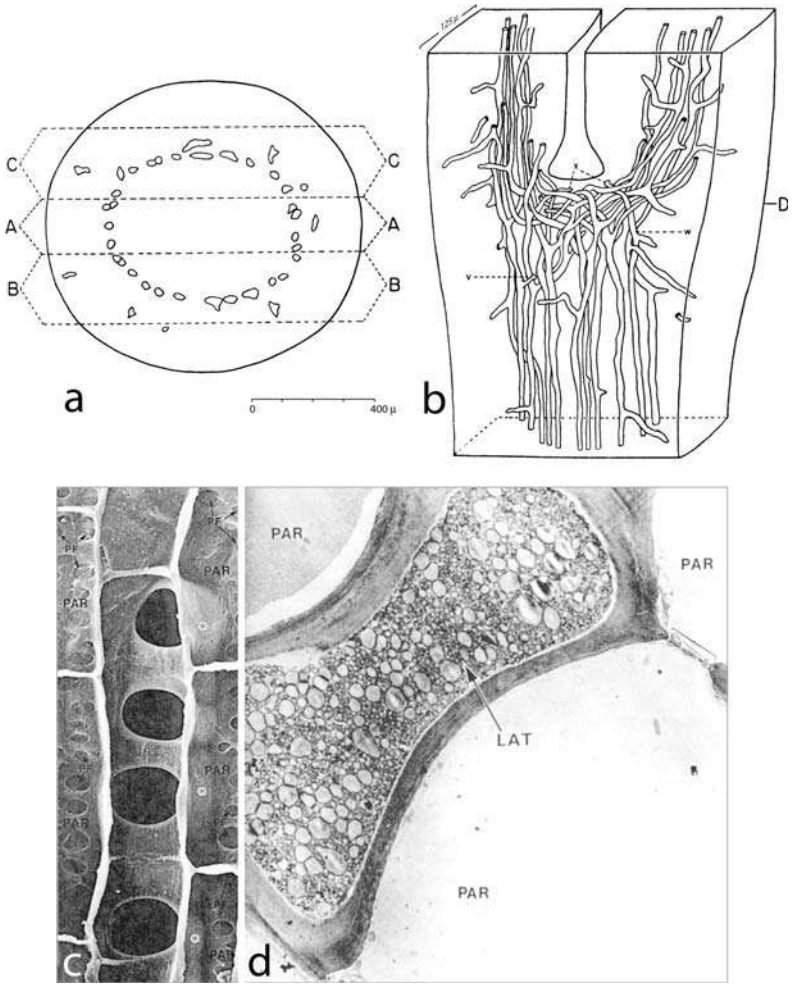

Figure 15.3 (a, b) Non-articulated laticifers in an embryo of *Nerium oleander* (Apocynaceae). (a) Drawing of a transverse section at the cotyledonary node indicated in (b) as D. (b) Three-dimensional drawing of a thick, longitudinal section indicated in (a) as B-B showing the complex system of laticifers. (c, d) Articulated laticifers in *Hevea brasiliensis* (rubber tree). (c) Scanning electron micrograph of an articulated laticifer and associated axial parenchyma cells (PAR) in the secondary phloem as seen in longitudinal section. Note the large perforations between this and a contiguous laticifer. The contents of this laticifer have been removed. PF, primary pit field. Magnification × 504. (d) Electron micrograph of a transverse section showing the thick, non-lignified primary cell wall and the cell contents, including numerous vesicles (lutoids) which contain polyterpenes and other compounds. LAT, laticifer. Magnification × 2584. (a, b) From Mahlberg (1961). Used by permission of the Botanical Society of America. (c, d) From de Faÿ *et al.* (1989). Used by permission of Springer-Verlag Wien.

single cells. As growth proceeds they increase in length acropetally by the addition of new cells without intrusive growth. As cells mature in the developing articulated laticifer, the end walls between longitudinally superposed cells are absorbed resulting in a coenocyte which may be much branched (see Esau, 1975). Thus, mature non-articulated and

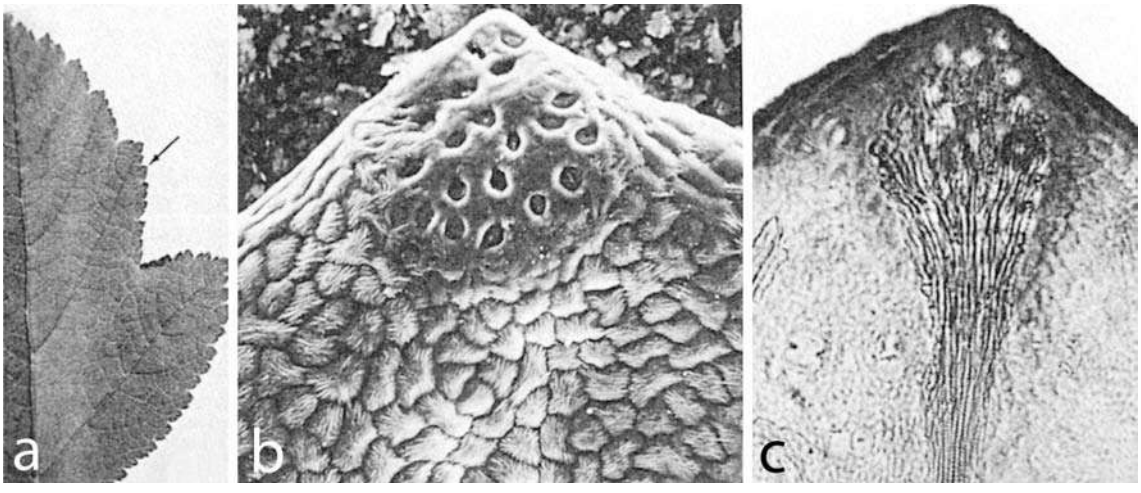

Figure 15.4 Hydathodes from the marginal teeth of a leaf of *Physocarpus opulifolius*. (a) Leaf showing location of the hydathode in (b) at arrow. Life size. (b) Scanning electron micrograph illustrating numerous water pores on the adaxial surface of a hydathode. Magnification × 200. (c) Hydathode from a cleared leaf showing the relationship between the water pores (light circular areas) and the tracheary tissue. Magnification × 140. From Lersten and Curtis (1982). Used by permission of the National Research Council of Canada.

articulated laticifers have a similar appearance, and both comprise a system of slender, branched or unbranched, tubes although they differ greatly in ontogeny.

Laticifers have non-lignified, primary walls, and contain latex, the composition of which may vary greatly in different species. The color of the latex varies from clear to white, brown, yellow, and orange. Polyterpenes are common constituents which, with other components, occur in small vesicles. In rubber-producing plants (e.g., *Hevea brasiliensis* and *Ficus elastica*) these vesicles are called **lutoids** (Fig. 15.3d). The vesicles may ultimately fuse forming a large vacuole. In addition to polyterpenes, laticifers may also contain alkaloids (as, for example, in *Papaver somniferum*, opium poppy), sugars, proteins, enzymes, starch grains, etc.

External secretory structures

External secretory structures occur in many forms, ranging from simple hydathodes and glandular hairs to complex salt glands and nectaries, among others. **Hydathodes** are modified stomata and associated tissues through which excess water is released from the plant through a process called **guttation**. This occurs when transpiration is low and root pressure is high. Although somewhat variable in structure, a typical hydathode (Fig. 15.4) which is located at the leaf margin (Fig. 15.4a), consists of parenchyma tissue, lacking chlorophyll, termed **epithem**, located between the end of a vein and the external pore (or pores) (Fig. 15.4b, c). The parenchyma (epithem), in contact with the substomatal chamber, unlike that associated with the substomatal chambers of typical stomata, is wettable, thus facilitating the passage of water to the exterior. The movement of water through the epithem may either be passive, the result of root pressure, or the result of active transfer, utilizing energy. In the latter case the epithem cells may function as, and have the structure of, transfer cells. The number of pores (Fig. 15.4b)

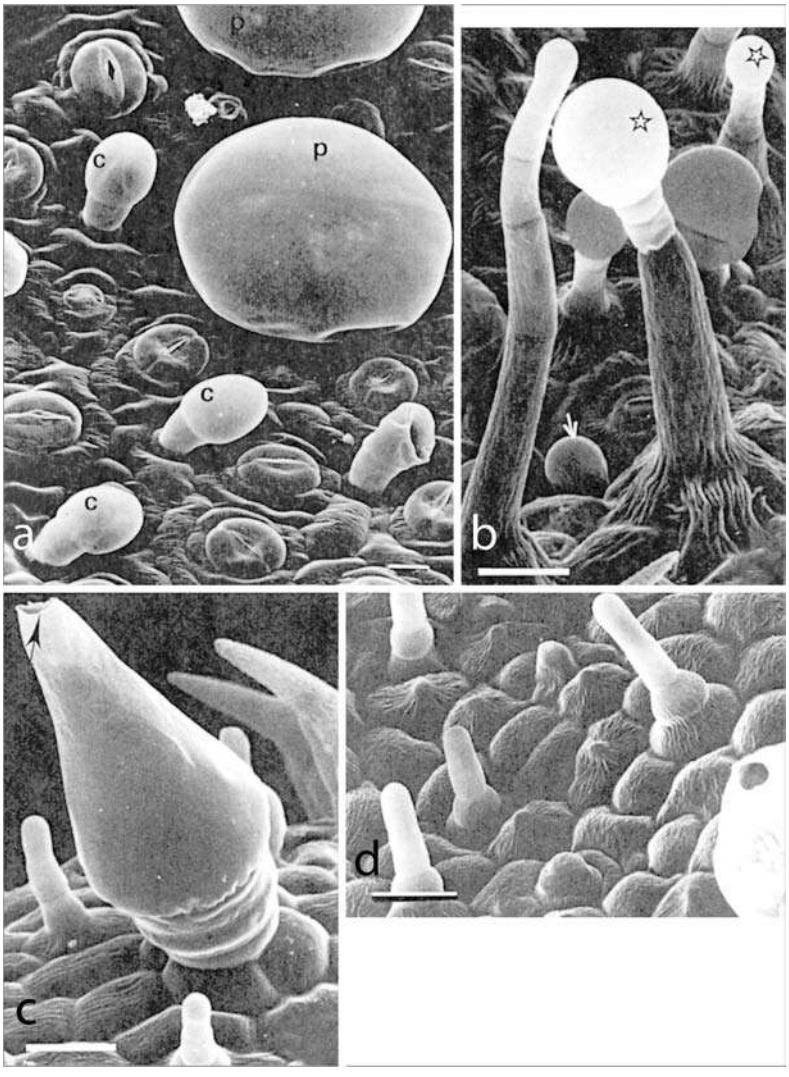

Figure 15.5 Glandular trichomes. (a) Peltate (p) and capitate (c) trichomes from the abaxial surface of a leaf of *Mentha* (mint). Bar = 10 μm. (b–d) Capitate trichomes from *Plectranthus ornatus*. (b) Long-stalked capitate trichomes. Arrow indicates short-stalked capitate trichome; stars indicate long-stalked capitate trichomes. (c) A conoidal trichome consisting of a large conical, glandular cell and a bicellular stalk. Arrow indicates apical pore. (d) Digitiform trichomes of three to four cells. Bars (b–d) = 25 μm. (a) From Colson *et al.* (1993). Used by permission of the National Research Council of Canada. (b–d) From Ascensão *et al.* (1999). Used by permission of Oxford University Press.

in a hydathode varies from one to many. Some hydathodes, especially those located at the tips of teeth on leaf margins, may consist simply of a single modified stoma without associated epithem.

It has been estimated that 20–30% of vascular plant species contain **glandular trichomes** on their aerial surfaces (Fahn, 1988; Duke, 1994). Although these trichomes are of diverse morphology (Fig. 15.5a–d), the glands, with few exceptions, are characterized by a globular appearance resulting from the separation of the cuticle from the walls of the secretory cells and the filling of the subcuticular space by chemical compounds produced by these cells (Duke and Paul, 1993; Duke, 1994; Bourett *et al.*, 1994). Perhaps the most common type is the **peltate trichome** (Fig. 15.6a–d), consisting of a stalk one or more cells long bearing an expanded gland of several cells. Among the compounds produced by plants, terpenoids and their derivatives are among the most

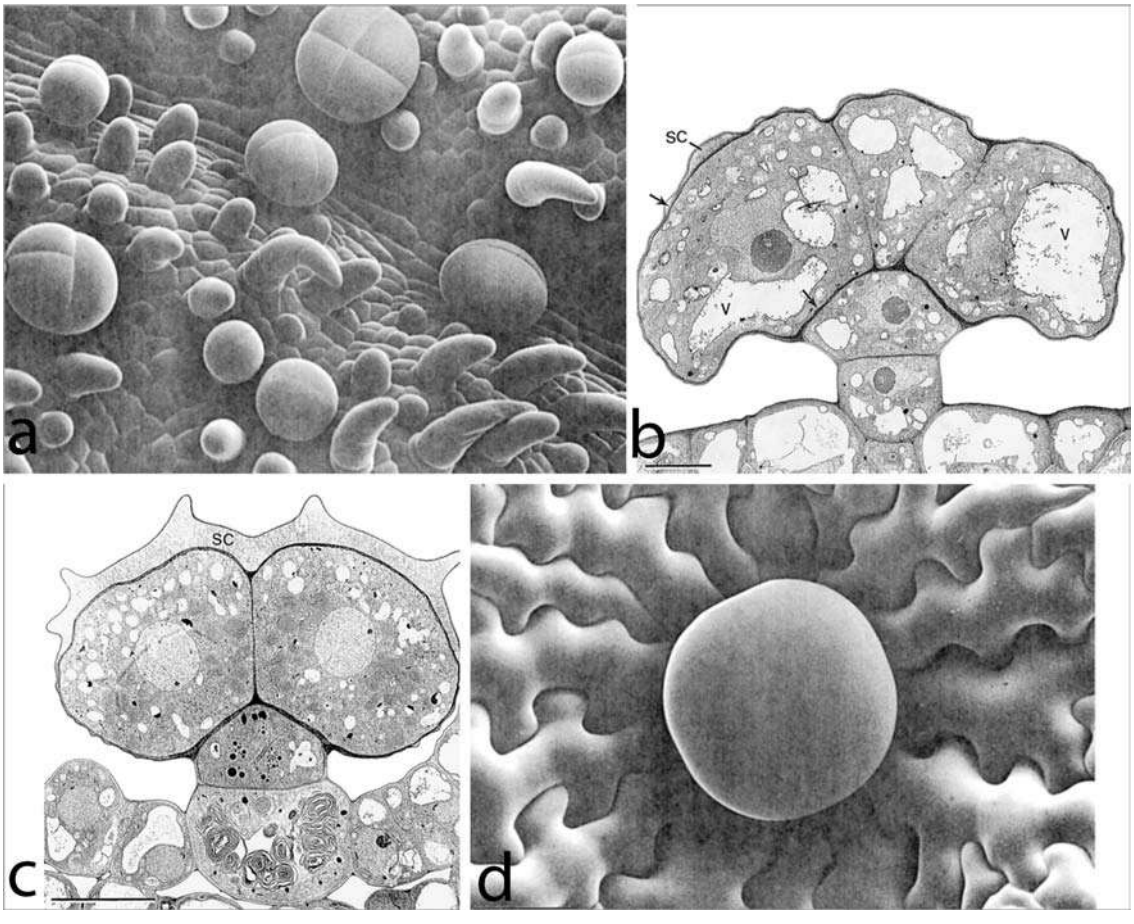

Figure 15.6 Peltate glandular trichomes of *Nepeta racemosa* (catmint). (a) Young peltate glands with two, three, or four secretory cells representing stages in development. These glandular trichomes are scattered among immature, non-glandular hairs. Bar = 25 μm. (b) Transmission electron micrograph of a sectional view of a peltate gland. The cuticle is pulled slightly away from the cell wall but there is very little material within the subcuticular cavity (sc). Secretory cells contain large vacuoles (v). Arrows indicate electron-opaque cell wall. Bar = 5 μm. (c) A sectional view of a peltate gland at a more mature stage with a somewhat distended cuticle and a large quantity of material in the subcuticular cavity. Bar = 10 μm. (d) A mature peltate gland with a fully extended cuticle which obscures the sutures between secretory cells. Bar = 25 μm. From Bourett *et al.* (1994). Used by permission of the University of Chicago Press.

common in glandular trichomes. Some are highly toxic whereas others provide the flavors of spices such as oregano and of essential oils such as mint, lavender, and sweet basil. Others form the basis for fragrances in perfumes (e.g., Werker *et al.*, 1993; Bourett *et al.*, 1994; Ascensão *et al.*, 1999).

Glandular trichomes are abundant on the surfaces of young leaf primordia and develop very early (Werker *et al.*, 1993; Bourett *et al.*,

1994). By leaking from the glands, their contents are apparently spread over the surface of the primordia, protecting them from insect damage by various biological effects, among which are insecticidal, repellent, and behavior-modifying effects as well as feeding deterrents (Duke, 1994). In addition, the young regions of some plants become coated with resinous materials, derived from glandular hairs, in which insects may become entrapped. Such coatings are also thought to reduce solar heating or water loss through evaporation (Duke, 1994). Glandular trichomes that produce resinous and other sticky compounds are called **colleters**. They are common on the young leaves and flower parts of many species of woody dicotyledons in a large number of families. Some are of complex structure, even containing laticifers and vascular tissue (Thomas, 1991).

Glandular hairs may also contain potent insecticidal phytotoxins. For example, artemisinin, a sesquiterpenoid compound, produced by *Artemisia annua*, is highly toxic to the plant that produces it as well as to other plant species. Because it is sequestered in the subcuticular space in the glands, however, *Artemisia* is protected from its toxic effects. Artemisinin and other toxic substances produced in glandular trichomes probably function as a defense against insects and microbial pathogens (Duke, 1994). It is interesting to note, that artemisinin is also an important antimalarial drug, effective against *Plasmodium falciparum* strains that have become resistant to more commonly used drugs.

An especially interesting and important role of chemical substances produced in glandular trichomes is **allelopathy**, the inhibition of one plant species by chemicals produced by another. The phytotoxin 1,8-cineole (a monoterpene) produced by species of *Salvia* (Kelsey *et al*., 1984), is thought to inhibit competitors by volatilization from the ground litter (Muller and Muller, 1964; Duke, 1994).

We shall consider in detail the structure of several types of glandular hairs including those of *Nepeta racemosa* (catmint), *Cannabis sativa* (hemp, marijuana), and the stinging hairs of *Urtica dioica* (stinging nettle).

The peltate oil glands of *Nepeta* (Fig. 15.6a–d), typically borne on the abaxial surface of the leaves, consist of a short stalk, composed of a basal cell located within the epidermis and a single stalk cell upon which rests a cluster of four secretory cells, covered by a cuticle (Fig. 15.6b) (Bourett *et al*., 1994). The aromatic oil is synthesized within these cells and transferred granulocrinously to the exterior, expanding the cuticle (Fig. 15.6c). Upon complete expansion of the cuticle in mature glands, the sutures between the four secretory cells disappear (Fig. 15.6d).

The glandular trichome of *Cannabis sativa* is very similar in external appearance to that of the peltate glands of other taxa, but differs strikingly in that the secretory cavity of the mature gland is bounded by both a cuticle and a subcuticular wall (Fig. 15.7a–d) (Kim and Mahlberg, 1991; Mahlberg and Kim, 1991). During early stages of secretory cavity development, the outer walls of the secretory cells become "loosened." Precursor materials of cutin and, presumably, the active ingredient in the drug marijuana (tetrahydrocannabinol), are thought to form

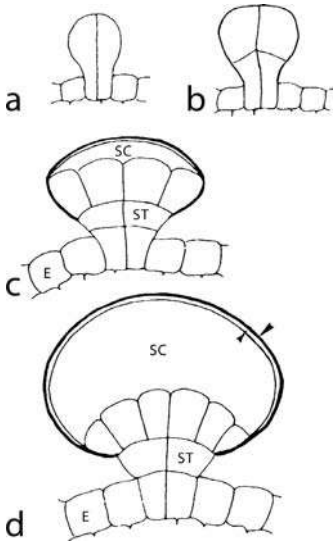

Figure 15.7 Diagrams illustrating the development of the glandular trichome in *Cannabis sativa*. (a) A cell of the protoderm expands and divides anticlinally followed by (b) a periclinal division in each cell forming an upper and a lower tier of two cells each. (c) By a series of anticlinal divisions in the upper tier a discoid layer of secretory cells (SC) is formed. Periclinal divisions in the lower tier result in the formation of the stipe (ST) and the basal cells which comprise a part of the epidermis (E). (c, d) The secretory cavity develops, as the cuticle (large arrowhead) expands, and cell wall substance, possibly derived from the outer walls of the secretory cells, forms a subcuticular wall (small arrowhead). See the text for more detail. From Kim and Mahlberg (1991). Used by permission of the Botanical Society of America.

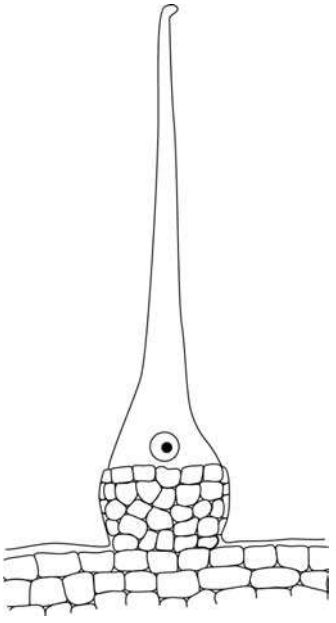

Figure 15.8 Glandular hair of *Urtica dioica* (stinging nettle).

in hyaline areas in the walls, become membrane-enclosed, and move in these vesicles into the developing secretory cavity, nearly filling it. Wall material, referred to by Kim and Mahlberg (1991) as "wall matrix," derived from the outer walls of the secretory cells, moves through the developing cavity in a hydrophilic phase between the vesicles, and is deposited under the cuticle, forming the subcuticular wall. The substructure of this wall has not been well defined, and it is not clear whether or not it contains cellulose microfibrils. However, Kim and Mahlberg (1995) have described the presence in the wall of elongate fibrils in parallel pairs. Vesicles in the secretory cavity enlarge and some migrate to the subcuticular wall where the vesicular membrane disintegrates. Precursor compounds of cutin apparently move through the wall, are synthesized into cutin and, thus, contribute to the expanding and thickening cuticle (Mahlberg and Kim, 1991; Kim and Mahlberg, 1995). This unusual development wherein cutin precursors contained in vesicles and non-vesiculate subcuticular wall material are transported through a non-living space characterizes both *Cannabis* and *Humulus* (hops) (Kim and Mahlberg, 2000).

The stinging hairs of *Urtica dioica* (Fig. 15.8) consist of a cluster of basal cells, both epidermal and subepidermal in origin, in which rests the base of a long needle-like cell with a rigid, siliceous wall and a small bulbous tip. Upon contact with an animal, the tip breaks off releasing the toxic substances in the cell as it penetrates the skin. The composition of the toxic material has not been definitively determined but has been reported to contain a histamine and an acetylcholine (see Esau, 1965).

Salt glands (Fig. 15.9) provide a mechanism for the plant to rid itself of excess salt absorbed from the environment. This is an essential function of plants living in saltmarshes and salt-infiltrated soils in coastal marine areas. Salt glands of several types are modified multicellular trichomes borne on stems and leaves. Among the best known are those of members of the Tamaricaceae and Chenopodiaceae. In many species of *Atriplex* the gland consists of a large, bladder-like cell attached

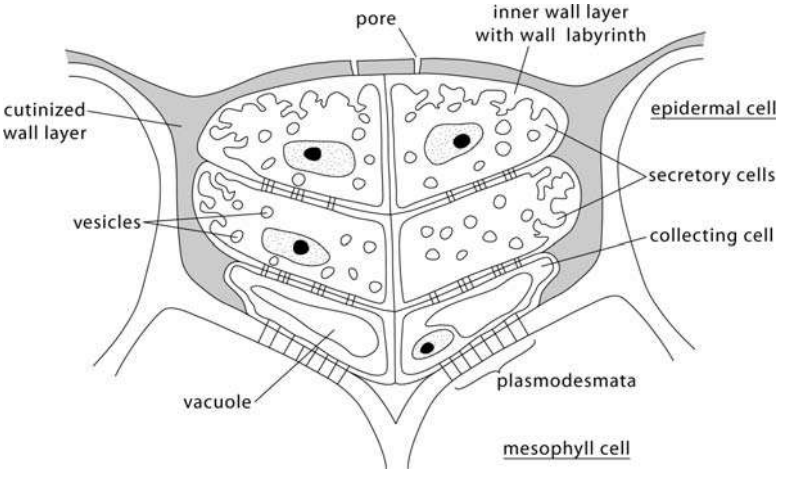

Figure 15.9 Salt gland of *Tamarix aphylla* (tamarisk). Note that the gland, which consists of two basal collecting cells and four secretory cells, is sunken within the epidermis. Salt is transferred symplastically from the leaf mesophyll into collecting cells and secretory cells, and apoplastically through the wall labyrinth to the exterior. See the text for more detail. Redrawn from Thomson *et al.* (1969). Used by permission of Dr. W. W. Thomson.

terminally to a uniseriate stalk consisting of one to several cells. Salt moves apoplastically from the xylem of a nearby vein to parenchyma cells subtending the base of the gland and symplastically through plasmodesmata in the walls of the stalk cells and the bladder where it is deposited within its vacuole (see Osmond *et al*., 1969). Upon disintegration of the gland the salt is released, forming a white residue on the surface of the leaf or stem. The movement of salt ions into the gland against a concentration gradient requires an expenditure of energy. Salt is prevented from moving back into the leaf or stem through the cell wall apoplast by the presence of cutinized transverse and radial walls of cells subtending the gland.

A very different, more complex type of salt gland characterizes *Tamarix aphylla* (tamarisk) (Fig. 15.9). It is also a modified, multicellular trichome, but one that is sunken within the epidermis. Salt in solution is transported symplastically by way of plasmodesmata through two basal collecting cells into the several secretory cells that comprise the bulk of the gland. The secretory cells are transfer cells with extensive wall ingrowths and heavily cutinized walls except in the region of contact with the two basal cells. The protoplasts of the transfer cells contain numerous small vesicles into which the salt accumulates. Fusion of the vesicles with the plasma membrane empties the salt into the wall where it then moves through the inner, uncutinized layer toward the surface of the gland and is released to the exterior through small pores. Movement of salt back into the leaf through the wall along the concentration gradient is prevented by the cutinized layer enclosing the gland (see Thomson *et al*., 1969).

Unlike salt glands that function to eliminate a substance potentially harmful to the plant, **nectaries** benefit plants in very different ways. By secreting a sugar solution (nectar) that attracts bird and insect pollinators, floral nectaries (Fig. 15.10a) play a significant role in plant reproduction. Whereas extrafloral nectaries (Fig. 15.10b, c) which occur on the stem, leaves, leaf petioles, midribs, stipules, and flower pedicels play no role in reproduction, they attract insects, the presence of which may prevent predation by animals or other insects.

Nectaries are highly variable in morphology, some being no more than a small cluster of secretory cells, others being raised mounds of secretory tissue of various forms (circular or kidney-shaped), whereas some are conspicuous outgrowths containing vascular tissue and both secretory and non-secretory parenchyma. Floral nectaries in many flowers take the form of a continuous ring around the base of the gynoecium (Fig. 15.10a; see Chapter 18 for another illustration). The movement of sugar solution derived from the phloem into the nectaries as well as from them to the exterior of the protoplasts can be either eccrinous (i.e., apoplastic) or granulocrinous. If eccrinous, the secretory cells have the structure of, and function as, transfer cells. An interesting example of granulocrinous transfer occurs in *Lonicera japonica* (honeysuckle). Sugar secretion occurs through short epidermal hairs, each consisting of a single large bulbous cell. Prior to secretion, many small ER and/or Golgi vesicles containing a sugar solution fuse with the

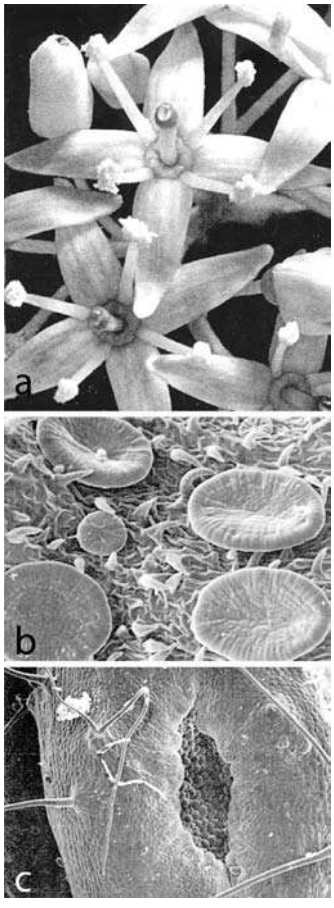

Figure 15.10 Nectaries. (a) The floral nectary of *Cornus sanguinea* (dogwood) surrounds the style at the base of the corolla. (b, c) Extrafloral nectaries. (b) Flattened, scale-like nectaries on the stem of *Bignonia capreolata*. (c) Nectary of *Gossypium hirsutum*, embedded in the midvein on the abaxial surface of the leaf. Note the numerous, raised secretory cells in the cavity. (a) From Jaeger (1961). Used by permission of Chambers Harrap Publishers, Ltd. (b, c) From Elias (1983). Used by permission of Columbia University Press.

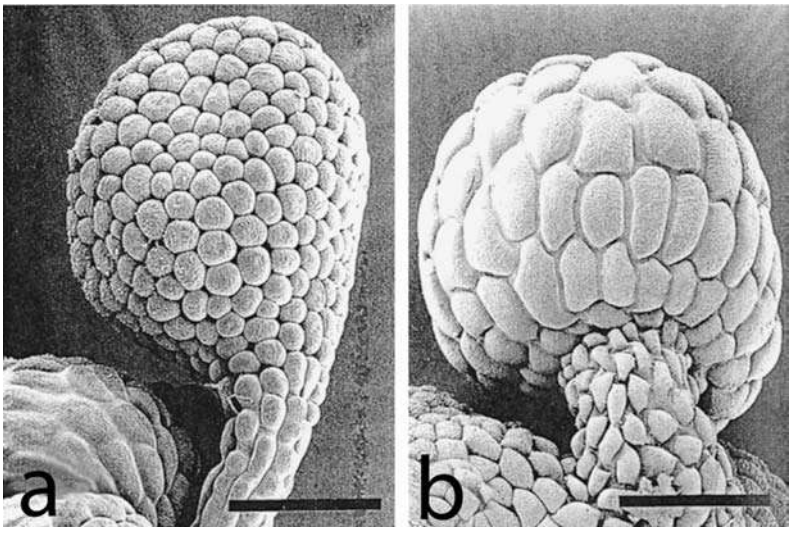

Figure 15.11 Secretory glands on anther connectives. (a) Anther gland of *Stryphnodendron* sp. Bar = 50 μm. (b) Anther gland of *Adenanthera pavonina*. Bar = 120 μm. From Luckow and Grimes (1997). Used by permission of the Botanical Society of America.

extensive plasma membrane lining the wall ingrowths, thus extruding their contents into the wall and ultimately into an expanding nectar-filled cavity between the wall and the cuticle. The nectar is released by rupture of the cuticle. In some members of the Myrtaceae, e.g., *Chamelaucium uncinatum*, sugar is transferred granulocrinously from the protoplasts, and through modified stomata into subcuticular cavities. The nectar moves to the exterior through openings in the cuticle that reflect the positions of the subtending stomata (O'Brien *et al*., 1996). Less well known than nectaries, and uncommon among plants (occurring in the Violaceae and some mimosoid Leguminosae), are secretory glands on anther connectives (Fig. 15.11a, b). They are thought to provide a food reward for pollinators. In some species they secrete a sticky material by which pollen is attached to the body of insects. In others they may function as **osmophores**, structures that emit a perfume which becomes a reward for pollinators such as euglossine bees (see Beardsell *et al*., 1989; Luckow and Grimes, 1997).

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Chapter 16

The root

Perspective: evolution of the root

The anatomy of the root reflects its origin, its subterranean environment, and its function. The first vascular plants (Rhyniophyta) lacked roots, and absorption of water and nutrients was facilitated by rhizoids. Roots evolved in the seed plant clade (rhyniophytes, trimerophytes, progymnosperms, seed plants) as well as in lycophytes, sphenophytes, and ferns in response to the pressures of a land environment and increasing plant size. During their evolution important functions such as anchorage, absorption and transport of minerals and water, and storage of photosynthate were established. In some ways, however, roots changed relatively little through time, resulting from the subterranean environment in which they evolved, and the fact that roots were, thus, not exposed to the same intense selection pressures as stems.

The seed plant root (Fig. 16.1a, b) is considered by most researchers to be an evolutionarily modified stem although it has also been suggested that it might be an entirely new organ that evolved independently of the stem. The predominant view is supported by the fact that the structure of the root of extant plants is remarkably similar to the anatomy of the stem of their ancestors. Even in many plants with stems of siphonostelic or eustelic structure, the roots are protostelic (Fig. 16.1b), also a feature of the stems of very primitive plants. Roots with central piths have an alternate arrangement of xylem and phloem that may reflect a protostelic origin.

The origin of the root in the lycophyte clade was apparently quite different from that in the seed plant clade. The zosterophyllophytes, from which the lycophytes are thought to have evolved, lacked roots. In the most highly specialized lycophytes, the Lepidodendrales, roots were borne on stigmarian appendages which were similar to stems in anatomy. The roots were helically arranged and are considered by many paleobotanists to be leaf homologs. It is hypothesized, therefore, that in this clade roots and leaves evolved from similar structures (see Stewart and Rothwell, 1993). The roots of all lycophytes, herbaceous and arborescent, are of remarkably similar anatomy, thus supporting the concept of a single origin of roots in this group. Within vascular

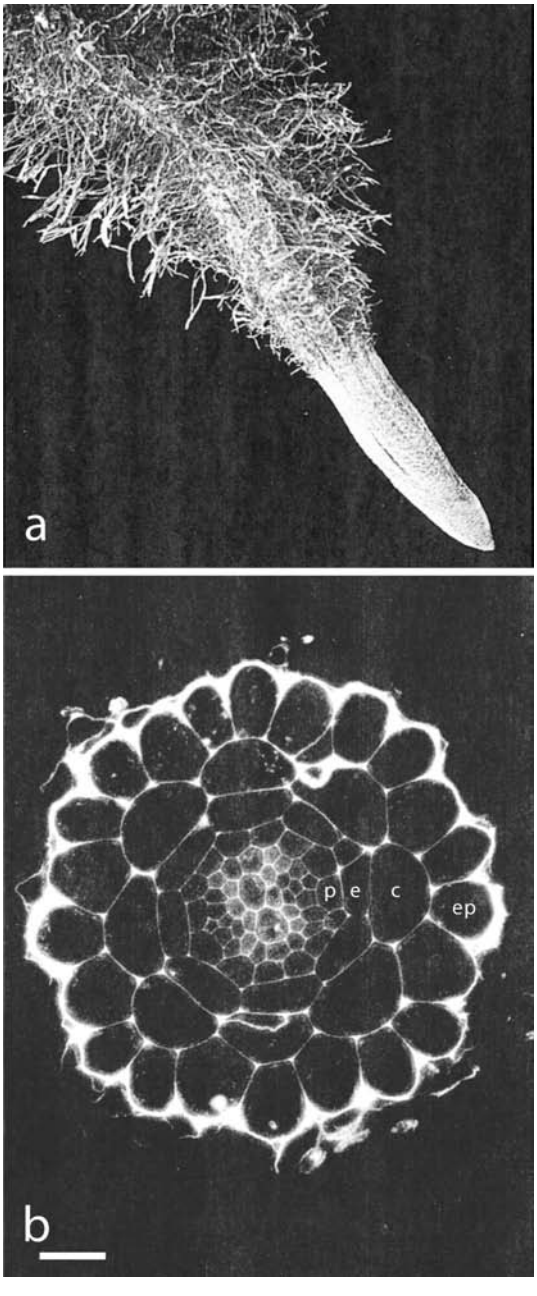

Figure 16.1 (a) Part of the root of a seedling of *Rhaphanus sativus* (radish) showing the root tip and a zone of numerous root hairs. Magnification × 20. (b) Transverse section of a root of *Arabidopsis thaliana* showing the central column (a protostele) of primary xylem and primary phloem enclosed by the pericycle (p), the endodermis (e), a single-layered cortex of eight large cells (c), and the epidermis (ep). Bar = 10 μm. (a) From Troughton and Donaldson (1972). Used by permission of the New Zealand Ministry of Research, Science and Technology. (b) From Bowman (1994). Used by permission of Springer-Verlag Heidelberg. © Springer-Verlag Berlin Heidelberg.

plants, however, it seems likely that roots are polyphyletic in origin, having evolved independently in seed plants and lycophytes (see Knoll and Niklas, 1987). The origin of roots in sphenophytes and ferns is unclear.

The major structural adaptations of roots are directly related to their functions. As plants increased in size during their evolution, the problem of anchorage became progressively more important, and this is reflected in root structure. Most large plants have tap root systems

which develop directly from the radicle in the embryo whereas smaller plants are often characterized by fibrous root systems consisting of many small roots that spread out laterally from the base of the stem. There are, however, many variations in the morphology of root systems, often related to the habitat of the plant.

As adaptations to the function of absorption, roots are characterized by the production of absorptive roots hairs in a region just proximal to the root apex. In addition, suberized Casparian bands in the walls of endodermal cells prevent back-flow of nutrients through the apoplast and out of the region of vascular tissue. A subepidermal exodermis, similar in structure to the endodermis, has the important function of restricting water loss from the root during periods of drought. In some taxa, absorbing roots are greater in diameter and have proportionately more vascular tissue than anchoring roots (Wilder and Johansen, 1992). The symbiotic relationship of most seed plants with fungi results in the formation of mycorrhizae that greatly facilitate the absorption of nutrients from the surrounding soil environment. Cluster roots enhance the absorption of phosphorus in mineral-deficient regions. In line with their function as absorbing organs, the roots of most plants penetrate the soil substrate. The apical meristem is covered by the root cap, a conical structure that protects and lubricates the root tip as it grows through the soil.

The structure of roots is also adapted to the function of storage. In roots that have primary structure only, the cortex is usually large, providing an expansive area for storage of photosynthate, often in the form of starch. In woody roots the phellogen differentiates in the pericycle which typically results in an early elimination of the cortex. Consequently, the secondary xylem which is highly parenchymatous becomes the major storage tissue. We shall discuss later, in more detail, each of these aspects of root structure and function.

Gross morphology

Gymnosperms and dicotyledons are characterized, typically, by tap root systems, whereas monocotyledons most commonly have fibrous root systems. The roots of extant ferns, sphenophytes, and lycophytes are usually adventitious roots that originate from stems. A **tap root** develops from a meristem at the lower end of the hypocotyl of the embryo. Once development of the root has begun in gymnosperms and dicotyledons its growth continues throughout the life of the plant. The main axis of a tap root system may extend to great depths in the soil, and often becomes woody, especially in trees, providing effective anchorage for these large plants. Lateral roots which develop from the tap root commonly branch, and extend outward for great distances. These lateral roots may also become woody and, with the main axis of the tap root system, are effective in maintaining the vertical orientation of the plant under adverse environmental conditions such as flooding and/or high wind velocities. Their location just beneath the soil surface

is also highly beneficial to the nutrition of the plant since they occupy nutrient-rich surface areas (Coutts and Nicoll, 1991). The biological and/or physical factors that result in the shallow subsurface orientation of lateral roots are not clearly understood. It has been observed that some of the lateral roots of a tree are **plagiogravitropic**, that is, they grow obliquely upward, but just prior to reaching the soil surface begin a downward deflection, thus maintaining their subsurface orientation (Coutts and Nicoll, 1991). The biological and/or physical signals that control the downward deflection of the roots are unknown.

In monocotyledons an initial tap root usually aborts early in development, and the root system becomes composed of numerous **adventitious roots**, lacking secondary growth, which develop from the base of the stem. **Fibrous root systems** thus formed are effective in anchorage as well as in nutrient absorption and transport.

Contractile roots and other highly specialized root systems

Although in seed plants, tap root and fibrous root systems are very common, highly specialized root systems may characterize plants growing in specific habitats or in which a particular function is enhanced. For example, mangroves, which grow in water, develop large prop roots that extend from the stem into the sub-aquatic substrate. The roots of plants growing in wet environments are often characterized by extensive development of cortical aerenchyma. The roots of some plants, such as carrot, rutabaga, beet, radish, etc. are fleshy storage organs, consisting almost entirely of parenchyma.

Cluster roots are common in many families of dicotyledons growing in regions deficient in phosphorus, and provide an important mechanism for the acquisition of this element, essential in plant development and function. Cluster roots consist of a group of small, determinate roots that are initiated in the pericycle opposite protoxylem strands (Skene, 2000). Organic acids and phosphatases which are released from these roots into the substrate function in phosphorus acquisition and, possibly, the absorption of other soil nutrients (Skene, 1998; Watt and Evans, 1999).

Contractile roots are common in many taxa of both monocotyledons and dicotyledons. They are especially common in plants characterized by bulbs or corms such as crocus and hyacinth as well as some that are not such as dandelion. By contracting, the roots pull the plant closer to the soil surface, or deeper within the soil. This adaptation assures that the bulbs or corms of such plants (called **geophytes**) become established in the soil at physiologically and ecologically effective depths (Pütz, 1991) where they or their developing aerial shoots will have access to light and adequate soil moisture (among other environmental factors), and will be protected from low winter and high summer temperatures.

The mechanism of root contraction in geophytes has been of considerable interest for many years. Recent histological studies have shown conclusively that root contraction in many geophytes is caused by a change in the dimensions and volume of cells in the inner and middle cortex. For example, in both *Chlorogalum pomeridianum* and *Hyacinthus orientalis*, members of the Liliaceae, the inner and middle cortical cells increase in radial dimension and decrease in longitudinal dimension. There is also a substantial increase in the volume of cells that comprise the outer part of the middle cortex. These changes result in shortening the root and the concomitant collapse of the outer cortical cells and epidermis (Jernstedt, 1984a, 1984b). Although the mechanism of change in cell shape is not well understood, there is a correlation between the change in cell shape and changes in cell wall structure, differential wall extensibility, and deposition of new cell wall material (see Wilson and Honey, 1966; Mosiniak *et al*., 1995). As the process of contraction continues over several periods of growth, the outer, collapsed layers of root tissue form conspicuous and characteristic ridges and folds.

Induction of the development of contractile roots in geophytes is apparently related to the depth of the planted bulb or corm. It was known as early as the late nineteenth century that deeply planted geophytes do not produce contractile roots. Research by Halevy (1986) demonstrated that contractile roots developed in *Gladiolus grandiflorus* only on small offshoot corms located close to the soil surface. He observed, further, that light and temperature fluctuations were essential for the development of contractile roots in this taxon. As growth of the aerial shoot began, two basal, sheathing leaves of specific lengths were produced. The upper sheathing leaf that extended above the soil level functioned as a light receptor which controlled depth. If the plant was deprived of either light or fluctuating temperatures, contractile roots failed to develop.

Whereas the corms of some taxa are pulled downward through the soil by contractile roots and must overcome the soil resistance, those of others, especially small, offshoot corms, move through channels in the soil made by a contractile root produced by the offshoot. In the latter situation, if the diameter of the corm and root are similar, the corm is pulled through the channel made by the contracting root with little or no soil resistance (Pütz, 1991). For more detail about the interesting subject of contractile roots, please refer to the references cited above.

Apical meristems

Several major histological patterns characterize the apical meristems of roots. In many pteridophytes there is a **single apical initial** from which all other tissues in the root are ultimately derived whereas lycophytes are characterized by a small **cluster of apical initials**. In most monocotyledons **three tiers of initials** have been recognized (Fig. 16.2a). By tracing cell lineages, the provascular column seems to arise from the basal tier, the ground meristem and the protoderm from the middle

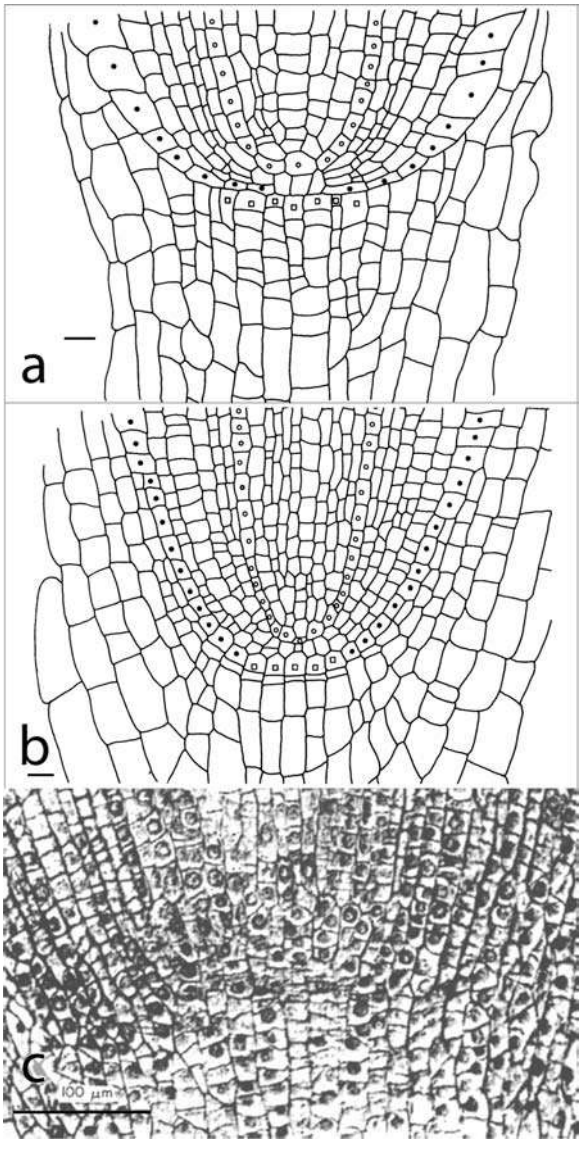

Figure 16.2 (a, b) Drawings of median longitudinal sections of the apical meristems of roots of a monocotyledon and a dicotyledon. (a) The apical meristem of *Triticum aestivum*, a monocotyledon, is characterized by three tiers of initials. The provascular column, the outer layer of which is indicated by circles, can be traced back to the basal tier, the ground tissue (unmarked) and protoderm (black dots) to the middle tier, and the root cap to the apical tier (calyptrogen) (squares). (b) The apical meristem of *Sinapis alba*, a dicotyledon, is also characterized by three tiers of initials. The provascular column (circles) can be traced back to the basal tier (as in the monocotyledon), the ground tissue (unmarked) to the middle tier, and the protoderm (black dots) and root cap to the apical tier (squares). Bar (a, b) = 20 µm. (c) Photograph of a median longitudinal section of the apical meristem of a root of *Vicia faba* consisting of a single zone of initials from which all tissue regions are derived, including a columella centrally located in the root cap. (a, b) From Clowes (1994). Used by permission of Blackwell Publishing Ltd. (c) From Clowes (1976). Used by permission of Elsevier.

tier, and the root cap (or calyptra, a term rarely used today) from the apical tier, often referred to as the **calyptrogen**. Three tiers have also been recognized in many dicotyledons (Fig. 16.2b). The provascular tissue can be traced through cell lineages to the basal tier, the ground meristem, alone, to the middle tier, and both the protoderm and the root cap to the apical tier. In some taxa, including many tree species, the root apex consists of a single zone of initials (Fig. 16.2c) from which all regions of the root appear to arise, including a **columella** centrally located in the root cap.

In roots of both monocotyledons and dicotyledons in which the various mature regions can be traced to distinct meristematic tiers, the apical meristems are considered to be **closed** (Fig. 16.2a, b). In

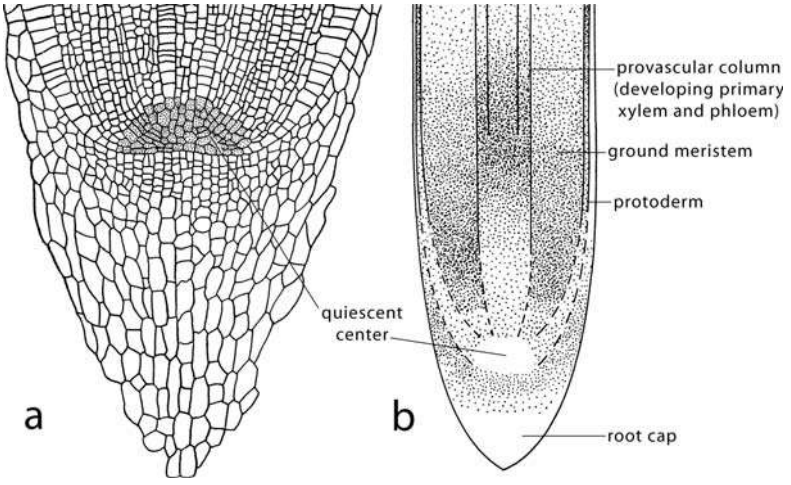

Figure 16.3 Median longitudinal views of root apices showing the quiescent center. (a) *Zea mays*. (b) *Allium cepa* showing distribution of cell divisions. Frequency of cell division is indicated by density of stippling. Light shading indicates low frequency, dark shading, high frequency. (a) From Clowes (1959). Used by permission of the Cambridge Philosophical Society. (b) From Jensen and Kavaljian (1958). Used by permission of the Botanical Society of America.

trees and other woody, as well as herbaceous, species of dicotyledons characterized by a single apical group of initials from which root cap, epidermis, cortex, and primary vascular system are all derived, the apical meristem is considered to be **open** (Fig. 16.2c). For exceptions and variations see Clowes (1994). Those who accept the concept that root apical meristems are composed of tiers of initials believe that the ultimate fate of the files of cells derived from the initials is restricted by cell lineages since these cells can be traced back to the initials. However, in many taxa a very low frequency of cell division has been observed in the region of the tiers of initials. This has led to the establishment of the concept of the **quiescent center** (see Clowes, 1959, 1961), a region of minimal cell division enclosed by a region of active cell division (Fig. 16.3a, b). According to Clowes, the quiescent center and the active initials which surround it comprise the **promeristem** in roots. Recent research has shown that the quiescent center plays an important role in development which we shall consider further in a later section.

The nineteenth-century German worker Hanstein proposed that the major tissue regions of the root were derived from a large meristem comprising the root tip. He recognized three distinct regions, or **histogens**, in this meristem, which he believed were derived from tiers of initials in the root tip. He proposed that the central histogen, called the **plerome**, gave rise to the vascular column, that a surrounding histogen, called the **periblem**, gave rise to the cortex, and that an outermost histogen, called the **dermatogen**, gave rise to the epidermis. If one excludes the apical tiers of initials in the concept, Hanstein's histogens become approximately equivalent to the provascular column, ground meristem, and protoderm located between the apical initials and the mature tissue regions. However, today we recognize that these are not permanent meristems or components of a larger meristem but, rather, transitional regions between the apical initials and mature tissue regions in which cell division, growth, and differentiation occur.

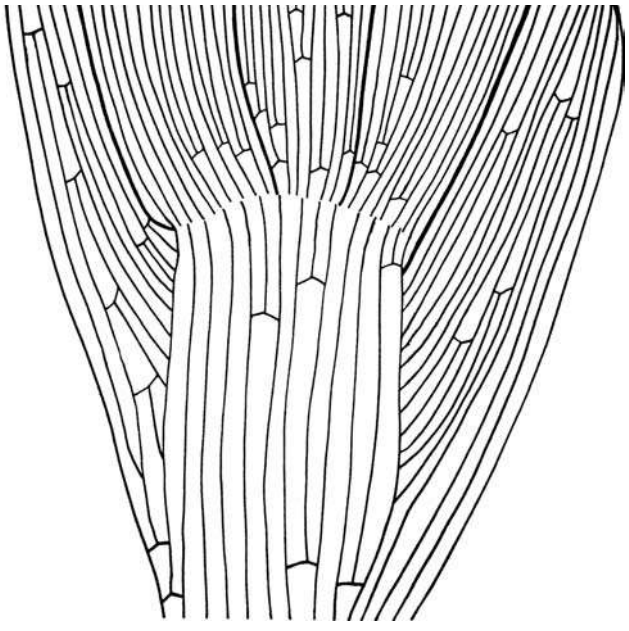

Figure 16.4 Arrangement of tissue domains in the root apex of *Vicia faba* as based on the Körper–Kappe concept. At levels at which new cell rows are formed there is a T-configuration. In the Körper (body) domain the T configuration is inverted whereas in the Kappe (cap) domain the T configuration in normal. This pattern is not, however, consistent as illustrated in *Vicia* in which the Körper includes not only the provascular tissue and ground meristem but also the columella (the central part of the root cap). Only the peripheral part of this root cap would be included in the Kappe domain. Note that the protoderm is also a part of the Kappe domain. From Clowes (1959). Used by permission of the Cambridge Philosophical Society.

Another way to look at root tip structure is the **Körper–Kappe** (body–cap) concept (Fig. 16.4) proposed by Schuepp in 1917. He noted that, during growth in the central region of the root tip at the level at which new files of cells form, there is an inverted T configuration, whereas in the outer region and in the root cap of some roots, the beginning of new files of cells is marked by a normal T configuration. The region in which the cross bar of the T faces the root apex is designated **Körper**, or body. The region in which the cross bar faces the base of the root is designated **Kappe**, or cap although in some taxa an inverted T configuration extends into the **columella**, the central part of the root cap (Fig. 16.4). In some cases Kappe configurations coincide solely with the root cap, and Körper configurations with the root tip proper (i.e., provascular column, ground meristem, and protoderm). In others Kappe is composed of root cap and protoderm, and may even include some of the outer ground meristem. When the Kappe of a particular root consists of root cap only we can conclude that there is a separate root cap initial. If the Kappe consists of root cap and protoderm, we know that the root cap and protoderm have a common initiating layer, or tier of initials. If the Kappe, in addition, includes some ground meristem, we can conclude that there is a cluster of apical initials, not distinctly tiered.

The quiescent center and its role in development

Although, as noted above, there has been great emphasis in the literature on the presence of tiers of cells that function as initiating layers in the roots of seed plants, work during the 1950s using radioactive isotopes demonstrated that the region in which these initials occur

in mature roots is, in fact, a zone of minimal cell-divisional activity. Consequently, this zone was labeled the **quiescent center** (Fig. 16.3) by the British botanist Clowes (Clowes, 1959, 1961). At about the same time, American botanists Jensen and Kavaljian, and the French botanist Buvat, arrived at similar conclusions in studies of the frequency of mitoses in root tips (Fig. 16.3b). Subsequently, the quiescent center has been documented in the root tips of many seed plants. Whereas early in development, the original tissue pattern in many species is apparently derived from tiers of meristematic initials in the root apex, with the establishment of the quiescent center the active zone of cell division is shifted to its periphery. Experiments in which auxin or gibberellin production was restricted by the use of chemical inhibitors (Barlow, 1992; Kerk and Feldman, 1994) and which led to increased cytokinesis in the quiescent center support the viewpoint that the low rate of cell division as well as the maintenance of the quiescent center are controlled, at least in part, by the level of hormone production in the root cap or root cap initials.

Studies of the embryogenesis of *Arabidopsis thaliana* have shown that the quiescent center and the columella of the root cap originate from direct derivatives of the hypophyseal cell of the developing embryo whereas the more proximal initials which enclose the quiescent center are derived from the apical cell of the globular embryo. The quiescent center and enclosing initials comprise the promeristem, described by Scheres *et al*. (1996) as the "functionally integrated root meristem." Genetic studies of root meristem development in *Arabidopsis* demonstrate that specimens which have the mutant *HOBBIT* (*hbt*) gene lack a quiescent center. In addition the calyptrogen (root cap meristem) develops abnormally resulting in a root cap lacking a columella, demonstrating that the *hbt* gene is required for normal root meristem development (Willemsen *et al*., 1998). Other studies, by these workers, of mutant embryos in which major tissue regions fail to develop suggest that regional identity of tissue domains is established early in embryo development. During normal embryogenesis in *Arabidopsis*, protoderm, ground meristem, and provascular tissue become defined very early as clonal domains that seem to be derived from specific initials. This supports the viewpoint that these tissue regions are derived, initially, as cell lineages from specific initials or groups (tiers) of initials as described above (see Scheres *et al*., 1996). This research group has shown, further, however, that following ablation (removal by killing) of initials from which a particular tissue type is directly derived, the adjacent cells that take over the positions of the ablated cells produce cells of the tissue type of the ablated initials. For example, if root cap columella cells were normally derived from the ablated initials, their replacements, which had originally been programmed to produce cells of vascular tissue "switch fate" and begin producing columella cells (see also van den Berg *et al*., 1997), thus supporting a conclusion that, in some species, root meristem cells and their derivatives develop according to position rather than as cell lineages, the predominant past viewpoint. Additional evidence of the function of the quiescent center has been

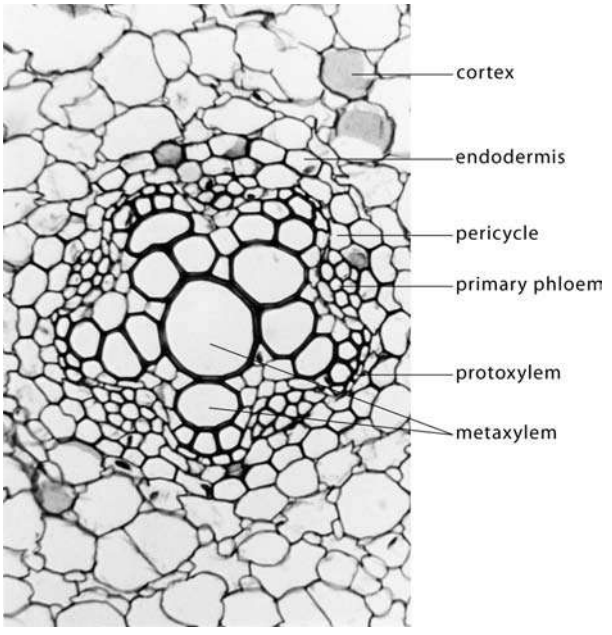

Figure 16.5 Transverse section of a root of *Ranunculus* sp. (buttercup) illustrating the ribbed protostele with strands of primary phloem between the ribs. Magnification × 260.

provided recently by Ponce *et al*. (2000), who demonstrate that following excision of the root cap in *Zea mays* genes that code for cell wall proteins or enzymes are expressed in the regenerating root cap only after the quiescent center has been re-established.

These studies provide strong evidence for communication between the quiescent center and the associated apical initials, the operation of a system of positional information, and some control of development by the quiescent center in both *Arabidopsis* and *Zea* (see Scheres *et al*., 1996; Schiefelbein *et al*., 1997; Ponce *et al*., 2000).

Ponce *et al*. (2000) describe the quiescent center "as an architectural template in the root apical meristem of all angiosperm and gymnosperm root tips . . . [which with surrounding initials] may regulate the positional and structural expression of . . . genes [which control the differentiation of tissue regions in roots]." Evidence that the quiescent center has a significant role in development is one of the exciting conclusions to come from recent research in plant molecular biology.

Primary tissues and tissue regions

The arrangement of primary tissues in the root parallels that in the stem, yet differs in several distinctive ways. In roots of many plants the central region consists of a solid column of primary xylem (Figs 16.1b, 16.5) whereas in others there is a central pith. The column of primary xylem, whether with or without a pith, is often fluted, appearing ribbed when observed in transverse section. The primary phloem commonly comprises small longitudinal bundles between the ribs of xylem (Fig. 16.5). In some dicotyledons and many monocotyledons in

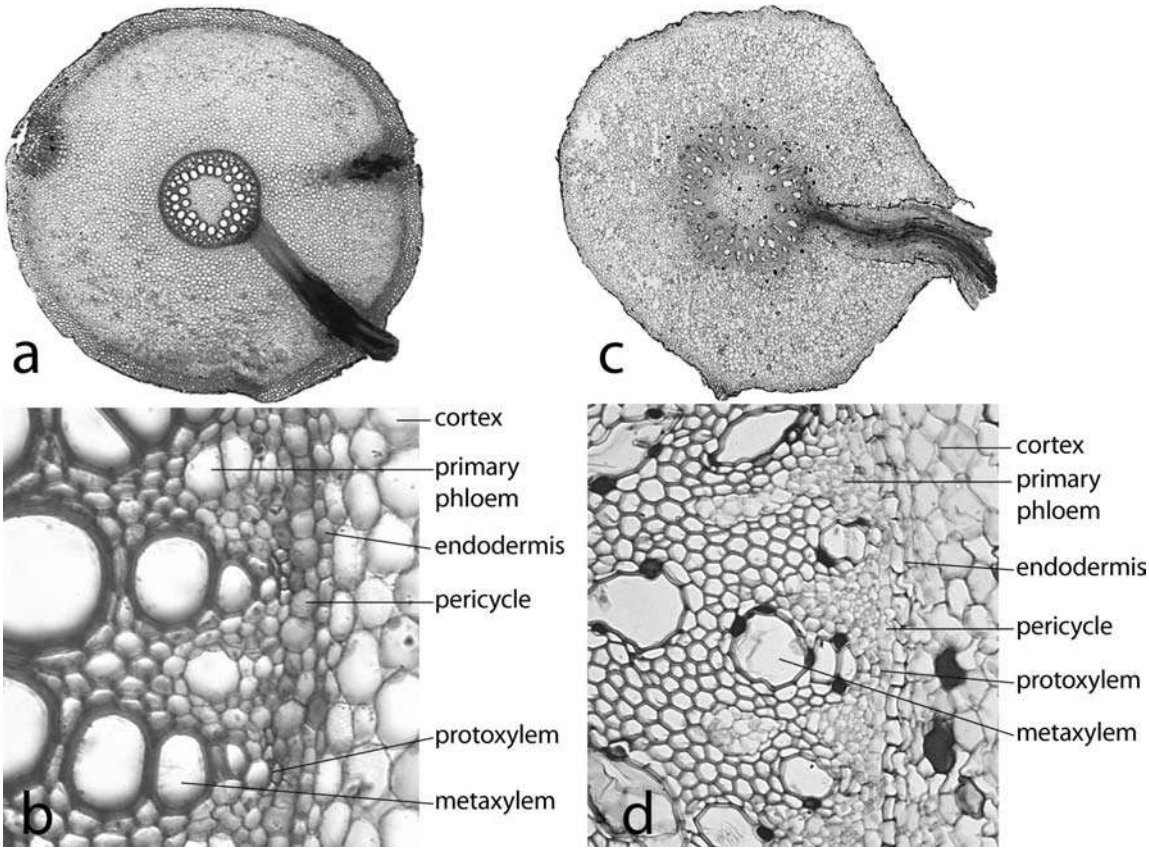

Figure 16.6 Roots of monocotyledons. (a) Transverse section of a root of *Smilax* containing a central column consisting of a compact cylinder of radiating primary vascular strands enclosing a well-defined pith. Magnification ×15. (b) Enlargement of a part of the central column in (a) illustrating histological details. Note the lateral root and the bundles of primary phloem that alternate with strands of primary xylem. Magnification × 275. (c) Transverse section of a root of *Zingiber officinate* (ginger) with a central column consisting of a pith and numerous alternating strands of primary xylem and primary phloem embedded in parenchyma. A lateral root extends through the cortex. Magnification × 12. (d) Enlargement of part of the central column of the root shown in (c). Magnification × 180.

which a pith is present, the xylem and phloem occur in alternating bundles (Fig. 16.6b, d). The primary xylem and phloem (and the pith, when present) plus the pericycle (Figs 16.1b, 16.5) comprise the **central column**.

The primary xylem is commonly two-ribbed, three-ribbed, four-ribbed, or five-ribbed, and is referred to as being diarch, triarch, tetrarch, or pentarch; but it may also be polyarch (Fig. 16.7a–e). Order of maturation of primary xylem is always exarch with protoxylem located in the tips of the ribs, or if considered in three dimensions, comprising the outermost edges of the ribs. The number of xylem ribs or bundles (where there is a pith) is a constant character in some taxa, but variable

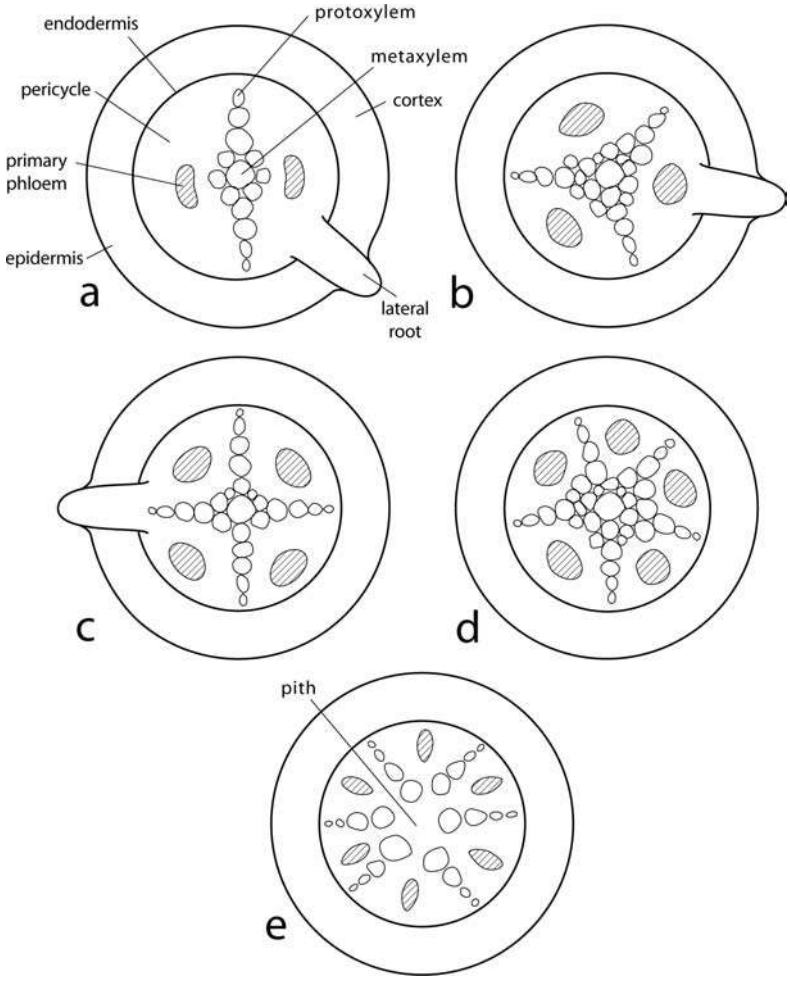

Figure 16.7 Diagrams illustrating patterns of primary xylem and primary phloem in roots. Note the alternation of bundles of primary phloem with ribs of primary xylem. These patterns are reflected in the terms applied to each variant. The terms indicate the number of ribs of primary xylem, as, for example (a) diarch, (b) triarch, (c) tetrarch, (d) pentarch, (e) polyarch. In polyarch roots, common in monocotyledons, there is usually a pith. Order of maturation of primary xylem is exarch in all roots.

in others. The histological characteristics of both primary xylem and primary phloem in roots are similar to those in stems. However, in roots it is more difficult to distinguish accurately protoxylem from metaxylem and protophloem from metaphloem because, during development, there is commonly less elongation of tissues in the region of first differentiation of these tissues than in stems; and, not surprisingly, there are often no protoxylem tracheids or vessel members with annular or helical secondary wall thickenings that would allow for stretching. Consequently, there is less obliteration of protophloem than is typical in stems.

The **pericycle** (Figs 16.5, 16.6b, d) is a narrow layer of potentially meristematic parenchyma between the vascular tissues and the endodermis from which lateral roots develop (see p. 302 for a detailed discussion of lateral root development). In roots with secondary growth, the phellogen also develops within the pericycle.

The **endodermis** (Figs 16.1b, 16.5, 16.6b, 16.8a) is a highly specialized, single layer of cells that comprises the innermost layer of the

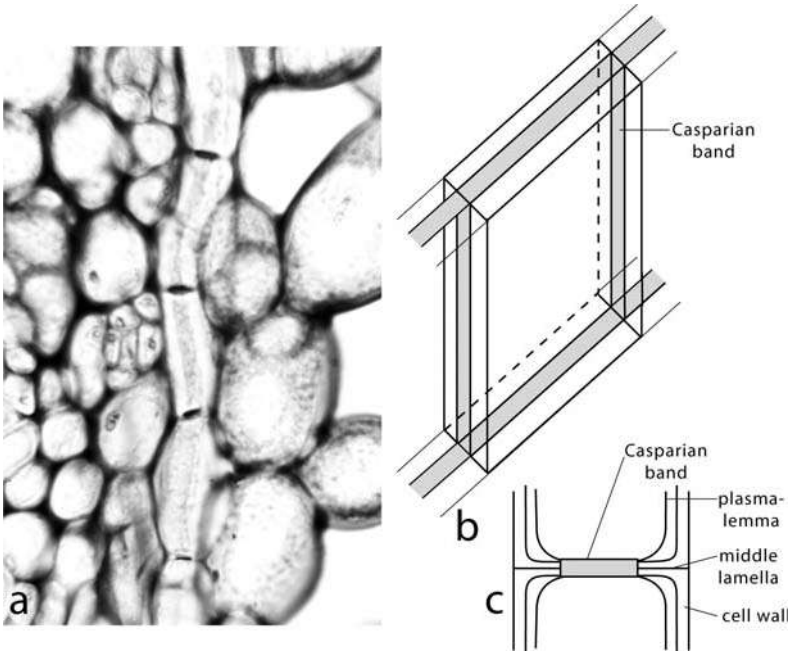

Figure 16.8 Endodermis illustrating Casparian bands. (a) Endodermis in the stem of *Acorus calamus*. Note Casparian bands in surface and sectional views. (b) Three-dimensional diagram of an endodermal cell showing the Casparian band in radial and transverse walls. (c) Sectional view showing that the suberized Casparian band extends through the walls of contiguous cells. Note that the plasma membrane of each cell is tightly attached to the Casparian band. Upon plasmolysis, the plasma membrane pulls away from the walls except in the region of the Casparian band.

cortex. Although it is characteristic of roots where it serves very important functions (see below), it also occurs in leaves, stems, or rhizomes of some angiosperms, the leaves of many pteridophytes, and the leaves of some conifers (Lersten, 1997). The endodermis consists of tabular cells, the transverse and radial walls of which are characterized by the presence of a continuous suberized and often lignified region in the primary wall called the **Casparian band** (Fig. 16.8a, b, c) (see Schreiber, 1996), a prominent feature of seed plants, but which also occurs in many species of pteridophytes (Damus *et al*., 1997). In addition to suberin and lignin, the Casparian bands may also contain cell wall proteins and carbohydrates (Schreiber *et al*., 1999). In roots, the Casparian bands in the endodermis as well as in the exodermis of many plants (see below) regulate the apoplastic uptake and loss of water and solutes through the radial and transverse cell walls (Hose *et al*., 2001). The Casparian band extends through the walls and middle lamella of contiguous cells, and is in contact with the plasma membranes of these cells which adhere tightly to it. Upon plasmolysis of the protoplasts, the plasma membranes are pulled away from the cell walls except in the region of the bands (Fig. 16.8c), often forming taut sheets resulting in so-called **band plasmolysis**. In addition to the Casparian band, the inner layer of the primary walls in many taxa become impregnated with suberin and is known as the **suberin lamella**. In many plants the suberin lamellae are covered by a cellulosic layer of variable thickness which may become lignified (see Seago *et al*., 1999; Ma and Peterson, 2001a). Solutes that move into the root are prevented by the Casparian bands from moving through the transverse and radial walls and by the suberin lamellae from moving through the tangential walls of endodermal cells.

Consequently, transport across the endodermis into the central vascular tissue must occur via plasmodesmata (at least in many angiosperms) which are not severed by development of the suberin lamellae (see Verdaguer and Molinas, 1997; Ma and Peterson, 2001a, 2001b), or apoplastically through the tangential walls of **passage cells**, thin-walled endodermal cells that lack suberin lamellae (Clarkson, 1991; Peterson and Enstone, 1996). Furthermore, as the concentration of ions in solution increases to the *inside* of the endodermis, the Casparian bands prevent the diffusion of ions out of the vascular column through the transverse and radial walls of the endodermal cells (see Clarkson and Robards, 1975; Clarkson, 1991; Peterson *et al*., 1993). In many monocotyledons which lack secondary growth and herbaceous dicotyledons that produce only small quantities of secondary tissue the endodermis may become very thick-walled and persist for many years or for the life of the plant. The presence of passage cells may be especially important in such plants. Another possible function of passage cells in the endodermis is the transfer of calcium and magnesium into the transpiration stream. When the epidermis and central cortex die they are the only cells exposed to the soil solution that are capable of ion uptake (Peterson and Enstone, 1996). No plasmodesmata have been observed in the endodermal cell walls in the roots of conifers so it appears likely that movement of solutes through the tangential walls of these cells is apoplastic (see Verdaguer and Molinas, 1997).

The endodermis begins its development very close to the root tip, and is functional in the region of root hair development. In the primary (tap) root of *Quercus suber* (cork oak), for example, the developing endodermis was observed within about 1 mm of the junction of the root cap and the root proper, and at about the same level as the first evidence of maturation of protophloem elements (Verdaguer and Molinas, 1997). The Casparian band began to develop at 20–25 mm from the root tip opposite the protophloem, and plasmodesmata were apparent, except in the region of the Casparian band. By 70–80 mm from the root tip, the primary cell walls were covered on their inner surfaces by a uniformly thick suberin lamella except in the region of plasmodesmata and the Casparian band where it was very thin or absent. At maturity, the suberin lamellae were covered by a thin, cellulosic layer (Verdaguer and Molinas, 1997). Throughout development, the protoplast contained conspicuous ER and Golgi bodies and numerous associated vesicles which, presumably, transported, granulocrinously, precursor compounds of suberin, lignin, cellulose, and other components of the cell walls. The endodermal cell walls of all species previously reported, from pteridophytes to gymnosperms and angiosperms, are similar in ultrastructure, differing only in the thickness of the suberin lamellae (see references cited in Verdaguer and Molinas, 1997).

To the exterior of the endodermis, the **cortex** consists predominantly of parenchyma, but may contain extensive regions of collenchyma and/or sclerenchyma, especially near the periphery. The parenchyma tissue in the cortex typically contains a complex system of **intercellular air channels** which facilitates aeration, i.e., entry of

oxygen and release of carbon dioxide. Such tissue, often referred to as **aerenchyma**, is especially well developed in roots that grow in aquatic or highly moist environments (see Peterson, 1992; Seago *et al*., 2000a, 2000b).

A major function of the cortex in most roots is storage of photosynthate, usually in the form of starch. Entire tap roots of carrot, beet, rutabaga, etc. are highly specialized as storage organs. Even the secondary xylem in such roots is highly parenchymatous, and functions primarily in storage.

The roots of many herbaceous plants and the apical regions of roots of some woody plants are characterized by a specialized tissue immediately below the epidermis called the exodermis (Fig. 16.9). The **exodermis**, similar in both structure and function to the endodermis, controls the passage of water and solutes into and out of the root (Ma and Peterson, 2001a, 2001b). Its major function, however, is thought to be the restriction of apoplastic water loss from roots during conditions of low water potential resulting from drought (Enstone and Peterson, 1997; Taleisnik *et al*., 1999) or their presence in saline substrates (Taleisnik *et al*., 1999). The exodermis consists of one to several layers of cells characterized by suberin lamellae which comprise the inner wall layer. Casparian bands (Fig. 16.9) extend through the radial and transverse walls of contiguous cells. Band plasmolysis occurs in the exodermis, but is less common than in the endodermis (Enstone and Peterson, 1997). The presence of Casparian bands and suberin lamellae in exodermal cells prevents ions in the soil solution from moving through the apoplast of these cells into the cortex. Consequently, with the exception of passage cells that lack suberin lamellae, movement of ions through the exodermal cells must be symplastic, i.e., through plasmodesmata (Peterson, 1988; Peterson and Enstone, 1996).

The effectiveness of the exodermis in restricting water loss from roots is directly related to the degree of maturity of the tissue. During root development, cells of the exodermis have been observed to differentiate asynchronously in some species (e.g., *Zea mays*), with mature cells occurring in groups or "patches" (Enstone and Peterson, 1997) whereas others have reported a completely developed exodermis close to the root tip (Wang *et al*., 1995). Consequently, restriction by the exodermis of apoplastic water loss can be variable. Although Taleisnik *et al*. (1999) observed that water retention in root segments containing an exodermis was "significantly higher" than that in non-exodermal segments, they concluded that **rhizosheaths** (see Wang *et al*., 1991), sheaths of soil that form around roots in very dry soil, may be more effective than the exodermis in restricting water loss.

Prior to the formation of secondary tissues in roots in which little or no secondary tissues develop, the **epidermis** (Figs 16.1b, 16.9) functions primarily in absorption, enhanced by the presence of specialized root hairs (see later section). Since, however, the root tip is a site of active cell division and differentiation, the developing epidermis (protoderm) provides, in addition, a very important protective function. The nature of the surface of the protoderm is of great importance since it must not

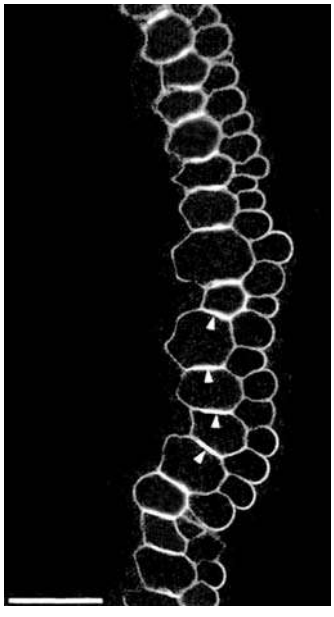

Figure 16.9 Casparian bands as seen in sectional views (at arrow heads) in the exodermis of the root of *Allium*. The layer of cells on the right is the epidermis. Bar = 50 μm. From Peterson (1988). Used by permission of Blackwell Publishing Ltd.

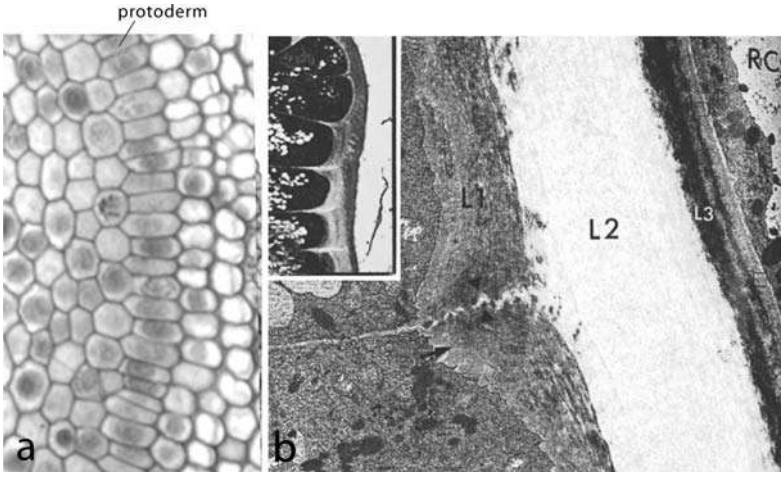

Figure 16.10 (a) Protoderm in the root tip of *Allium* with numerous nuclear division figures indicating cell divisional activity. Note also, the numerous recently formed anticlinal walls. Magnification × 343. (b) Highly magnified region of a transverse section of the root tip of *Zea mays* showing the primary wall (L1) of protodermal cells and outer L2 and L3 layers which comprise the pellicle, a protective structure. Magnification × 4800. Inset, a series of epidermal cells. Magnification × 490. (b) From Abeysekera and McCully (1993a). Used by permission of Blackwell Publishing Ltd.

only serve in protecting the root from insects and pathogens and the detrimental effects of moving through the soil, but also must accommodate the multiple developmental changes occurring in both the protoderm itself as well as more internal cells (Abeysekera and McCully, 1993a, 1993b, 1994). Among these changes are rapid cell divisions (Fig. 16.10a) and the consequent expansion of the protodermal surface as well as cell division and extension growth (elongation) of cells of the ground meristem and provascular column, among others. Abeysekera and McCully describe a specialized outer surface of the protodermal cells in *Zea mays* which they describe as a distinct structure consisting of three layers (Fig. 16.10b). They consider the primary cell wall of the protodermal cells, characterized by a helicoidal arrangement of cellulose microfibrils, to be the inner layer (L1) of this surface structure. The outer layers, L2 and L3, comprise the **pellicle**. These layers differ in both staining characteristics and structure from the underlying cell walls. L2 is thick with an amorphous texture and a smooth outer boundary which does not follow the contours of the protodermal cells. Fine microfibrils, difficult to distinguish, lie parallel to the long axis of the root. L3, the outer, very thin layer "is coarsely and irregularly fibrillar." The pellicle is a strong, elastic cover over the root tip of *Zea mays* that protects it during early development stages.

Development of the pellicle begins near the interface between the root proper and the root cap. It attains maximum thickness over the meristematic region and extends into the root hair zone where the L3 layer disappears and the L2 layer thins conspicuously, remaining only

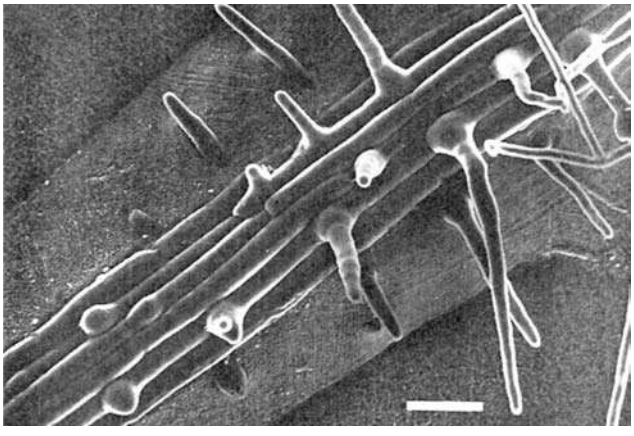

Figure 16.11 Developing root hairs in the root hair zone of *Arabidopsis thaliana*. Bar = 50 μm. From Schiefelbein and Somerville (1990). Used by permission of the American Society of Plant Biologists.

as "collars" around the base of root hairs that have pushed through it and the primary cell wall during their development. Whereas it seems likely that the development of a pellicle is a common feature of root tips, there is, as yet, little evidence to support this view since it has been observed primarily in maize and a few other grasses (Abeysekera and McCully, 1993a).

Root hairs develop in a region that extends from just proximal to the apical meristem for one to several millimeters toward the base of the plant (Figs 16.1, 16.11). The formation of root hairs greatly expands the area of absorption. As development of the root proceeds, the **root hair zone** maintains its size and its position relative to the apical meristem with new root hairs being developed distally as older hairs die proximally. As might be expected, the root epidermis has no cuticle or only a very thin cuticle. In plants, usually herbaceous perennials, that live for years without secondary growth, the epidermis proximal to the absorbing zone may produce a thick cuticle and function as a protective layer. In others it disintegrates and is replaced by development of an exodermis (see above), the walls of which become lignified and suberized. Whereas cells of the exodermis often have the appearance of sclerenchyma, they typically retain a living protoplast.

Some aerial roots of tropical plants such as orchids have a **multiple epidermis**, that is, one consisting of several cell layers. This structure, the **velamen**, consists of non-living cells. Although it has often been considered to be a water-storage region, it is now thought to function primarily in preventing water loss.

Lateral transport of water and minerals in the young root

Perhaps the most important function of the young root is the absorption of water and minerals from the soil and their transfer, laterally, into the stelar region from which they move longitudinally through the primary xylem into the shoot. During their course across the root,

water and ions in solution must traverse a complex of structures and tissue regions. In general, water moves passively from the soil into the stelar region as it is being lost from the plant through transpiration. Nutrient ions, on the other hand, are actively absorbed across the plasma membranes of living cells and then transferred from cell to cell through plasmodesmata. As we now know, the movement of both water and ions into the region of the xylem is influenced by the presence of Casparian bands and suberin lamellae in the endodermis and in some plants by comparable structures in an exodermis. Whereas these structures, often impregnated with both suberin and lignin, increase the resistance to water flow, they do not entirely restrict it. Furthermore, it is generally believed that water moves across the plasma membranes of the cortical parenchyma cells relatively freely (see Steudle and Peterson, 1998). It should be noted, however, that water not only crosses cell membranes by diffusion through the lipid bilayer, but also through specialized water channel proteins in the plasma membrane called **aquaporins**. Roots have the ability to alter their water permeability in response to environmental signals, and such changes are thought to be related to changes in cell membrane permeability mediated by aquaporins (Javot and Maurel, 2002). Steudle and Peterson conclude that as water reaches the primary xylem, it moves through the lignified cell walls of vessel members primarily through the thin, highly porous pit membranes. In the young roots of *Zea mays*, pit membranes occupy only about 14% of the total surface area of metaxylem vessel members (Steudle and Peterson, 1998). They calculate that the vessel walls provide 10–30% of the resistance to radial water flow, but note that resistance would be variable depending on the area of wall surface comprised of primary wall. For example, in primary xylem vessel members with helical secondary wall thickenings and large areas of exposed primary wall, the resistance to water flow would be considerably less than in pitted vessel members.

Three **radial pathways** are generally recognized for the lateral movement of water in young roots (Fig. 16.12), an apoplastic path, a symplastic path through plasmodesmata, and a transcellular path, across cell walls, protoplasts, and plasma membranes. These parallel pathways are characterized by different degrees of resistance to flow, and all are probably utilized in variable degrees during the radial transport of water across the young root (Steudle and Peterson, 1998).

Nutrient ions, upon accumulation in high concentration in the stelar region of roots, would tend to diffuse outward through the apoplast along the concentration gradient were it not for the Casparian bands in the endodermal cell walls (see Peterson *et al*., 1993; Steudle and Peterson, 1998). Consequently, unlike the passive flow of water across the tissues of the root, nutrient ions are actively pulled through the root tissues against concentration gradients through plasmodesmata or across cell membranes. Ma and Peterson (2001b) concluded that in *Allium cepa* there was a high degree of ion transport across cell membranes between epidermis and exodermis, a high degree of plasmodesmatal transport of ions through the cortex, across the endodermis and into the pericycle, and a high degree of membrane transport from

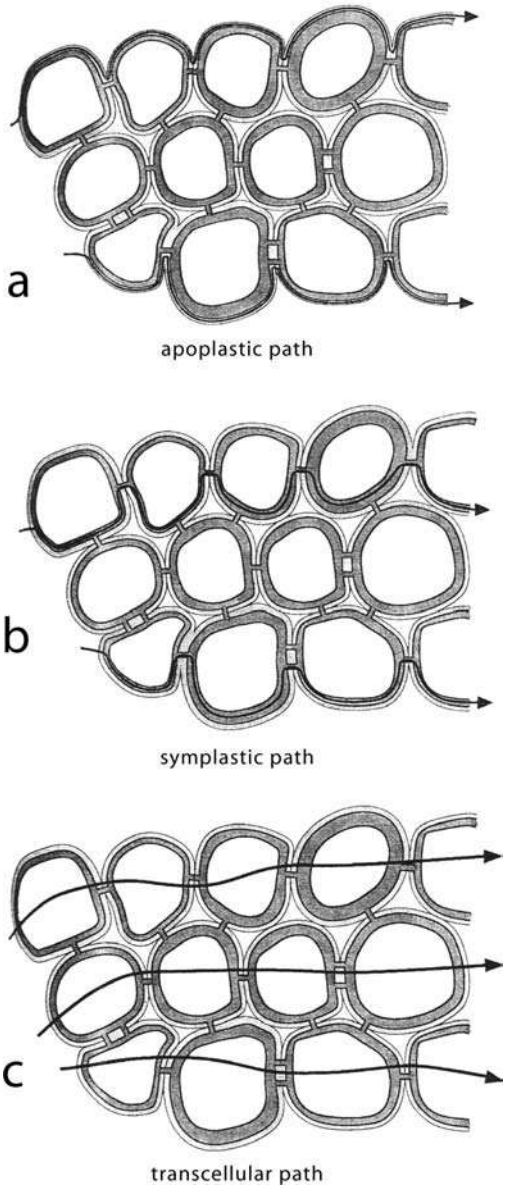

Figure 16.12 Diagrams illustrating the paths of lateral water movement within roots. (a) Apoplastic path: water moves through the cell walls (light shading) around the protoplasts (dark shading). (b) Symplastic path: water moves through the protoplasts of adjacent cells and across the walls between protoplasts through plasmodesmata. (c) Transcellular path: water moves across the walls, plasma membranes, and protoplasts. From Steudle and Peterson (1998). Used by permission of Oxford University Press.

pericycle into stelar parenchyma from which ions were transported directly into protoxylem vessel members. It seems likely that a similar pattern characterizes other taxa. (For more detail about the lateral transport of water and nutrient ions across the root, please see Steudle and Peterson (1998) and Ma and Peterson (2001b).)

Development of primary tissues

New cells produced by root apical meristems grow and differentiate. Often emphasis has been placed on cell elongation as the first stage in development. Recent studies, however, demonstrate, at least in *Zea*

mays, that cell growth is initially isodiametric (Baluska *et al*., 1990, 1993). During this phase of growth, cells increase essentially equally in length and width, and peripheral microtubules, which direct the orientation of cellulose microfibrils, become arranged transversely to the long axes of the cells in preparation for active cell elongation. Gibberellic acids are thought to regulate this change in orientation of microtubules and, thus, control the polarity of cell growth during the elongation phase (Baluska *et al*., 1993). Whereas the zone of isodiametric growth is conspicuous in maize, it is relatively inconspicuous in some other species (e.g., Bell and McCully, 1970).

Growth and differentiation immediately proximal to the root apical meristem occur in provascular tissue, ground meristem, and protoderm (Fig. 16.13a). Cell growth and increase in vacuolar volume (Fig. 16.13b) in these regions result from uptake of water and resulting turgor pressure. Maintenance of turgor pressure requires wall loosening resulting in increase in wall area which, with adequate solute concentration, results in water uptake and continued cell growth (Cosgrove, 1993; Pritchard, 1994). In addition to increase in cell size by turgor pressure, cell membranes and organelles as well as cell wall components are synthesized during growth. As in other parts of the plant, communication between cells or cell domains in roots (i.e., signaling and molecular trafficking) commonly takes place, symplastically, by way of plasmodesmata, although the transfer of small molecules may occur apoplastically. In a study of distribution of plasmodesmata in root tips of *Arabidopsis*, Zhu *et al*. (1998) found that primary plasmodesmata were abundant in transverse walls of all transitional tissue regions (i.e., protoderm, ground meristem, and provascular tissue). Although some secondary plasmodesmata occurred in transverse walls they were more frequent in longitudinal walls between cell files of adjacent tissues, and between different tiers of apical initials. They concluded, further, that plasmodesmatal distribution was tissue specific. Signals (e.g., hormones) that control gene expression in particular cells or tissue domains could be restricted by secondary plasmodesmata in the longitudinal walls between cells or tissues, and longitudinal flow of information could be facilitated by the abundant primary plasmodesmata in the transverse walls. However, Zhu *et al*. (1998) emphasized that during development, as cells elongated and differentiated (i.e., approached maturity) in the proximal regions of these tissue regions, primary plasmodesmata disappeared from the transverse walls, but the density of secondary plasmodesmata in the longitudinal walls remained constant.

Differentiation of mature tissues (Fig. 16.13c) from derivatives of provascular tissue, ground meristem, and protoderm is **acropetal**, that is, maturation proceeds from more proximal to more distal regions. In many taxa, the pericycle is the first tissue region to differentiate visually from provascular tissue. The primary phloem begins its differentiation earlier than the primary xylem and, thus, functional protophloem occurs closer to the apical meristem than functional protoxylem (Fig. 16.14). Provascular strands are also characterized by a latitudinal pattern of development. In a protostelic root, the first incipient

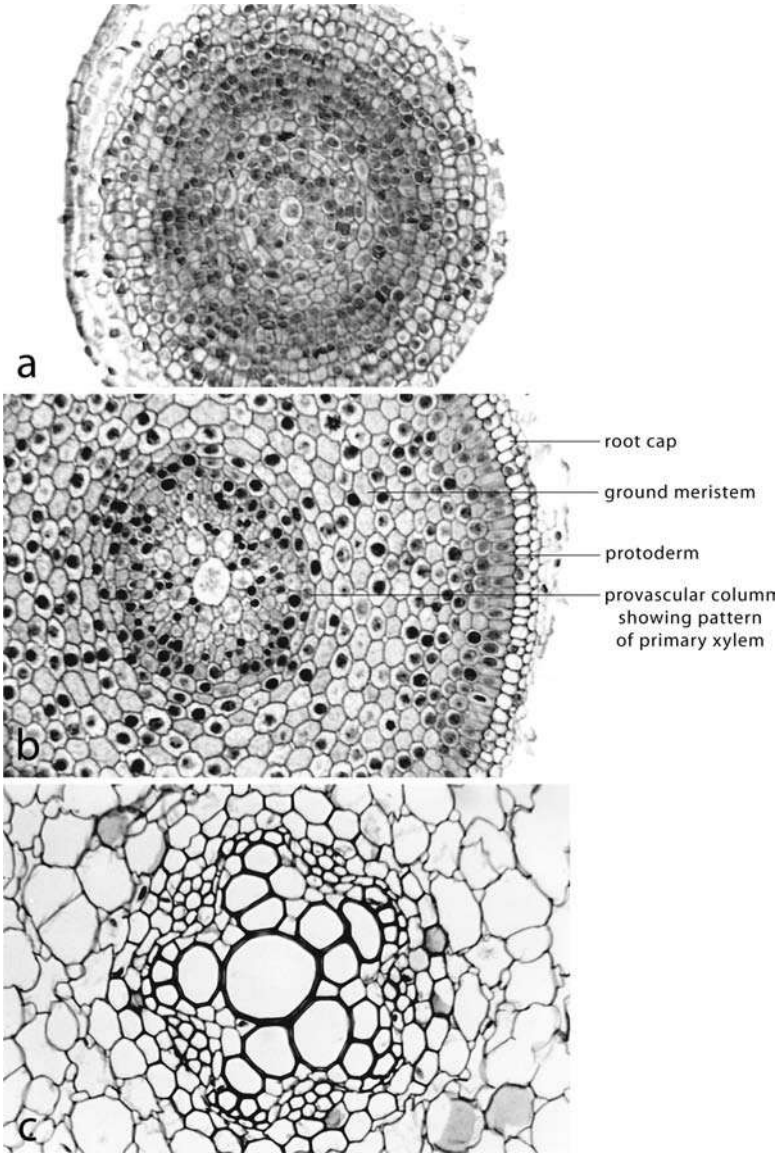

Figure 16.13 Transverse sections illustrating three stages in the development of the root of *Allium*. (a) Transverse section just proximal to the root cap in which tissue regions are immature and indistinct. (b) A more mature region showing well-defined protoderm, ground meristem, and provascular column. At this level the cells are more highly vacuolate, and the pattern of the primary xylem is apparent. (c) A mature region in which the tissues of the central column are distinct. Note the pentarch primary xylem column and the bundles of primary phloem between the ribs of xylem. Magnification (a–c) × 183.

primary xylem cells to become apparent are large, metaxylem cells in the center of the xylem column (Fig. 16.13a, b). As development proceeds in dicotyledons and gymnosperms, the ribbed pattern of the primary xylem column becomes apparent (Fig. 16.13b). However, the first primary xylem cells that acquire secondary walls and become functional are protoxylem cells at the ends of the ribs (Fig. 16.14). From the protoxylem, development continues toward the center of the primary xylem column through the metaxylem. Thus, development of the primary xylem is **centripetal**. This pattern of development is also referred to as **exarch** (Figs 16.13c, 16.14). Development in the bundles of incipient primary phloem is also centripetal in that the protophloem matures

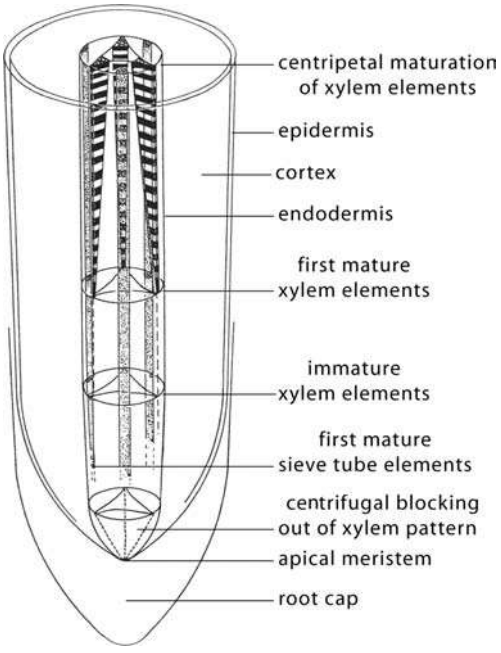

Figure 16.14 Diagram of a root of *Pisum* (pea) showing the spatial relationship between primary tissue regions and their relative levels of differentiation. Note that the primary phloem differentiates closer to the apical meristem than the primary xylem. From Torrey (1953). Used by permission of the Botanical Society of America.

first at the outer edge followed by maturation of metaphloem toward the center of the axis.

Controversy surrounds the nature of the tissue from which the pith differentiates in some roots. Some botanists consider this tissue to be ground meristem, others provascular tissue. The latter view is supported by the fact that plants that have a pith in their most basal regions are often characterized in more apical regions by its absence. In other words, in such plants, as the roots become older, the central meristematic tissue differentiates into primary xylem.

Concurrently with development of primary vascular tissues, cortical tissues develop through growth and differentiation of the ground meristem and its derivatives. Close to the root apex, periclinal divisions result in files of cells that increase the diameter of the root, followed by anticlinal divisions which, with cell elongation, result in increase in its length. Early in the process of differentiation, and close to the apical meristem, as cortical cells grow, the system of intercellular channels develops. The innermost layer of cells in the cortical region develops as the endodermis (Fig. 16.13c) at the same level as the root hair zone in the epidermis. Differentiation of cortical tissue is acropetal.

The protoderm (Fig. 16.13b) and the epidermis which differentiates from it have somewhat different origins in different major groups. In monocotyledons, the epidermis and the cortex have a common origin from the central tier of apical initials. By contrast, in many dicotyledons the epidermis and root cap are both derived from the basal tier of initials. However, in many dicotyledons (including many tree species) that lack tiers of initials, epidermis, cortex, vascular column, and root cap all originate from a single cluster of initials in the root apex (for

more detail, see the section above on apical meristems). In some taxa, in the incipient root hair zone, certain small cells from which root hairs will develop are formed by unequal divisions. These cells, called **trichoblasts**, differ from adjacent cells by having densely staining cytoplasm and larger nuclei. In other taxa, cells from which root hairs develop exhibit no apparent structural differences from adjacent cells. New root hairs develop at about the same level as the first mature protoxylem.

For many years, epidermal cells that produce root hairs have been used for the study of cell growth, especially cell elongation. Recent analyses of root hair development in *Arabidopsis thaliana* have provided significant information on the role of genes in development (e.g., Schiefelbein and Somerville, 1990; Dolan *et al*., 1994; Galway *et al*., 1994; Masucci and Schiefelbein, 1996; Berger *et al*., 1998; Schiefelbein, 2000). The production of root hairs in *Arabidopsis* and other members of the Brassicaceae is position dependent (Schiefelbein, 2000). Protodermal cells that will differentiate into root hair cells (trichoblasts) are located over the anticlinal walls of subjacent cells and those that will not produce root hairs are located next to them in contact with the outer periclinal walls of subjacent cells. Genetic studies have demonstrated the presence of genes in protodermal cells that specify those that will differentiate into either root hair cells or non-root hair cells (see Berger *et al*., 1998). Furthermore, ablation experiments in which adjacent cells moved into the space vacated by the killed cells clearly demonstrate that development of these cells is position dependent. Root hair cells that become located in the former positions of non-root hair cells, and non-root hair cells that move into the space vacated by root hair cells, take on the characteristics of the ablated cells (Berger *et al*., 1998). It is believed that root hair initiation is controlled by auxin and/or ethylene (Schiefelbein, 2000). Following initiation, wall loosening, controlled by expansin genes (see Baluska *et al*., 2000; Cho and Cosgrove, 2002), leads to the formation of an outward bulge in the periclinal wall of the trichoblasts followed by tip growth and elongation of the root hair. During root hair growth, the cytoskeleton is involved in the movement of vesicles containing the precursor compounds necessary for cell wall synthesis (see Chapter 5 for more detail on cell elongation).

Auxin and tissue patterning

The various histological patterns described above develop in tissues derived from the apical meristem. It is widely accepted that pattern formation is under genetic control and mediated by the hormone auxin, but the mechanism of this control of cell and tissue differentiation is only beginning to be understood (see also Chapter 5). Recent studies of patterning in the root tip of *Arabidopsis thaliana* indicate that histological pattern formation is influenced by auxin concentration gradients and PIN proteins that function as **auxin efflux transporters**

(proteins that transfer auxin from cells in one region to cells in another) (Sabatini *et al*., 1999; Friml and Palme, 2002; Friml *et al*., 2002; Benkova *et al*., 2003).

Auxin moves from apical regions of the shoot through the living cells of undifferentiated vascular tissues (provascular strands and the vascular cambial zone) to other parts of the plant (**polar auxin transport**). When it reaches the apical meristem of the root it is redistributed through the ground meristem and protoderm to the root cap and the more proximal regions of the root apex. Auxin can only leave cells by **PIN efflux transporters**. The PIN genes encode the auxin transport proteins which regulate the development and location of auxin concentrations and **auxin maxima**, sites of the initiation of tissue differentiation. Tissue differentiation proceeds along concentration gradients, and results in pattern formation (see Scarpella *et al*., 2006; Scheres and Xu, 2006).

In the root, high concentrations of auxin stimulate the induction of xylem, and low concentrations induce the production of phloem. It has been suggested that the alternate arrangement of ribs of primary xylem and strands of primary phloem in the root is controlled by alternate streams of auxin of different concentrations flowing toward the root tip (Aloni *et al*., 2006). In taxa characterized by exarch development of primary xylem, high concentration streams induce vessels of protoxylem followed by the induction of metaxylem vessels. Low concentration streams induce the alternate primary phloem strands. Because sieve tubes are induced and differentiate under the influence of low auxin concentrations, they mature before vessels in the xylem ribs and closer to the root tip. This early maturation possibly provides a conduit for the flow of cytokinins from the root cap as well as a non-polar flow of auxin through the sieve tubes and associated, differentiating cells of the provascular strands (Aloni *et al*., 2006).

Lateral root development

Initiation of lateral roots is **endogenous**, occurring, primarily, in the pericycle in seed plants and in the endodermis or cortex in pteridophytes. In many taxa there is a specific and constant position of lateral root initiation in relation to the ribs of the primary xylem. In pteridophytes lateral root initiation is always directly opposite the ends of the xylem ribs whereas in seed plants the site of initiation is variable, sometimes opposite the ends of xylem ribs, sometimes opposite the strands of primary phloem, sometimes between the ends of ribs and the adjacent strands of primary phloem (Fig. 16.7a–c).

In gymnosperms and angiosperms lateral **root primordia** are initiated in the pericycle proximal to the zone of elongation by periclinal divisions (Fig. 16.15a) followed by anticlinal divisions and cell growth (Fig. 16.15b). Prior to primordium formation in *Arabidopsis*, auxin accumulates at the sites of primordium initiation (Benkova *et al*., 2003). Subsequently, under the control of PIN efflux transporter proteins,

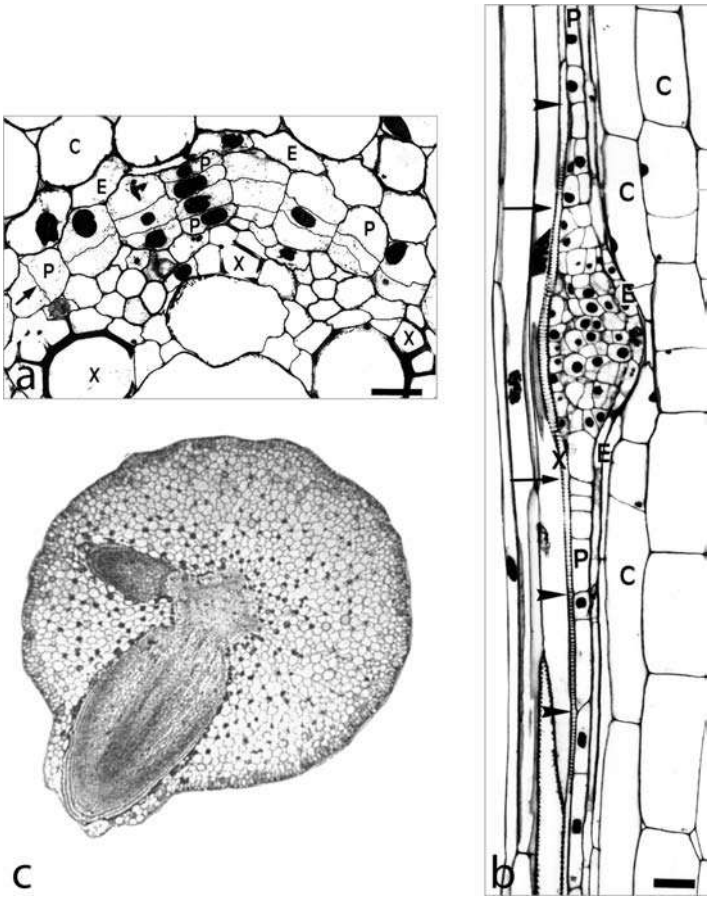

Figure 16.15 Lateral root development in *Allium*. (a) Transverse section showing short files of cells formed by periclinal divisions in the pericycle at the site of lateral root initiation. C, cortex; E, endodermis; P, pericycle; X, xylem. Arrow indicates an anticlinal wall in a cell in the pericycle. Bar = 50 μm. (b) Radial longitudinal section illustrating the young lateral root. Bar = 50 μm. Arrowheads indicate sites of proliferation of pericycle cells around the developing lateral root primordium; arrows delimit the root primordium. (c) Transverse section of a root of *Salix nigra* (black willow) with lateral roots. The larger lateral root has grown through the cortex, rupturing the epidermis. At this stage primary tissue regions are apparent behind the apical meristem. (a, b) From Casero *et al.* (1996). Used by permission of Springer-Verlag Wien. (c) From Eames and MacDaniels (1925).

auxin is transferred into the primordia and auxin concentration gradients are established with their maxima occurring at the tips of the primordia. Under the influence of PIN genes, the various tissue regions differentiate.

Recently, Aloni *et al.* (2006) have suggested that lateral root initiation is dependent on three hormonal signals, auxin, cytokinin, and ethylene. They note that auxin promotes, whereas cytokinin restricts, lateral root development. Ethylene also promotes lateral root development, but is known to interrupt auxin transport. On these and other bases (please see Aloni *et al.*, 2006 for details, and references sporting these conclusions) Aloni and co-workers present an interesting hypothesis to explain the role of each of these hormones in lateral root initiation. They suggest that auxin, the primary hormonal signal, is transported downward in the young root through differentiating protoxylem as well as through the pericycle. Cytokinin, produced in the root cap, and which inhibits lateral root initiation, moves upward through differentiating vascular tissue toward the zone of lateral root initiation. Local increase of auxin in immature protoxylem vessels stimulates synthesis of ethylene which moves laterally into the pericycle where it blocks the downward flow of auxin. The result is a local increase of auxin at this

level which stimulates lateral root initiation. The upward movement of cytokinin prevents lateral root initiation in the zone of elongation near the root tip. This hypothesis can be appropriately applied to the role of hormones in lateral root initiation in a main root which is characterized by a ribbed stele and in which lateral roots are produced opposite the ends of ribs of primary vascular tissue. It is not as easily applied to roots in which lateral roots are initiated opposite strands of primary phloem located between ribs of primary xylem, or in other locations.

In general, following primordium formation, and as development of the lateral root continues, anticlinal divisions often occur in the endodermis opposite the initial site of cell division in the pericycle, and in some species the endodermis becomes biseriate locally. Periclinal divisions in the endodermis result in the formation of a sheath over the developing lateral root as it pushes its way through the cortex, and a root cap and transitional tissue regions – provascular tissue, ground meristem, and protoderm – differentiate in the apical region of the young lateral root (Fig. 16.15c).

Connections between the lateral and the parent roots develop by the differentiation of vascular tissues within parenchyma tissue in the intervening region (e.g., Casero *et al*., 1996). It is especially important to understand the structure of the vascular tissues that connect parent and lateral roots because lateral roots play a significant role in absorbing and transporting water and minerals from the soil solution into the main root. In both maize (McCully and Mallet, 1993; Shane *et al*., 2000) and barley (Luxova, 1990) the vascular systems of main and lateral roots are connected by an extensive vascular plexus (Fig. 16.16), the components of which differentiate from parenchyma in the pericycle. This plexus consists of a mixture of numerous small, short tracheary elements (some of which are vessel members) and xylem parenchyma bounded by sieve tube members, all described by McCully and Mallett (1993) as primarily cuboidal (Fig. 16.16b, c). The tracheary elements which are connected to each other by bordered pits apparently provide an effective apoplastic conduit for the movement of water and solutes from lateral roots into the main root. The pits in the contiguous walls between vessel members of the primary xylem of the main root and the tracheary elements of the lateral roots, termed **boundary pits**, are very large and have conspicuous pit membranes (Fig. 16.16a). Because the boundary pit membranes have very small pores and can filter out particles with mean diameters as small as 4.9 ± 0.7 nm, Shane *et al*. (2000) concluded, with other evidence, that boundary pit membranes are efficient filters for microbes and particulates.

The primary phloem which is largely peripheral to the tracheary tissue in the vascular plexus connects directly to that of the main root. McCully and Mallett (1993) also observed sites of direct contact between sieve tube members and tracheary elements (Fig. 16.16a), and conclude that, as in the leaves of a few grasses (see Eleftheriou, 1990) and ferns (Evert, 1990), these might play a role in nutrient recycling between the xylem and the phloem.

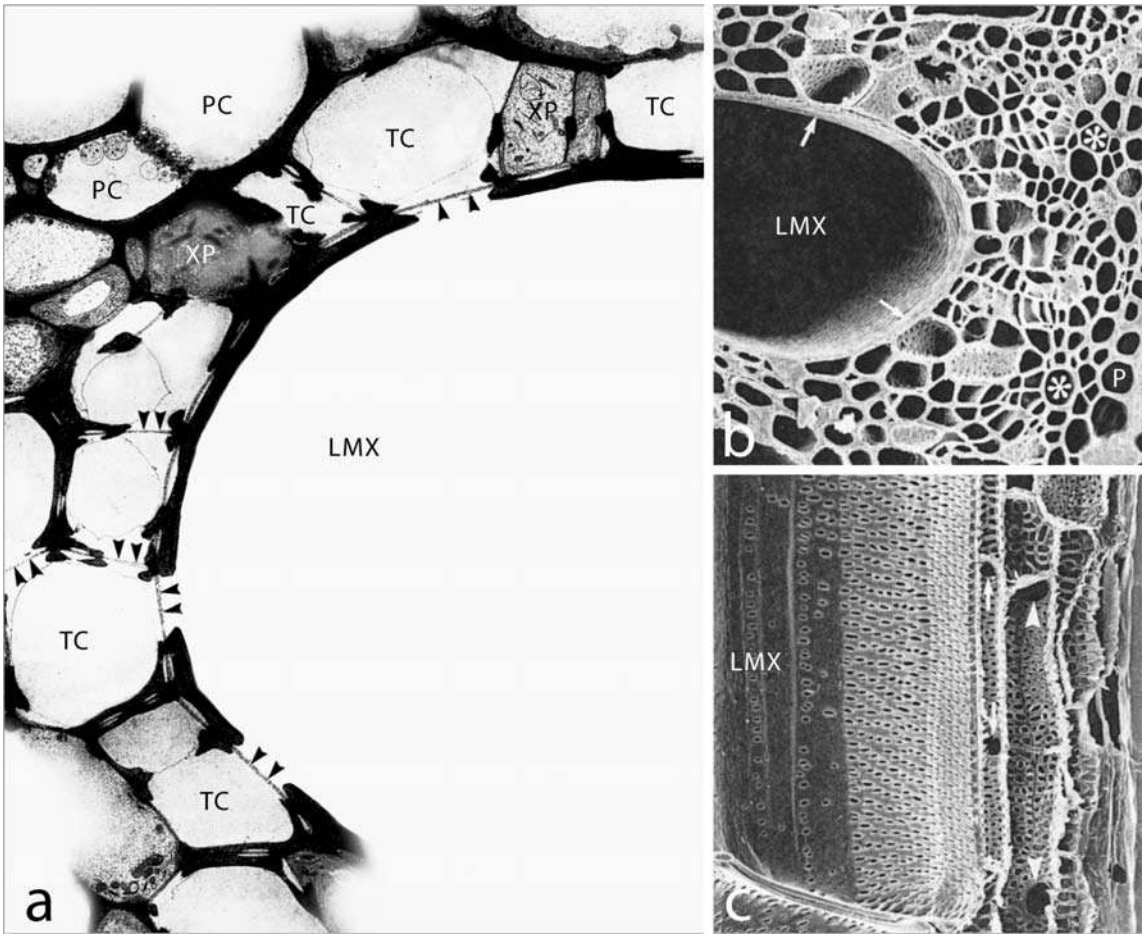

Figure 16.16 Vascular connection between the main root and a lateral root of *Zea mays*. (a) Transmission electron micrograph of a transverse section of part of a late metaxylem vessel member (LMX) of the main root. The wall of this vessel member, facing the exterior of the root, is bounded by numerous tracheary connector elements (TC) of the lateral root. The contiguous walls between the connector elements, and between connector elements and the vessel member of the main root, contain bordered pit-pairs with wide apertures and uniformly thick pit membranes (arrowheads). XP, xylem parenchyma; PC, connector sieve elements. Magnification × 2750. (b) Scanning electron micrograph of a transverse section of a late metaxylem vessel member and associated tracheary connector elements of a lateral root. Asterisks indicate sieve tube members; arrows indicate tracheary connector elements. P, pericycle of the main root. Magnification × 194. (c) Scanning electron micrograph of a longitudinal section through a region similar to that shown in (b). Some of the tracheary connector elements are vessel members. Note the vessel member end wall perforations (arrows and arrowheads). Magnification × 262. (a) From McCully and Mallet (1993). Used by permission of Oxford University Press. (b, c) From Shane *et al.* (2000). Used by permission of Oxford University Press.

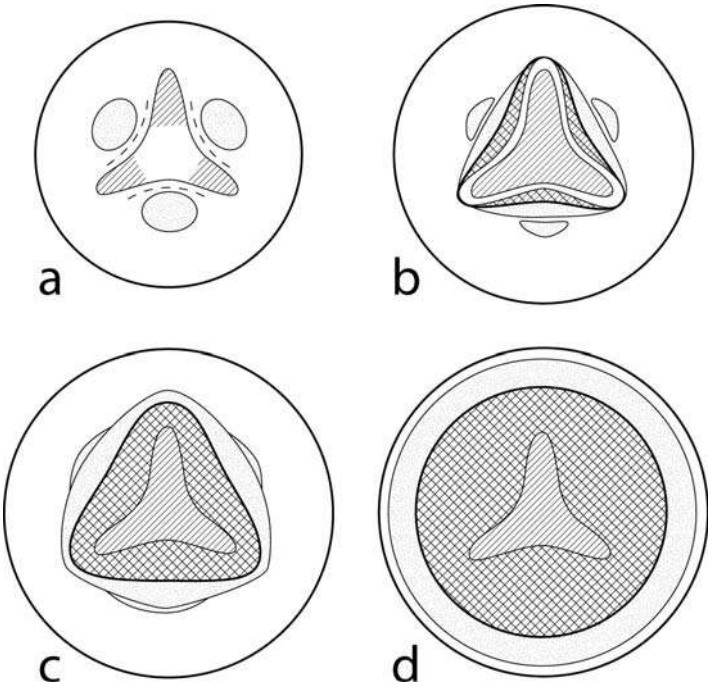

Figure 16.17 Diagrams of transverse sections illustrating the origin of secondary tissues in roots. Primary xylem is lined; secondary xylem is cross-hatched; primary phloem is unshaded; secondary phloem is stippled. (a) Differentiation of primary xylem is incomplete. The vascular cambium is indicated by dashed lines. (b) As the cambium produces secondary xylem and phloem, the primary phloem is compressed. The cambium is indicated by a heavy line. (c, d) With continued activity, the vascular cambium attains a circular outline in transverse view, and subsequent increments of secondary xylem and phloem will appear as cylinders.

Adventitious roots

Roots that arise from stems, other plant parts (e.g., the fleshy leaves of plants such as *Sedum* and *Begonia*), and regions of main roots other than the pericycle proximal to the zone of elongation are called **adventitious roots**. Such roots may originate from callus tissue associated with wounds, or endogenously from pericyclic parenchyma, from interfascicular parenchyma, and in old roots, from vascular rays or the axial parenchyma in secondary phloem. As noted earlier in this chapter, the root system of most monocotyledons is composed of adventitious roots that develop at the base of the stem, but in some grasses they also develop from axillary shoots. The root systems of pteridophytes consist of adventitious roots that develop in internodal regions or at nodes in association with leaves. In some extinct ferns, e.g., *Botryopteris*, adventitious roots were even borne on petioles.

Secondary growth

As in the stem, the production of secondary vascular tissues in roots is initiated by activity of the vascular cambium. The cambium differentiates first from provascular tissue in the bays between ribs of primary xylem and to the inside of the strands of primary phloem (Fig. 16.17a). These regions of the cambium commonly become active in producing secondary xylem and phloem before the cambium has become continuous around the outer edges of the primary xylem ribs (Fig. 16.17b),

differentiating in these latter regions from pericycle. Because of this developmental pattern, the cambium only gradually attains a circular form as viewed in transverse section (Figs 16.17b–d, 16.18a). In many plants, especially woody plants, as secondary phloem and xylem are produced, the primary phloem is compressed and obliterated. In some herbaceous perennials in which secondary xylem is produced in limited quantities, little or no secondary phloem may be produced and the metaphloem functions as the conduit for transfer of photosynthate throughout the life of the plant (Fig. 16.18c, d). In such plants protophloem is usually compressed and obliterated.

If no secondary vascular tissues, or only small amounts are produced, a periderm does not develop and the cortex is retained for the life of the plant (Fig. 16.18c). In such plants the epidermis may develop a thick cuticle, thus becoming the protective outer boundary of the root system, or an exodermis may develop in the outermost cortex, comprising a protective layer. The part of the outer cortex in contact with and to the interior of the exodermis may consist of one to several layers of sclerenchyma. This region and the exodermis comprise the **hypodermis**. Root structure of this type is characteristic not only of many herbaceous taxa of both dicotyledons and monocotyledons, but also of some large plants such as the palms.

The tracheids and vessel members in the secondary xylem of roots are commonly large in transverse dimensions and thin-walled (Fig. 16.18b–d). Both secondary phloem and secondary xylem in roots are characterized by large amounts of parenchyma, including that of abundant, large rays. These adaptations are directly related to the storage function of roots.

In roots that produce large amounts of secondary vascular tissues, a phellogen differentiates within the outer pericyclic parenchyma shortly after the beginning of cambial activity. As secondary growth leads to diametric expansion of the root, the continuity of the phellogen is maintained by numerous anticlinal divisions that result in an increase in its circumference. The single-layered phellogen produces phellem to the exterior and phelloderm to the interior, producing a periderm that is in contact with the secondary phloem (Fig. 16.18a, b). Cut off from a source of water and photosynthate, the cortex and epidermis die and slough off. In old roots, rhytidome similar to that in stems develops, but as it develops the outer part decays. Consequently the rhytidome remains relatively thin and the root surface smooth.

The root cap: its function and role in gravitropism

The **root cap** covers the apical meristem of the root and, traditionally, has been thought of, primarily, as a protective structure. We now know that it has other very important functions. As new root cap cells are continually produced by the root cap meristem, they gradually move to the periphery and ultimately are sloughed off. Initially they function

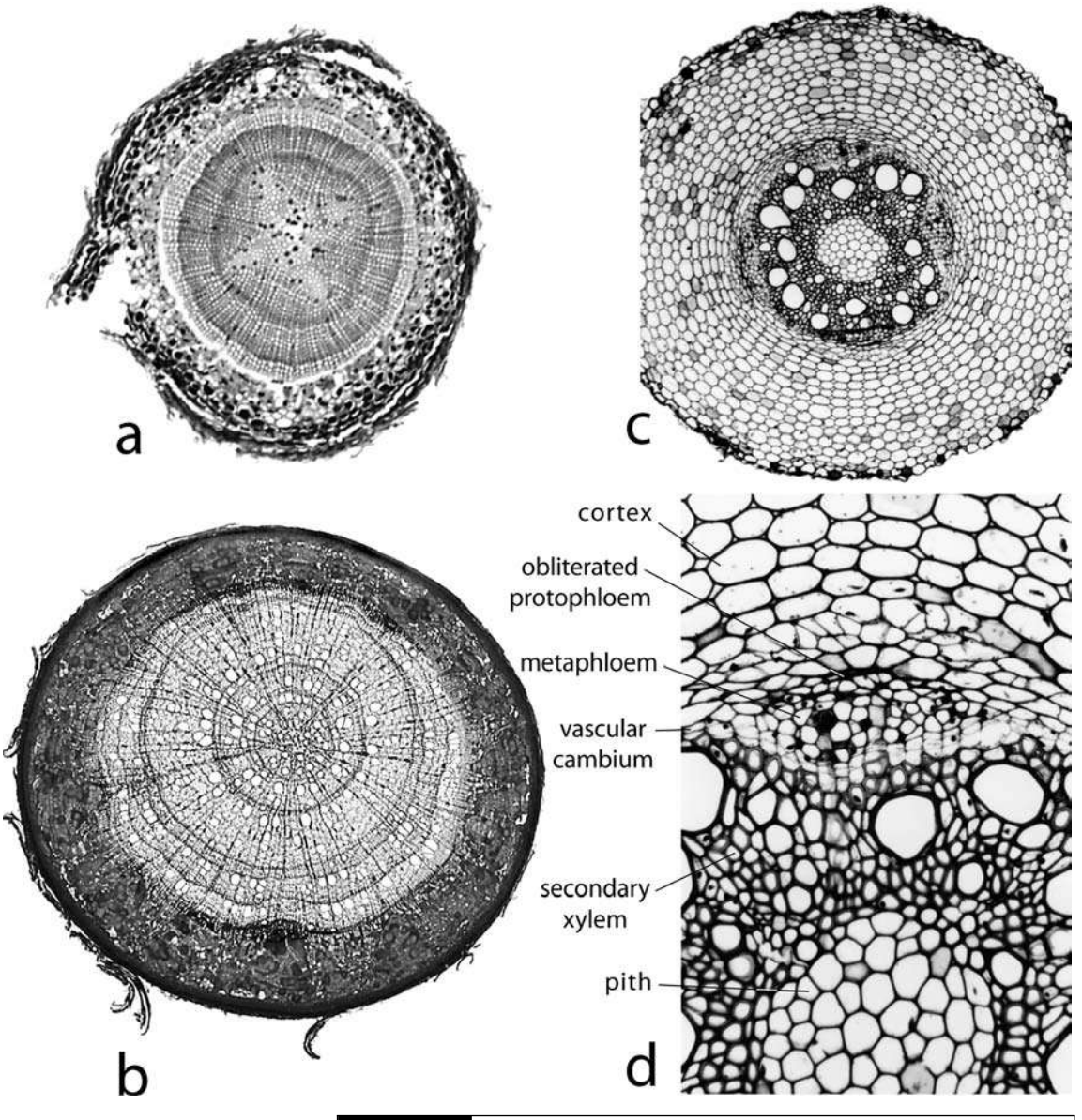

Figure 16.18 Transverse sections of roots with secondary tissues. (a) A root of *Cedrus deodara* with tetrarch primary xylem. Note that the vascular cambium was not continuous around the ends of the primary xylem ribs until near the end of the first growing season. Periderm is in contact with the secondary phloem. The cortex and epidermis have sloughed off. Magnification × 43. (b) A root of *Tilia americana*. The secondary xylem contains numerous rays and very large vessels. Note the periderm in contact with the secondary phloem. Magnification × 24. (c, d) Root of *Pelargonium*. Note the pith, the cortex, and the large vessels in the secondary xylem. (d) The vascular cambium produces little or no secondary phloem, and the metaphloem functions as the major conduit for the transport of hormones and photosynthate for the life of the plant. Note the compressed and obliterated protophloem. Magnification (c) × 50, (d) × 185.

as statocytes (perceptors of gravity), but as they near the periphery they become secretory cells that produce and secrete polysaccharide mucilage (Barlow, 1975, 2002), thought to function in lubricating the root as it pushes its way through the soil. The secretion of mucilage is granulocrinous (see Schnepf, 1993). Golgi vesicles containing mucilage fuse with the plasma membrane of cells in the outer part of the root cap, and the mucilage is thereby released into the cell walls through which it migrates to the exterior, coating the root tip. This coat of mucilage protects the root tip from desiccation, prevents or decreases the probability of entry into the root of toxic substances, and facilitates the exchange of ions.

Both shoots and roots sense and respond to gravity. This response is called **gravitropism**. Shoots are negatively gravitropic whereas roots are positively gravitropic. A shoot that has been beaten down by heavy rain or blown down by strong wind has the ability to perceive this change in orientation and, through a series of physiological signals, to mediate a pattern of growth that results in a reorientation to an upright position (Blancaflor and Masson, 2003). This response is highly adaptive because an upright orientation of the shoot is essential for efficient photosynthesis and, consequently, continued growth. Gravitropism results in the downward growth of roots, thus controlling the orientation of the root system in the substrate. This is also highly adaptive since it leads to anchoring the root system in the substrate and placing it in a position to absorb water and mineral elements from the soil. The degree to which roots are **gravitropic**, is highly variable. Tap roots are strongly gravitropic whereas lateral roots vary from being only slightly to being not at all responsive to gravity.

The gravity response in the roots of seed plants is initiated in the root cap when a deviation from the vertical orientation of the root tip is perceived. For root curvature to occur a biochemical signal, such as a plant hormone, must be activated. Upon its transmission to the site of differential growth, the zone of elongation, root curvature occurs.

Specialized cells of the root cap, called **statocytes**, contain **amyloplasts** (plastids containing starch), also known as **statoliths**. When the root tip is vertical, the amyloplasts are located near the distal transverse walls of the statocytes (Fig. 16.19a, b). However, when the root tip is horizontal, the amyloplasts sink toward the lateral walls (Fig. 16.19c), and cells in the upper part of the elongation zone of the root begin to grow faster than those in the lower part which results in its downward curvature and a return of the amyloplasts to their original position near the distal transverse walls of statocytes in the root cap. The mechanism of this gravitropic response and the precise role of the amyloplasts is unclear. It is surmised that in a root that is not oriented vertically a chemical signal, such as a hormone, when transferred to the zone of elongation, will accumulate in higher concentration in the lower than in the upper region of the zone. Since auxin, the hormone long believed to control root curvature, inhibits growth in high concentrations, cell elongation will occur in the upper region of the elongation zone and be restricted in the lower, resulting in a downward curvature of the

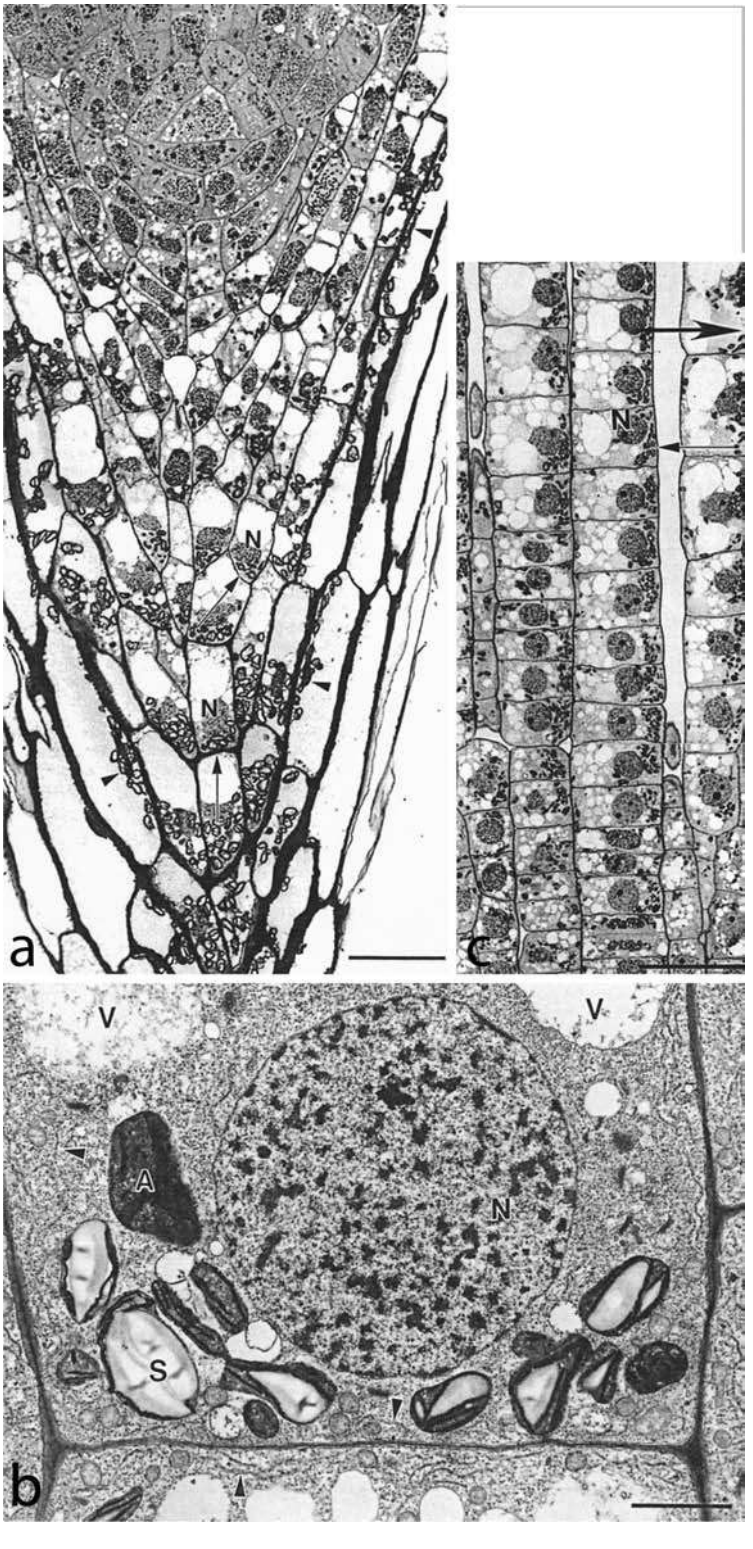

Figure 16.19 Gravitropic responses of amyloplasts (statoliths) in cells of the root cap and in cells of the cortex in the elongating region of roots of *Equisetum hyemale* (horsetail). (a) Median longitudinal section of the root tip showing the apical initial (asterisk) and the root cap. In this root, grown and fixed in vertical orientation, the nuclei and statoliths (amyloplasts) of the central cells of the root cap have sedimented against the lower transverse walls (arrows). N, nucleus. Bar = 50 μm. (b) Transmission electron micrograph of sedimented nucleus and amyloplasts in a cell from a vertically grown root. A, amyloplast; N, nucleus; S, starch; V, vacuoles; arrowheads indicate peripheral endoplasmic reticulum. Bar = 3 μm. (c) Longitudinal section of a root grown in a horizontal orientation. The root tip is below the bottom of the page. All nuclei and amyloplasts in cells of the inner cortex in the zone of elongation have sedimented toward the periclinal walls (small arrow). The large arrow indicates the gravity vector. Bar = 50 μm. (a–c) From Ridge and Sack (1992). Used by permission of the Botanical Society of America.

root. This concept of differential growth related to differential distribution of auxin, and resulting in positive geotropism in roots, was proposed by Cholodny and Went in the early part of the twentieth century. The **Cholodny–Went hypothesis** has been widely accepted for many years and recently has been strongly supported by the work of Ottenschläger *et al*. (2003). On the other hand, it also has been challenged on several bases. The most serious challenge comes from experiments that have shown, conclusively, in several species that when auxin synthesis is inhibited, the gravitropic curvature response still occurs (see Evans, 1991; Konings, 1995; Evans and Ishikawa, 1997). In this regard, it is interesting to note that Aloni *et al.* (2006) have demonstrated that cytokinins are constantly produced, and occur in high concentration, in statocytes in the root cap. They are transported through plasmodesmata to the root elongation zone. It is possible, therefore, that both cytokinin and auxin play roles in the growth response to gravity in roots, with cytokinin stimulating the initial, rapid downward bending and auxin, the longer, slower bending of the elongation zone (Aloni *et al*., 2006).

It has been further demonstrated that root curvature can occur in the absence of amyloplasts, and it has been surmised that sedimentation of other cell organelles might serve the same function. In this regard, it is interesting to note that in *Equisetum*, sedimentation of the cell nuclei occurs simultaneously with that of the amyloplasts, usually following them and coming to rest just above them (Fig. 16.19b, c).

The cytoskeleton has also been implicated in the regulation of gravitropism. Amyloplasts have been shown to be enclosed by, or attached to, actin microfilaments. It has been postulated that the movement of amyloplasts during sedimentation would place tension on the actin network which would, in turn, activate a sequence of hormonal signals causing gravitropic curvature of the root (Baluska and Hanstein, 1997; Yoder *et al*., 2001; Hou *et al*., 2003). On the other hand, many studies, in which the actin microfilament system has been disrupted or even depolymerized by various chemical compounds, have shown that gravitropic curvature still occurs. Other studies have demonstrated that the gravitropic response is inhibited or even enhanced (Hou *et al*., 2003). In the face of such contradictory evidence, it is clear that there is still much to be accomplished before we understand the mechanisms by which the physical signals from amyloplast sedimentation are translated into the biochemical signals that control the gravitropic bending response (Hou *et al*., 2003).

Although research in many laboratories has resulted in advances in our knowledge of the factors related to gravitropism in roots (see Blancaflor, 2002; Blancaflor and Masson, 2003), the role of amyloplasts, the routes of transport of the mediating signal to the zone of elongation, the mechanism and control of cell wall relaxation (wall loosening) required during cell elongation, the role of the cytoskeleton, if any, even the nature of the signal which elicits differential cell elongation in the gravitropic response are still not clearly understood. The excellent paper by Blancaflor and Masson (2003) should be consulted

for a comprehensive review and discussion of this fascinating area of research.

Mycorrhizae

The root tip with its root hairs is an efficient region of water and mineral absorption from the soil under optimal conditions of water and mineral availability. The area through which absorption occurs, however, in a single root is relatively small. Furthermore, under conditions of drought, the volume of soil that provides the source of water and minerals for a root tip can be depleted. Consequently, as an adaptation to such conditions, mycorrhizae which greatly enhance the root's absorptive capacity have evolved.

A **mycorrhiza** is the structural combination of a fungus and a root (Fig. 16.20a) resulting in a mutually beneficial symbiotic relationship. The fungus may be either an ascomycete or a basidiomycete. According to Bonfante and Perotto (1995) mycorrhizae occur in approximately 90% of terrestrial plant species. They have not been observed in either the Brassicaceae or Cucurbitaceae, and are rare in aquatic land plants and plants such as sedges that grow in wet substrates. Two major types have been recognized, ectomycorrhizae and endomycorrhizae.

In an **ectomycorrhiza** the fungus forms a dense sheath of hyphae around the root tip with numerous branching hyphae extending from this sheath into the surrounding soil and others penetrating the epidermis and cortex. These internal, much-branched, coenocytic hyphae penetrate the parenchyma tissue through intercellular channels forming a network of hyphae, called the **Hartig net**, between, but in intimate contact with, cells of the cortex. The parenchyma cells associated with the Hartig net are thought to function like transfer cells. Photosynthate is transported into the hyphae in this region, providing a source of nutrition for the fungus, and water and minerals are transported from the hyphae into the cortical cells, benefiting the plant by greatly enhancing the supply of water and minerals, especially in mineral-poor, and dry, soils.

A large majority of vascular plants, possibly up to 80% (Bonfante and Perotto, 1995), are characterized by endomycorrhizae. An **endomycorrhiza**, unlike an ectomycorrhiza, lacks a conspicuous, enclosing sheath or mantle of hyphae although in some forms (called **ectendomycorrhizae**) hyphae form a thin enclosing sheath around the root tip (Fig. 16.20a). In both types, hyphae penetrate the root and proliferate within the cortex (Fig. 16.20b) through intercellular channels. Some hyphae penetrate the walls, but not the plasma membranes, of the parenchyma cells. They form complex, much-branched structures called arbuscules (Fig. 16.20b, c) that become almost completely enclosed by the plasma membranes. Enclosed by the walls of the cells and in intimate contact with the protoplasts through the plasma membranes (Fig. 16.20d) (although *not within* the protoplasts), the **arbuscules** form efficient regions of transfer of photosynthate to the fungus and water and minerals to the plant. Some hyphae form vesicles in the

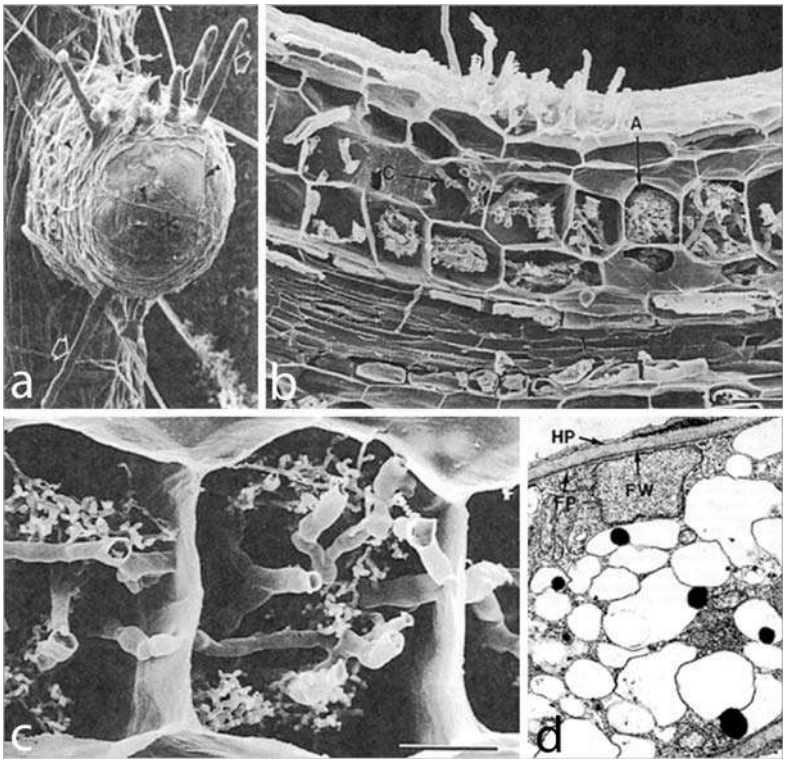

Figure 16.20 (a) Scanning electron micrograph of an endomycorrhiza of *Pinus banksiana*. Note the root tip with unusual apical root hairs (arrows) and a thin mantle of fungal hyphae. A typical endomycorrhiza lacks a hyphal mantle. Magnification × 61. (b) An infected endomycorrhizal root of *Acer saccharum* showing large fungal hyphae (hyphal coils) (C) and arbuscules (much-branched smaller hyphae) (A) in cells of the cortex. Magnification × 198. (c) Close-up of cortical cells showing hyphal coils and arbuscules. Magnification × 1250. (d) Transmission electron micrograph of vacuolated intracellular hyphae. HP, host plasmalemma; FP, fungal plasmalemma; FW, fungal wall. Magnification × 7324. (a) From Scales and Peterson (1991). Used by permission of the National Research Council of Canada. (b–d) From Yawney and Schultz (1990). Used by permission of Blackwell Publishing Ltd.

intercellular channels in which glycogen and/or lipids are stored. Thus, the term **vesicular–arbuscular mycorrhiza** is often used in preference to endomycorrhiza. For more detail about this complex and important area, see Yawney and Schultz (1990), Brundrett and Kendrick (1990), Scales and Peterson (1991), Bonfante and Perotto (1995), Smith and Smith (1997), Massicotte *et al*. (1999), Armstrong and Peterson (2002), Blancaflor *et al*. (2001), and Yu *et al*. (2001).

Nitrogen fixation in root nodules

Whereas nitrogen is constantly being taken from the soil it is also constantly being added to the soil by some plants through the process

of **nitrogen fixation**. This recycling of nitrogen contributes signficantly, with other factors, in preventing the depletion of soil nitrogen. Although nitrogen is an essential element in plant metabolism, atmospheric nitrogen cannot be utilized by most plants. Through time a symbiotic relationship between roots and several soil microorganisms has evolved by which atmospheric nitrogen is converted into a form that plants can use. This process, nitrogen fixation, takes place in root nodules in many taxa of the Fabaceae (Leguminosae) (see Pate *et al*., 1969; Hirsch, 1992; Subba-Rao *et al*., 1995) as well as in several other families of dicotyledons. The only gymnosperms known to fix nitrogen are several members of the cycads in which the symbiont is a cyanobacterium (blue-green alga).

In the Fabaceae the endophytic microsymbiont is the bacterium *Rhizobium*. There is a high degree of specificity between *Rhizobium* species and their host plants, thus a species that will infect one legume genus will not infect another. Infection of the root system which occurs through root hairs stimulates the development of root nodules of distinctive structure. The bacteria aggregate within cells in the center of the nodule. This region is surrounded by a parenchymatous tissue containing vascular bundles which, in turn, is enclosed by an endodermis. Exterior to the endodermis is a cortex characterized by a complex system of intercellular air channels. The endodermis retards the entry of oxygen into the center of the nodule preventing denaturation of nitrogenase, essential to the process of nitrogen fixation which occurs in this region. The nitrogenase is provided by the *Rhizobium*, and a protein, hemoglobin, is provided by the host plant. Sugar utilized as a source of energy required in the process is also provided by the host plant. Numerous plasmodesmata connect the *Rhizobium*-containing cells with the surrounding parenchyma cells. These plasmodesmata are thought to be the conduits by which sugar is transported into the cells where nitrogen fixation occurs, as well as the means by which the resulting amino acids are transported out of this region into the surrounding parenchyma.

In other families, the endosymbiont is usually an actinomycete, the most common being *Frankia*. Well-known taxa of woody dicotyledons that fix nitrogen in root nodules include *Alnus* of the Betulacaceae, *Ceanothus* (tea bush) in the Rhamnaceae, *Eleagnus* (oleaster) of the Eleagnaceae, and *Myrica* (sweet gale) of the Myricaceae. Root nodules in which *Frankia* species are the endosymbionts resemble those of the legumes, except that the actinomycete is usually confined to the cortex. The hemoglobin present in cells in which nitrogen fixation occurs may provide oxygen for metabolism while inhibiting oxygen denaturation of nitrogenase.

Several cycads are known to produce root nodules containing the cyanobacteria *Anabaena* or *Nostoc*. Nitrogen fixation in root nodules of the cycad *Macrozamia* is of significance in the ecology of some Australian forests. *Anabaena* is also known to form a symbiotic relationship with the heterosporous fern *Azolla*. In several Asian countries, colonies of *Azolla* infected with *Anabaena* living in rice paddies contribute, upon death,

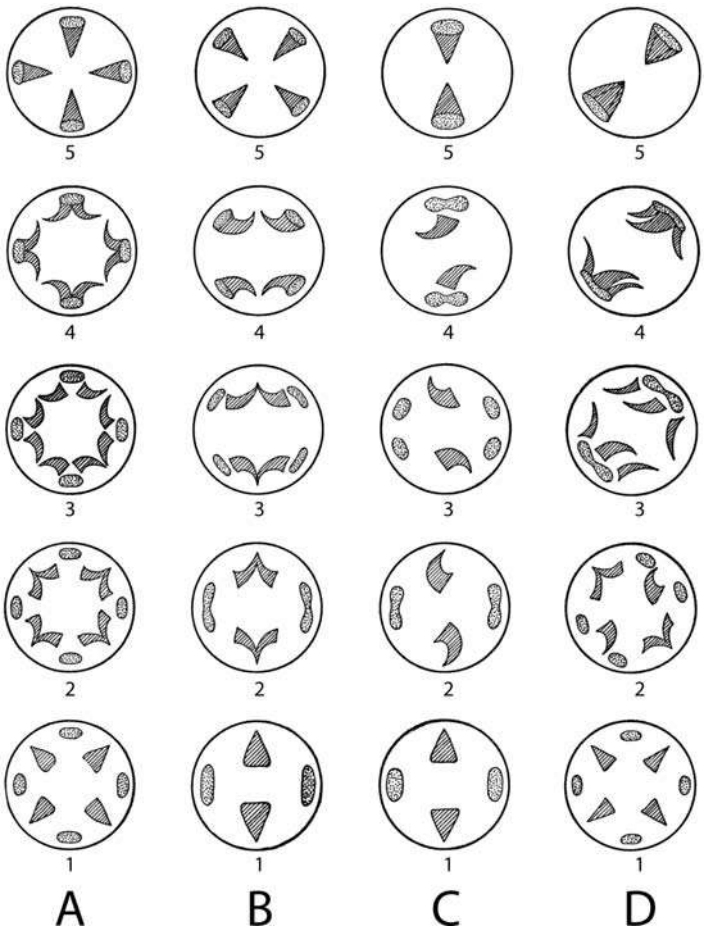

Figure 16.21 Diagrams of four types of root–stem transition (A–D). Diagrams in the lower row, A1–D1, represent roots. Those at level A5–D5 represent stems, with intermediate stages at successive levels between, illustrating separation, rotation, and fusion of primary vascular bundles. Primary xylem is lined; primary phloem is stippled. From Eames and MacDaniels (1925).

significant quantities of nitrogen which can be utilized subsequently by the rice plants.

Root–stem transition

Primary vascular tissues in the developing roots of many seed plants are radially arranged in separate longitudinal bundles or strands whereas in the stems of the same plant they occur together, most commonly in collateral bundles. Furthermore, the order of maturation (or direction of differentiation laterally) is exarch in the root and endarch in the stem in seed plants. Consequently, in the transition region between root and stem there is a reorientation of the primary xylem and primary phloem. This transition commonly takes place over a short distance in the hypocotyl of the embryo in provascular tissue, but in some species, e.g., *Pisum sativum*, it may extend through several internodes. Esau (1965) indicates that in many species the change in orientation of vascular tissue is completed in the cotyledons. A recent example of a transition of this type has been described in *Arabidopsis thaliana* by Busse and

Evert (1999). These changes which would not be conspicuous in the embryo would, however, be clearly expressed upon differentiation of primary vascular tissues in the axis of the developing sporophyte. When the vascular tissue is observed at successive levels in the mature state it becomes apparent that in some taxa the bundles of primary xylem divide and become reoriented in relation to bundles of primary phloem so that collateral bundles with endarch order of maturation are formed. In other taxa, both xylem and phloem bundles divide. One may develop a three-dimensional comprehension of this reorientation of vascular tissues by studying a diagram of vascular tissue orientation at successive levels through the transition region (Fig. 16.21).

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Chapter 17

The leaf

Perspective: evolution of the leaf

All vascular plants except their most primitive ancestors are characterized by leaves (see Chapter 1). As the primary photosynthetic organs, leaves are of great significance not only to the plant but also to many other organisms, including humans, that rely on plants as a source of food. Botanists interested in plant evolution believe that leaves evolved in at least two ways, and in possibly five independent lines in vascular plants (see Niklas, 1997). The leaves of lycophytes are considered **enations** because they are thought to have evolved as simple outgrowths from stems. These leaves, often referred to as **microphylls**, are commonly small although those of some extinct taxa attained great lengths (up to 1 meter in some members of the Lepidodendrales). Like all microphylls, however, they were vascularized by only a single midvein. In seed plants and ferns (possibly also in sphenophytes) leaves are thought to represent evolutionarily modified lateral branch systems. This hypothesis (the telome hypothesis) is based on the fact that the earliest seed plant ancestors were leafless, but bore small lateral branch systems. The fossil evidence indicates that over time, three-dimensional branch systems became flattened and subsequently laminate. Seed plant leaves which, on average, are much larger, and much more complex than those of lycophytes in both gross morphology and internal structure, are often referred to as **megaphylls**. For more detailed discussions of the evolution of leaves see Steward and Rothwell (1993) and Taylor and Taylor (1993).

Leaves may be classified in several categories: **foliage leaves** (which function in photosynthesis), **cataphylls** (bud scales and scales on underground stems which function in protection and/or storage; the first cataphylls to develop are often called **prophylls**), **hypsophylls** (floral bracts which are thought to have a protective function), and **cotyledons** (the first leaves produced in the embryo which may be thin, or thick if they function in storage and provide a direct source of nutrition for the developing seedling).

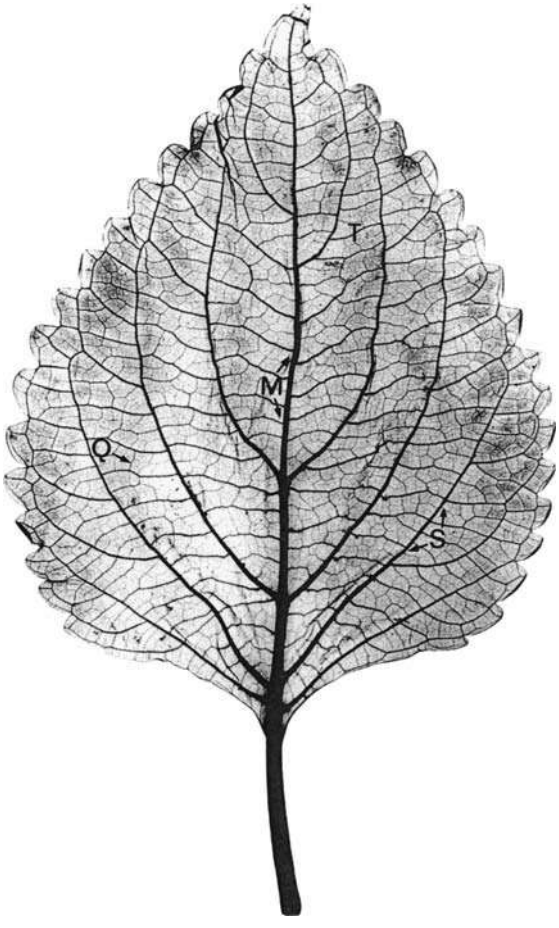

Figure 17.1 Cleared leaf of *Coleus blumei*, a dicotyledon, showing its broad, laminate form and complex system of veins (vascular bundles). M, midrib; S, secondary vein; T, tertiary vein; Q, quaternary vein. From Fisher (1985). Used by permission of the Botanical Society of America.

Basic leaf structure

Although diverse in morphology and anatomy, all leaves share many features in common. The leaves of many seed plants consist of a stalk-like petiole and a relatively thin, broad laminate blade characterized by transectional dorsiventral symmetry (Figs 17.1, 17.2). Internally a vascular skeleton is enclosed by parenchymatous mesophyll which, in turn, is enclosed by an epidermis (Fig. 17.2a, b). In many ways the anatomy of the leaf resembles that of the stem. In some dicotyledons, for example, the leaf traces that enter the petiole base of large leaves divide and become arranged in a cylinder although other tissues in the petiole have a dorsiventral arrangement, characteristic of most leaves. Furthermore, the petiolar vascular supply as well as that in the leaf proper in some dicotyledons and many conifers is enclosed by a pericycle and endodermis (Fig. 17.3). The mesophyll may contain collenchyma and/or sclerenchyma.

Although similar in anatomy, leaves of most plants differ fundamentally from stems in that they are determinate in growth. That is, their

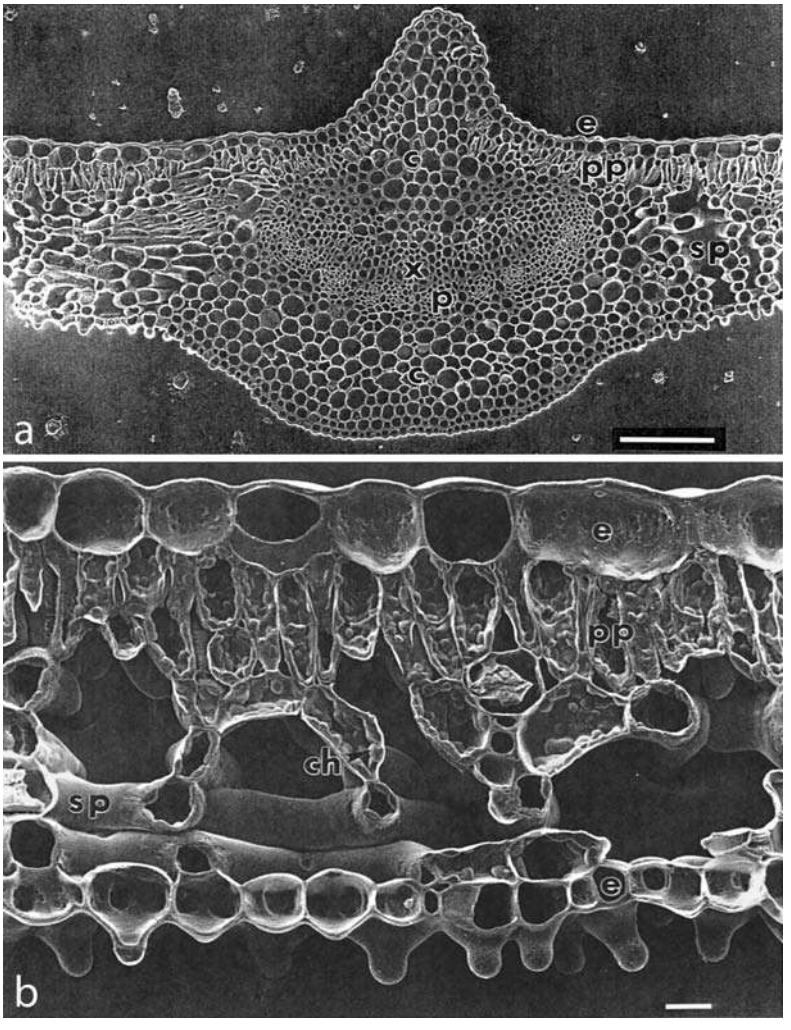

Figure 17.2 Scanning electron micrographs of transverse sections of leaves of *Erythroxylon coca* showing dorsiventral symmetry. (a) Section of the midrib. e, epidermis; pp, palisade mesophyll; sp, spongy mesophyll. x, primary xylem; p, primary phloem. Bar = 100 μm. (b) Section illustrating chloroplasts (ch) in palisade and spongy parenchyma and large air spaces in the spongy mesophyll. Bar = 10 μm. (a, b) From Ferreira *et al.* (1998). Used by permission of the University of Chicago Press.

meristems cease to function after a genetically predetermined period of growth, and their size is thereby restricted. The leaves of several ferns, however, may continue their development over long periods of time, and are, therefore, essentially indeterminate. Several dicotyledons, e.g., *Guarea* and *Chisocheton* in the Meliaceae, also produce relatively indeterminate leaves characterized by continued apical growth for up to 4 years (see Fisher and Rutishauser, 1990). Leaves of deciduous plants live for only one growing season. Those of "evergreen" plants are termed persistent, and remain on the plant for 2 or more years.

Although the leaves of a majority of plants have broad, relatively thin blades, others may be thick and fleshy or, as in some monocotyledons, tubular. In many conifers, there is an absence of specialization into blade and petiole. Whatever the morphology of a leaf, in

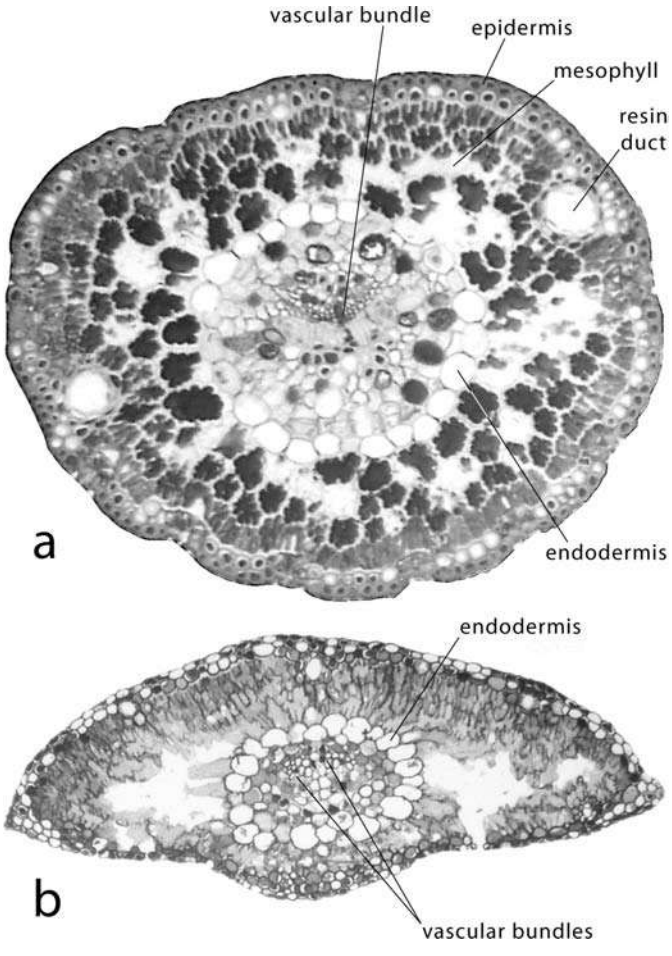

Figure 17.3 Transverse sections of conifer leaves. (a) *Pinus monophylla*, with a single vascular bundle enclosed by an endodermis. Magnification × 99. (b) *Pseudolarix* sp. with two vascular bundles. Magnification × 76.

gymnosperms and angiosperms, **adaxial** and **abaxial** surfaces (adaxial, oriented toward the stem and abaxial, oriented away from the stem) are, with rare exceptions, reflected in its internal anatomy, especially in the arrangement of primary xylem and phloem in the veins. You will remember that in seed plants the vascular bundles of the stem eustele are commonly **collateral**, that is, xylem comprises the inner part of the bundles and phloem the outer. Consequently, as vascular bundles (i.e., leaf traces) diverge into the leaf, the primary xylem will be oriented toward the upper, adaxial surface of the leaf, the primary phloem toward the lower, abaxial surface (Fig. 17.2a). This information can be especially useful to paleobotanists who study fragments of leaves in the fossil record. Orientation based on position of vascular tissues may be difficult or impossible in some tubular leaves such as that of *Allium* and some other monocotyledons.

In seed plants the leaf vascular system originates from one, two, three, five, or more leaf traces that diverge from axial bundles of the stem eustele and enter the leaf base (Beck *et al*., 1983; see also Chapter 6).

In petiolate leaves of dicotyledons, there may be a single bundle in the petiole of small leaves that in the blade will become the midvein. This single bundle may be an extension of the single leaf trace, or may result from the fusion of two leaf traces. In larger leaves the petiole vascular system is usually supplied by three or more leaf traces, a large median trace and two, four, or more smaller lateral traces. The median trace will become the midvein. In leaves supplied by five or more traces, the laterals frequently become arranged in an arc, and in very large leaves, as noted above, following branching of the laterals, a cylinder of vascular bundles may be formed. Even in such cases, however, the median bundle (midvein) with xylem and phloem oriented toward the adaxial (upper) and abaxial (lower) surfaces of the leaf lamina, respectively, is usually easily identified. In some taxa, the midvein may consist of several vascular bundles including the extension of the median trace and branches of the adjacent lateral traces (Beebe and Evert, 1990). In monocotyledons, petioles commonly contain numerous vascular bundles in a parenchymatous ground tissue.

As the result of branching of the leaf traces or petiolar vascular system during development, a complex anastomosing system of veins is produced in the blades of many leaves. In most dicotyledons, a **reticulate venation system** develops (Figs 17.1a, 17.4a, b) whereas in many monocotyledons a system of interconnected, more or less **parallel veins** is common (Fig. 17.4c, d). In some primitive gymnosperms such as *Ginkgo*, there is an open, **dichotomous system**. In the compound leaves of cycads a single vein services each pinna in *Cycas*, but in some other genera there are many essentially parallel veins that may run the length of the pinnae with some of these dichotomizing. In the cycad *Stangeria* each pinna contains a midvein with laterals. The leaves of conifers are vascularized by a single vein or two veins (Fig. 17.3) that result from the dichotomy of a single leaf trace.

Vascular bundles of the venation system are enclosed by **bundle sheaths**, consisting of parenchyma (sometimes collenchyma or sclerenchyma) one or more cells thick (Fig. 17.5). In some angiosperms cells of the bundle sheaths are characterized by Casparian bands or suberin lamellae similar to those of an endodermis which apparently provide apoplastic barriers to solute transport. In leaves of some taxa, walls or ribs of tissue called **bundle sheath extensions** extend from the veins to the upper and/or lower epidermis (Fig. 17.5). These are supporting structures, often composed of sclerenchyma, that are also thought to be pathways of transport between the veins and the epidermis.

The leaf **mesophyll**, the primary photosynthetic tissue of the leaves of dicotyledons, is predominantly parenchymatous, but in many taxa sclerenchyma and/or collenchyma provide support especially along the leaf margins and around vascular bundles. Whereas in the leaves of some angiosperms the mesophyll is essentially homogeneous, in most it is divided into upper and lower histological regions (Fig. 17.2b). The upper region, the **palisade mesophyll**, consists of one or more relatively compact layers of elongate cells oriented at right angles to the

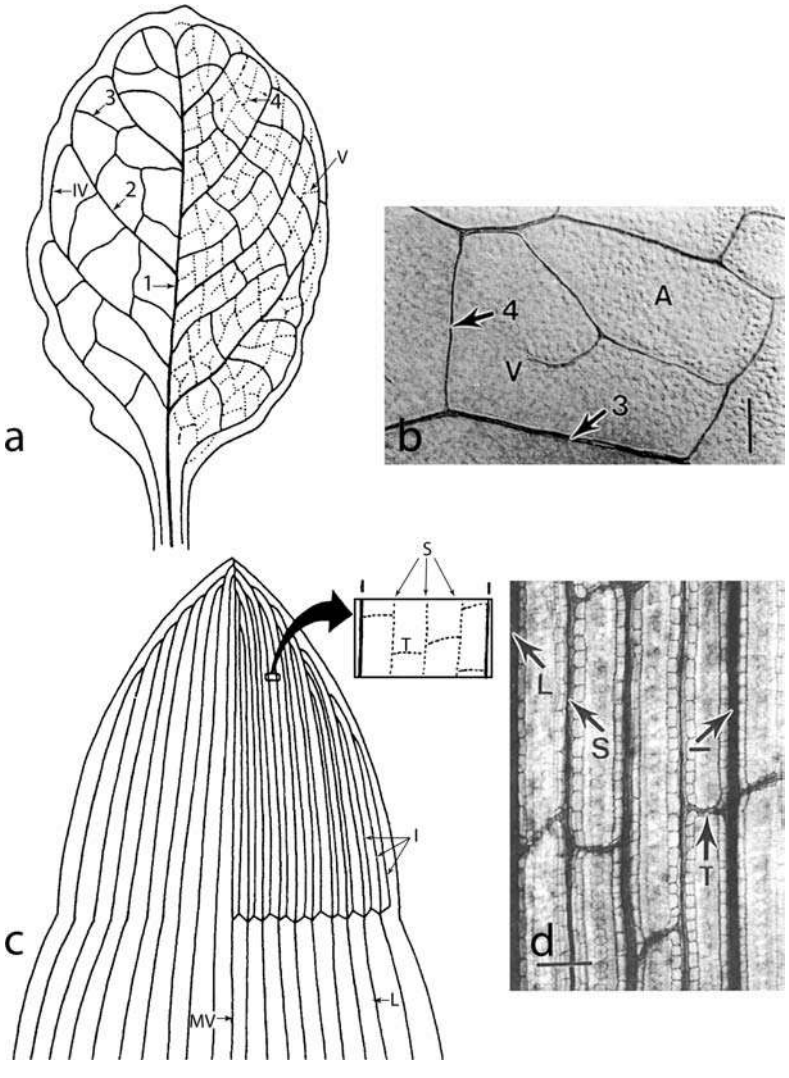

Figure 17.4 Venation patterns in dicotyledon and monocotyledon leaves. (a) Diagram of the reticulate venation pattern in *Arabidopsis thaliana* showing different vein orders. Secondary veins (2) are joined by an intramarginal vein (IV). V, freely ending veinlet. (b) Part of a cleared leaf of *Arabidopsis* showing tertiary (3) and quaternary (4) veins enclosing an areole (A) containing a freely ending veinlet (V). Bar = 100 μm. (c) Diagram of a leaf of *Zea mays* (maize) showing the midvein (MV), large (L), intermediate (I), and small (S) longitudinal veins, and transverse veins (T). (d) Part of a cleared leaf blade of *Zea mays*, showing vein orders as in (c). Bar = 100 μm. Note the parallel pattern of veins in *Zea* as contrasted with the reticulate pattern in *Arabidopsis*. (a–d) From Nelson and Dengler (1997). Used by permission of the American Society of Plant Biologists.

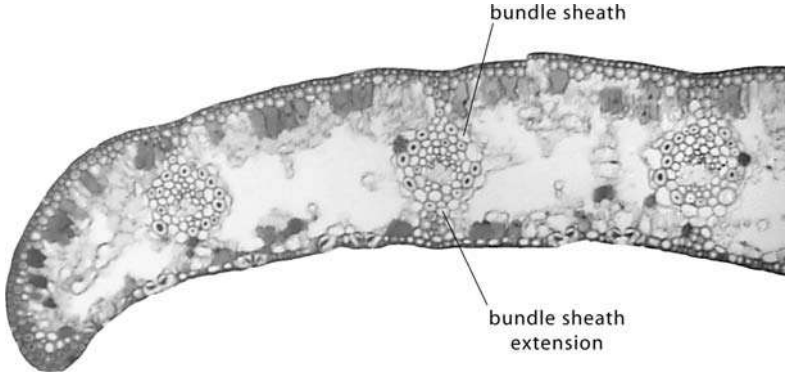

Figure 17.5 Transverse section of a pinnule of *Zamia* (a cycad) illustrating a vascular bundle sheath and the bundle sheath extension. Magnification × 80.

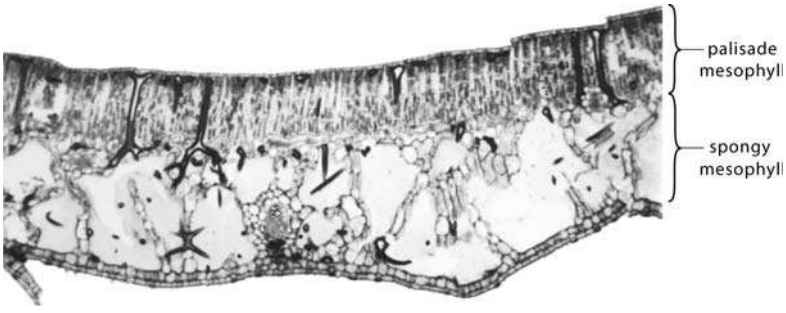

Figure 17.6 Transverse section of the leaf of the aquatic plant *Nymphaea*. Note the very extensive air spaces in the spongy mesophyll. Magnification × 50.

epidermis. The number of layers is often correlated with light intensity; the higher the light intensity in which the plant grows, the greater the number of layers. The lower region, the **spongy mesophyll**, is composed of loosely arranged, irregularly shaped cells between which are extensive interconnected air spaces and channels. Such tissue is generally referred to as **aerenchyma**. Air channels also characterize the palisade mesophyll, but the volume of air within the tissue is considerably less than that in the spongy mesophyll. The looseness of the spongy mesophyll, i.e., the volume of air space within it, may be related to the exchange of O_2 and CO_2. For example the spongy mesophyll in floating leaves of aquatic plants (Fig. 17.6) has proportionately larger air spaces than that in leaves, the lower surfaces of which are in contact with the atmosphere.

In some members of the Leguminosae, e.g., *Glycine* (soybean) and *Calliandra*, and in several other dicotyledon families, the veins are connected by sheets of parenchymatous tissue called **paraveinal mesophyll** (Fig. 17.7a, b) (Kenekordes *et al*., 1988; Liljebjelke and Franceschi, 1991; Lersten and Curtis, 1993). This tissue, one or two layers thick, in essentially the same plane as the veins, is thought to function in the transport of photosynthate and nitrogenous compounds between the mesophyll and the veins (Franceschi and Giaquinta, 1983a, 1983b).

The leaves of some xeromorphic plants exhibit little or no difference between upper and lower mesophyll regions as, for example, those of many conifers, including *Pinus* (pine). The uniform mesophyll of *Pinus* (Fig. 17.3) and some other conifers is composed of cells characterized by distinctive infoldings of the cell wall. A lack of differentiation of palisade and spongy mesophyll also characterizes some herbaceous perennial dicotyledons and many grasses (Fig. 17.8). Some xerophytes, on the other hand, including the gymnosperms *Araucaria*, *Podocarpus*, and *Callitris*, as well as some angiosperms (e.g., *Atriplex* in the Chenopodiaceae, species of *Acacia* in the Leguminosae, and species of Myrtaceae) have palisade mesophyll in both upper and lower parts of their leaves. Such mesophyll is referred to as being **isobilateral** (Fig. 17.9a). Of 39 xeromorphic species from many families studied by Burrows (2001), the leaves of nearly 50% were isobilateral, and most of these were **amphistomatous** (with stomata in upper and lower epidermises) (see Beerling and Kelly, 1996). The adult leaves of some species of *Hakea* (Proteaceae)

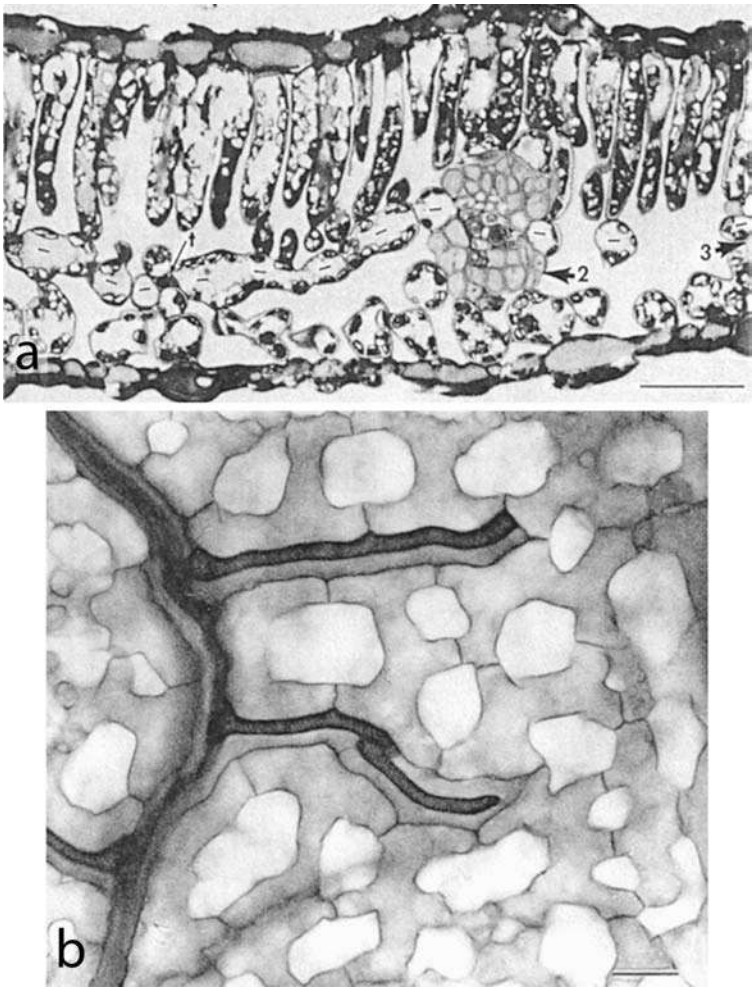

Figure 17.7 Paraveinal mesophyll in leaves of *Calliandra tweedii* (Leguminosae). (a) Transverse section of a leaf showing a single-layered paraveinal mesophyll (cells containing dashes) in sectional view extending between veins of several orders. Vein order is indicated by numbers. Bar = 50 μm. (b) Paradermal section showing the paraveinal mesophyll in surface view. Note its reticulate nature; also the veins consisting of tracheary elements and parallel parenchyma cells. Bar = 20 μm. From Lersten and Curtis (1993). Used by permission of the Botanical Society of America.

(see Groom *et al*., 1997) are circular in section with a cylindrical, one- to several-layered mesophyll (Fig. 17.9b). The leaf mesophyll may contain various secretory ducts and cavities such as resin canals in conifers, oil cavities containing aromatic compounds in *Mentha* and *Eucalyptus*, laticifers in many dicotyledons, etc.

The leaf **epidermis** is a compact parenchyma tissue lacking intercellular spaces (except the openings of stomata between guard cells) (Figs 17.2b, 17.10a, b). Stomata are interspersed within this tissue, and are especially common in the lower epidermis, a condition termed **hypostomatous**; but in some taxa (e.g., floating aquatic species) stomata are restricted to the upper epidermis (**epistomatous**). Stomata seem to occur randomly in the epidermis of dicotyledons (Fig. 17.10a), but a recent analysis (Larkin *et al*., 1996) indicates that stomatal spacing may be non-random and controlled by cell lineages associated with stomatal development as well as the cell lineages of neighboring cells. In monocotyledons with parallel venation, stomata typically occur in

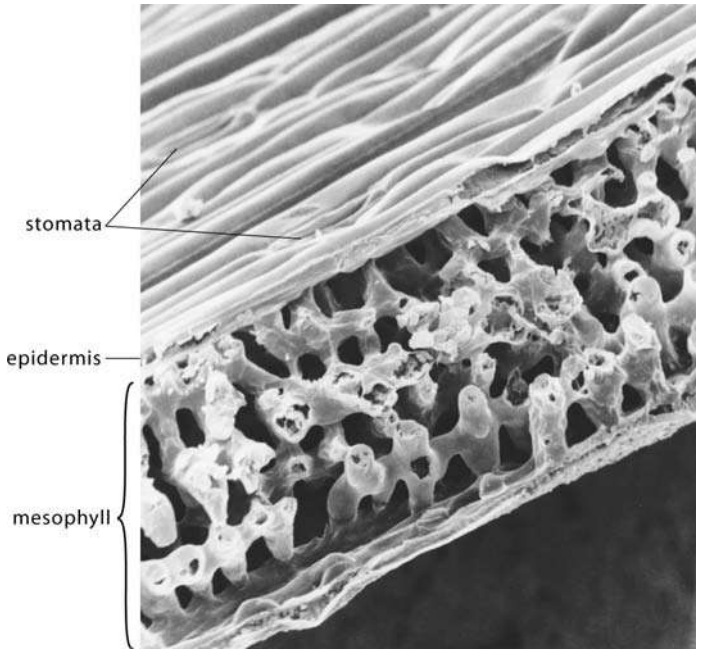

Figure 17.8 Scanning electron micrograph of a grass leaf which lacks differentiation of palisade and spongy parenchyma. Magnification × 87. Photograph by P. Dayanandan.

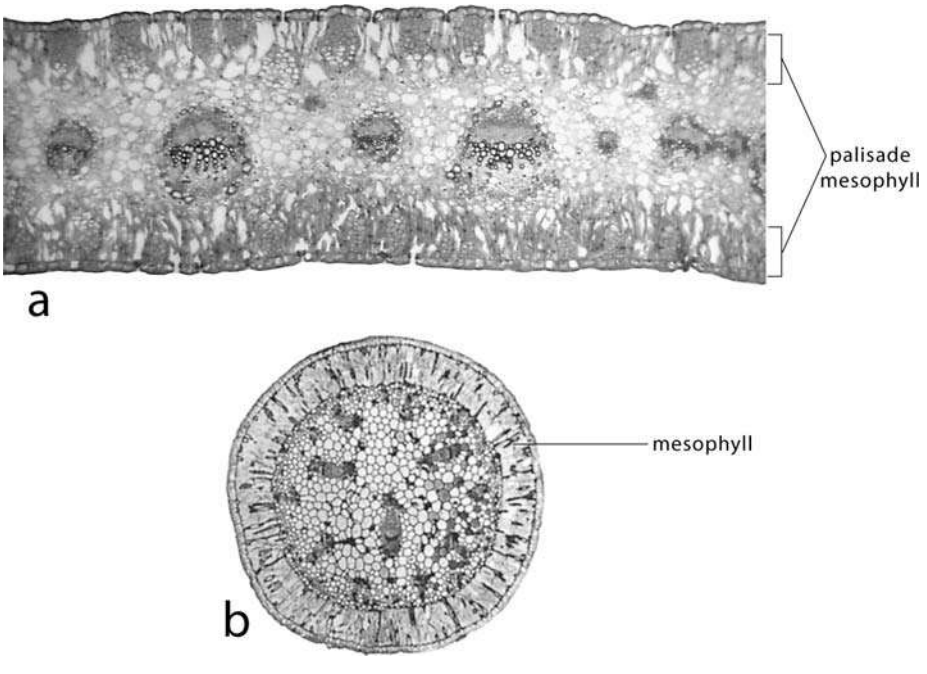

Figure 17.9 (a) Transverse section of a leaf of *Welwitschia mirabilis* with an isobilateral mesophyll (palisade mesophyll in both upper and lower regions of the leaf). Magnification × 52. (b) Transverse section of a leaf of *Hakea erinacea*, circular in section, and containing a cylindrical palisade mesophyll. Magnification × 18. (b) From Groom *et al.* (1997). Reproduced with permission of CSIRO Publishing, Melbourne, Australia.

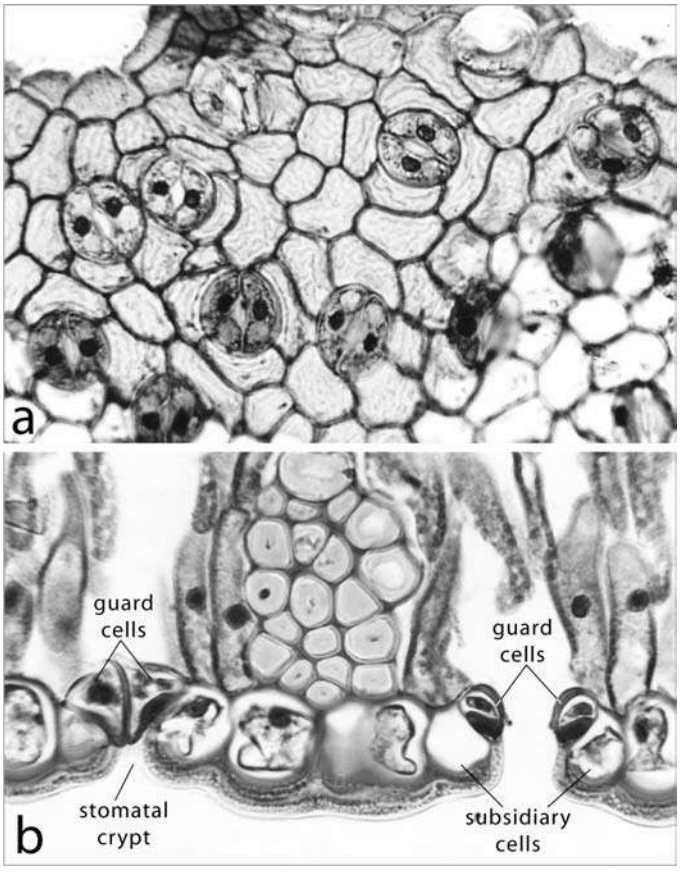

Figure 17.10 (a) Surface view of a leaf epidermis showing stomata with open apertures. Magnification × 297. (b) Stomata in the lower epidermis of *Welwitschia mirabilis*. In this xerophyte, stomata are sunken in stomatal crypts. Note that the guard cells are overlain by the subsidiary cells; also that there is an air space in the mesophyll beneath each stoma. Magnification × 526.

parallel rows. In mesophytes and hydrophytes stomata occur at the same level as other epidermal cells or, especially in aquatic plants, may be raised above this level. The stomata of xerophytes are typically sunken in depressions in the leaf surface called **stomatal crypts** (Fig. 17.10b), and in many species occur in both lower and upper epidermises. In some taxa, the epidermis contains sclereids, as well as (in grasses) cork and silica cells. A variety of unicellular and/or multicellular trichomes (hairs) characterize the leaf epidermis. In leaves that roll or curl under conditions of water stress (e.g., leaves of many grasses), there are rows of large, thin-walled bulliform cells (Fig. 17.11) in the upper epidermis which, through loss of turgor, are thought to facilitate this process. Bulliform cells occur in grooves in the leaf surface that parallel major veins. During leaf development, increase in turgor in bulliform cells may assist in the unrolling of young leaves. In most plants the epidermal cells (with the exception of stomatal guard cells) lack chloroplasts. However, in some highly reduced aquatic species and a few ferns that grow in very low light intensity chloroplasts occur in all epidermal cells. Except in the epidermis of immersed aquatic plants the epidermis is covered by a variably thick cuticle. (For more detail on the epidermis, especially the morphology of stomata and trichomes, see Chapter 8.)

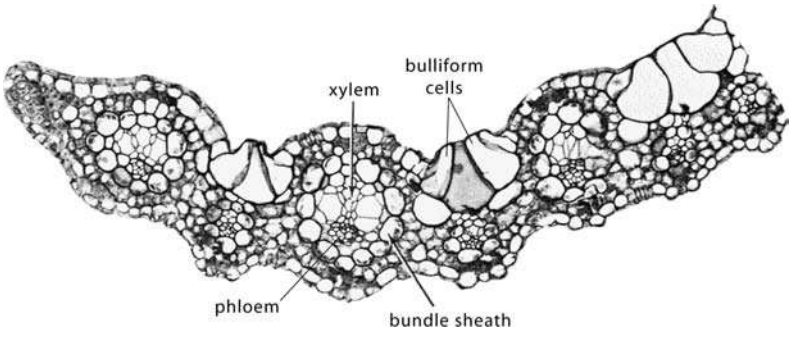

Figure 17.11 Transverse section of part of a leaf of *Saccharum* showing bulliform cells in the upper epidermis. Note also the conspicuous bundle sheaths. Magnification × 141. From Esau (1977). Used by permission of John Wiley and Sons, Inc.

Leaf development

Leaf primordia, produced by the apical meristem, begin their development by periclinal divisions in a subsurface layer on the flank of the apical dome. Additional periclinal as well as anticlinal divisions in both subsurface and surface layers result in a protuberance commonly called the **leaf primordium buttress**. In pteridophytes, a single apical initial, formed at the tip of the buttress, is the ultimate source of all additional cells produced during the development of the leaf. In many gymnosperms and angiosperms, a small cluster of cells forms the apical meristem of the leaf primordium. Factors that control the initiation of a leaf primordium are, as yet, not clearly understood, but it is widely accepted that growth hormones such as auxin and gibberellin stimulate primordium formation. It has been demonstrated that the application of the protein expansin to the apical meristem can also lead to the formation of primordium-like outgrowths (Fleming *et al*., 1999). Expansin is thought to cause a loosening of the microfibrils and the extensibility of cell walls at sites of primordium development (Lyndon, 1994; see also Cho and Cosgrove, 2000). This leads to an outward buckling of cells on the surface of the apical meristem, supporting the view of Green (1999) that physical factors may in some degree control the formation of primordia. For a more detailed discussion of the initiation of leaf primordia, please see Chapter 5. Auxin is also known to play a significant role in the continuing development of leaves following primordium formation.

Leaf morphogenesis in dicotyledons can be considered to consist of three phases, **leaf** (or **primordium**) **initiation** (described above), primary morphogenesis, and expansion and secondary morphogenesis (Fig. 17.12) (see Dengler and Tsukaya, 2001). During **primary morphogenesis**, cell division and cell growth in the young leaf primordium result in the formation of a primordial leaf axis, often called a **phyllopodium**, which has a dorsiventral symmetry, and which, ultimately, will become the petiole and midrib of the leaf. Early during this phase, as the phyllopodium increases in thickness, the leaf lamina begins to form as outgrowths on either side resulting from cytokinesis in **marginal meristems**. Some researchers prefer the term

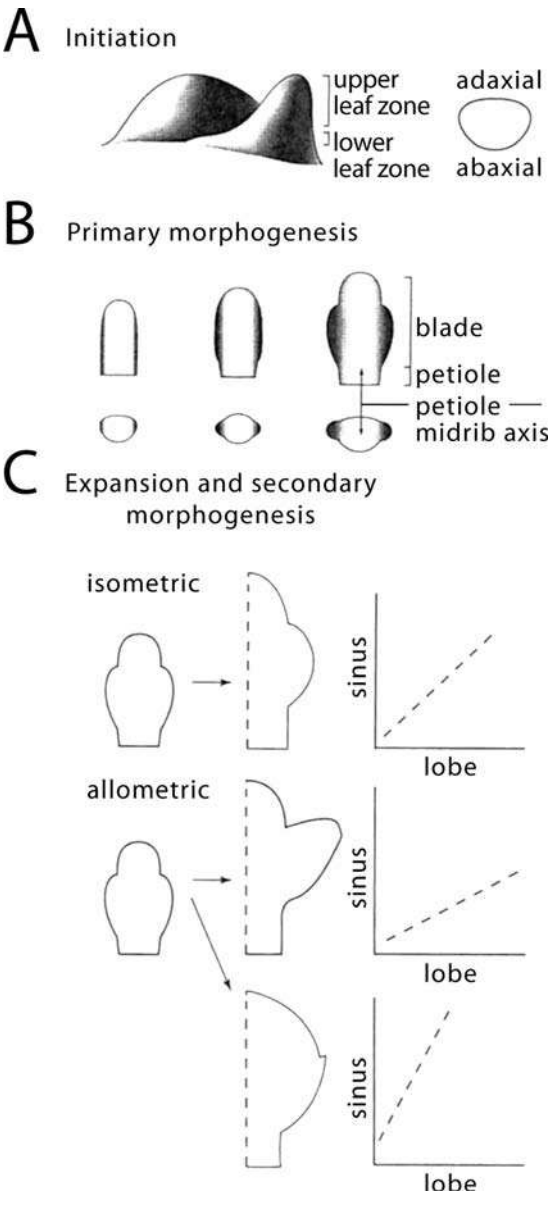

Figure 17.12 Diagrams illustrating three phases of leaf morphogenesis. During leaf initiation (A), the leaf primordium expresses both longitudinal symmetry (upper and lower leaf zones) and dorsiventral symmetry (differences between adaxial and abaxial sides). During primary morphogenesis (B), the marginal meristem (blastozone) (shaded) expresses morphogenetic potential to form the blade, lobes, and leaflets. In the top row is an adaxial view of the phyllopodium (young leaf). The bottom row shows transverse sectional views of the developing blade. During expansion and secondary morphogenesis (C), there is both isometric and allometric expansion of lobes and sinuses produced during primary morphogenesis. From Dengler and Tsukaya (2001). Used by permission of the University of Chicago Press.

marginal blastozone over marginal meristems (Hagemann and Gleissberg, 1996) because it emphasizes the morphogenetic potential of the lateral regions of the phyllopodium. Continued activity in the marginal meristems results in the lateral expansion of the developing leaf blade, each half of which commonly extends upward at an angle on either side of the phyllopodium. In plants with compound leaves, the marginal meristems become subdivided, and each subdivision, from which, ultimately, a leaflet will develop, is characterized by its own phyllopodium with apical and marginal meristems. With continuing cell division in apical and marginal meristems followed by cell expansion, the entire

leaf primordium usually curves upward and, in woody perennials, with other immature leaves and bud scales, comprises a vegetative bud. In some plants with petiolate leaves, a basal meristem, proximal to the marginal meristems, develops in the phyllopodium. The activity of this meristem results ultimately in the development of the leaf petiole. In other taxa, the petiole results from the suppression of activity of the marginal meristems. At an early stage, provascular tissue begins to differentiate in the phyllopodium and developing blade in a pattern that will, ultimately, reflect the mature system of veins.

During **expansion and secondary morphogenesis** (Fig. 17.12), the young leaf continues its growth and differentiation, ultimately achieving its mature size and form. During this phase, which covers a much longer time period than primary morphogenesis, there is an increase in surface area and volume of several thousandfold (Dale, 1988; see also Dengler and Tsukaya, 2001) and, according to Dale (1988), about 95% of the cells that comprise the mature leaf are formed. In young leaf primordia and very young leaves of most vascular plants, the marginal meristems are two or more layers thick. The outer layer can be considered a protoderm comparable to that from which the epidermis of the stem develops. The marginal meristems are, however, short-lived and subsequent meristematic activity is intercalary and diffuse (Donnelly *et al*., 1999). Subsequent growth and differentiation lead to the development of the internal leaf parenchyma. Some parts of the leaf parenchyma will differentiate as mesophyll and other parts as provascular tissue from which the system of veins will ultimately develop. Characteristics of the leaf margins and distinctive features of lobing develop, and the leaves achieve their final form. During this period of expansion and differentiation, the leaf may retain the basic form established during primary morphogenesis (**isometric growth**), or differences in morphology may occur (**allometric growth**) (Fig. 17.12) which is the more common growth pattern (Dengler and Tsukaya, 2001).

The morphology of mature venation systems is highly diverse. It is not surprising, therefore, that the development of venation systems is also highly variable. There are some common patterns of development, however, which we shall consider, using as examples a dicotyledon leaf with reticulate venation and a monocotyledon leaf with parallel venation.

In the leaves of many dicotyledons the venation system is initiated by the acropetal differentiation of a central provascular strand in the phyllopodium (Fig. 17.13A) which will become the midvein in the mature leaf. As the laminae expand, the various branch orders of the venation system differentiate in a heirarchical manner, always preceded by the differentiation of provascular strands (Fig. 17.14). The major (second-order) veins develop first (Fig. 17.13B, C) (Dengler and Kang, 2001). These veins, which reflect leaf shape, provide conduits for the transport of nutrients into the developing leaf. Third-, fourth-, and higher-order veins (Fig. 17.14) develop subsequently, beginning in

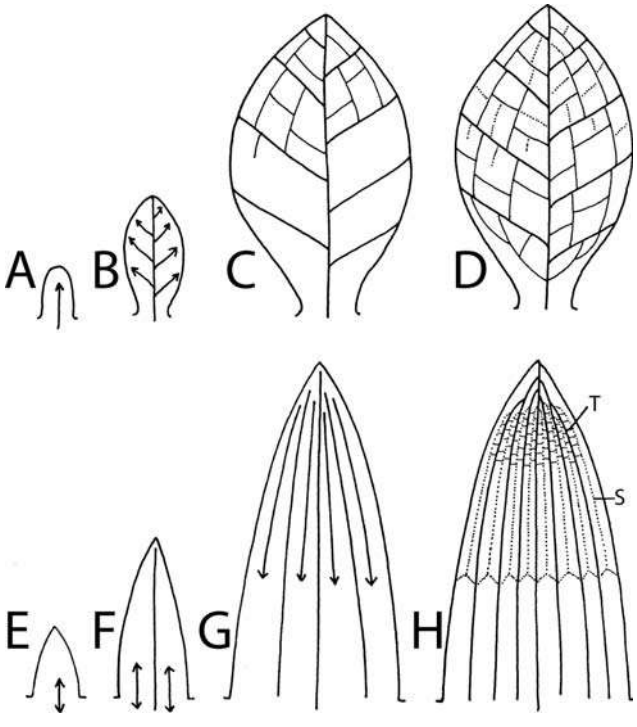

Figure 17.13 Vascular pattern ontogeny in the leaves of dicotyledons and monocotyledons. (A–D) *Arabidopsis thaliana*, a dicotyledon; (E–H) *Zea mays*, a monocotyledon. See the text for detailed descriptions. From Nelson and Dengler (1997). Used by permission of the American Society of Plant Biologists.

the apical regions of the leaf and proceeding basipetally (Fig. 17.13C, D). Last-order veins enclose small regions of parenchyma called areoles into which extend one or several vein endings (Figs 17.4b, 17.13D). Every mesophyll cell is, thus, in contact with, or very close to, a vascular bundle.

At the stage in which provascular tissue differentiates, the developing lamina consists commonly of five cell layers. The two outer layers are protoderm from which the upper and lower epidermis will differentiate (Fig. 17.14a). The three inner layers are ground meristem, sometimes called **promesophyll**. It is in the median layer of this tissue that the successive orders of provascular tissue will differentiate (Fig. 17.14a, b) and from which, ultimately, mature veins containing primary xylem and phloem will develop. Whereas the vascular strands of the venation system are derived solely from the median layer of ground meristem, the adaxial and abaxial layers of this tissue contribute to the development of the bundle sheath and bundle sheath extensions in many dicotyledons.

Development of the leaf vascular system in monocotyledons, although generally similar to that of dicotyledons, differs in several important ways. The initial ("midvein") provascular strand differentiates both acropetally and basipetally (Fig. 17.13E) in the base of the developing leaf primordium, followed by provascular strands of large veins which first differentiate acropetally and subsequently basipetally, connecting with vascular bundles of the stem vascular system

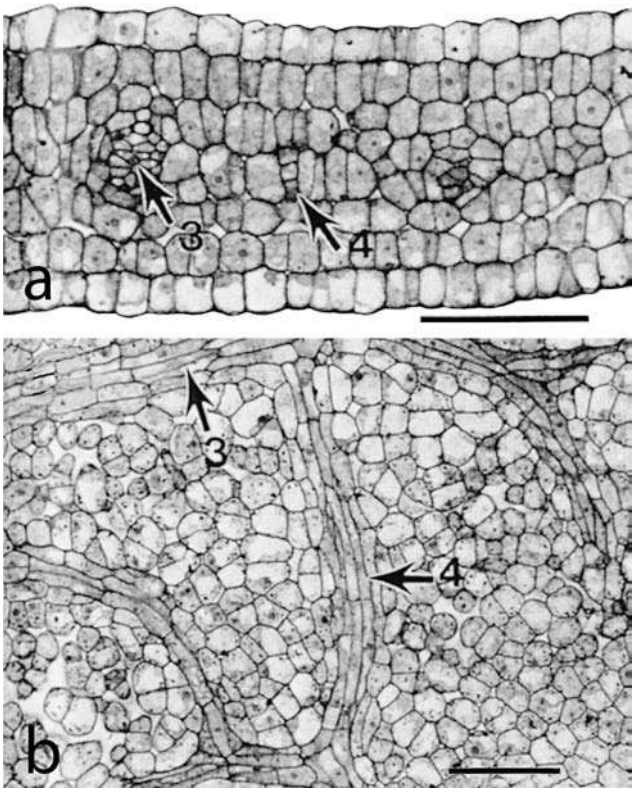

Figure 17.14 Immature leaves of *Arabidopsis thaliana* showing protoderm, ground meristem (promesophyll), and provascular strands. (a) Transverse section. Note provascular strands (arrows) that will develop into third- and fourth-order veins. Bar = 50 μm. (b) Paradermal section showing provascular strands that will develop into third- and fourth-order veins. Bar = 50 μm. From Nelson and Dengler (1997). Used by permission of the American Society of Plant Biologists.

(Fig. 17.13F, G). Intermediate veins are initiated in the apical region of the young leaf and differentiate basipetally (Fig. 17.13G), some of which will connect with the stem vasculature. Finally, small longitudinal and transverse veins are formed in the apical region of the leaf with transverse vein formation proceeding basipetally (Fig. 17.13H). Strong evidence indicates that polar auxin transport, possibly from leaf margins, influences the differentiation of provascular tissue, and ultimately mature veins (Dengler and Kang, 2001). PIN genes, which encode auxin transport proteins, control the establishment and location of auxin concentration gradients and auxin maxima. In leaves of *Arabidopsis*, components of the venation system are initiated at auxin maxima, first at the tip of the leaf primordium and subsequently along the primordium margins. From these sites, the midvein and lateral veins differentiate along auxin concentration gradients (Scarpella *et al*., 2006; Scheres and Xu, 2006). Meristematic activity continues in the more basal region after it has ceased in the more apical region of the developing leaf. Consequently, differentiation of most tissues at this late stage of development is basipetal.

During leaf development, the frequency (or rate) of cell division within different regions of the developing leaf may be directly related to its mature shape. However, rate of cell division alone may not be a controlling factor since cell growth (i.e., increase in size of individual

cells) may also play an important role in leaf morphogenesis (see Fleming, 2002). For example, if the rate of cell division is high, but the new cells remain very small in a part of the leaf (e.g., a leaf lobe), there will be little change in form. Likewise, if the rate is low, but new cells become large, there may also be little change in form. If, however, frequency of cell division is high and the new cells become large the lobe will increase in size and, depending on the relative difference in rate of cell division and degree of growth, the shape of the lobe will also change. An important goal in understanding leaf morphogenesis is determination of the mechanism which controls the integration of frequency of cell division and cell growth (Fleming, 2002). Since in many leaves the greatest frequency of cell division is in their more basal region, such leaves may be broader at the base than at the apex. In many plants the activity of adaxial and abaxial meristems along the developing midrib result in its increase in thickness, especially on the abaxial side. Stipule primordia may develop on either side of the leaf primordia.

Although the patterns of development presented above are generally applicable to the leaves of many vascular plants, significant variations characterize different major taxa. In conifers and some dicotyledons which have leaves that are angular to nearly circular in transverse section, marginal meristems are absent or largely inactive. In some conifers and other taxa that possess linear leaves, a basal meristem, often considered an intercalary meristem, and its derivatives provide most of the tissue of the mature leaf. Differentiation in such leaves is almost entirely basipetal. In many monocotyledons the base of the leaf primordia may encircle the apical meristem resulting, in the mature state, in leaves with leaf sheaths. In the grasses *Zea*, *Avena*, or *Triticum*, for example, a leaf primordium originates as a broad protuberance on one side of the apical meristem (Fig. 17.15). As development continues, the base of the primordium encircles the young stem, and ultimately develops into the leaf sheath. In grasses such as these, characterized by "open" sheaths, the margins of the developing sheaths overlap each other, thus encircling the shoot apex (Fig. 17.15). The regions of overlap of successively formed primordia occur on opposite sides of the shoot apex. Distally, the primordium narrows and, with primarily intercalary growth, the blade elongates and expands, becoming mature prior to the sheath which retains its meristematic potential longer than the blade. In some monocotyledons, e.g., *Allium*, the leaf primordium is "closed," and forms a hood over the apical meristem. Thus, the mature leaf is tubular. The unifacial leaves of some monocotyledons (e.g., *Iris*) result from the extensive activity of adaxial meristems, and little or no activity of marginal meristems. Development of palm leaves is unusually complex involving the formation in the leaf primordium of plications or folds which subsequently separate into individual leaflets. The details of this process are controversial. For detailed discussions of development in palm leaves please see Tomlinson (1961) and Periasamy (1962, 1965).

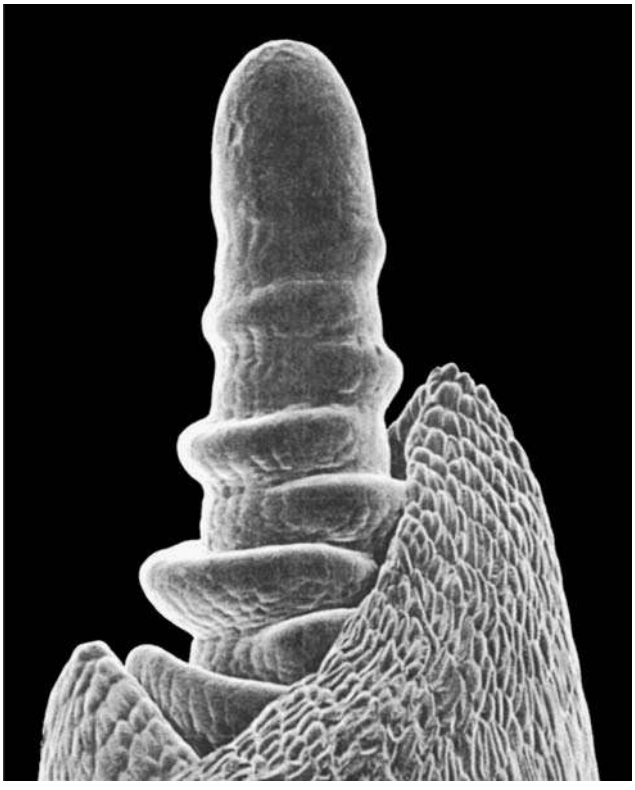

Figure 17.15 The shoot apex of *Triticum* illustrating the form and pattern of development of leaf primordia and the resulting overlapping leaf sheaths which encircle the stem. Magnification × 181. See the text for more detail. From Troughton and Donaldson (1972). Used by permission of the New Zealand Ministry of Research, Science and Technology.

The role of the cytoskeleton in leaf development

In the leaf, as in other regions of the plant, microtubules play an important role in cell growth and the development of cell form. This is especially apparent in the development of cells of the mesophyll and the resulting system of intercellular spaces. Microtubules become oriented just beneath or in contact with the plasma membrane, and cellulose microfibrils are synthesized in an identical pattern in the developing cell wall (Fig. 17.16a). If the microtubules are oriented in rings, the thickened rings of new cell wall resist outward expansion as the cells grow, but the regions of thin wall between the rings bulge out resulting in tubular cells with regularly spaced constrictions, as in *Triticum aestivum* (Jung and Wernicke, 1990). On the other hand, if the system of microtubule bundles and the cell wall thickenings are arranged in a reticulum, as in *Nigella damascena* (Wernicke *et al*., 1993) and *Adiantum capillis-veneris* (Panteris *et al*., 1993) the regions of thin wall between thickenings of the reticulum extend outward (Fig. 17.16b) forming multilobed cells (Fig. 17.16c) which comprise a tissue with extensive intercellular air spaces.

The mechanism by which the microtubules attain their characteristic pattern in the cells is not fully understood, but it has been suggested that their positioning might be controlled by the actin microfilaments

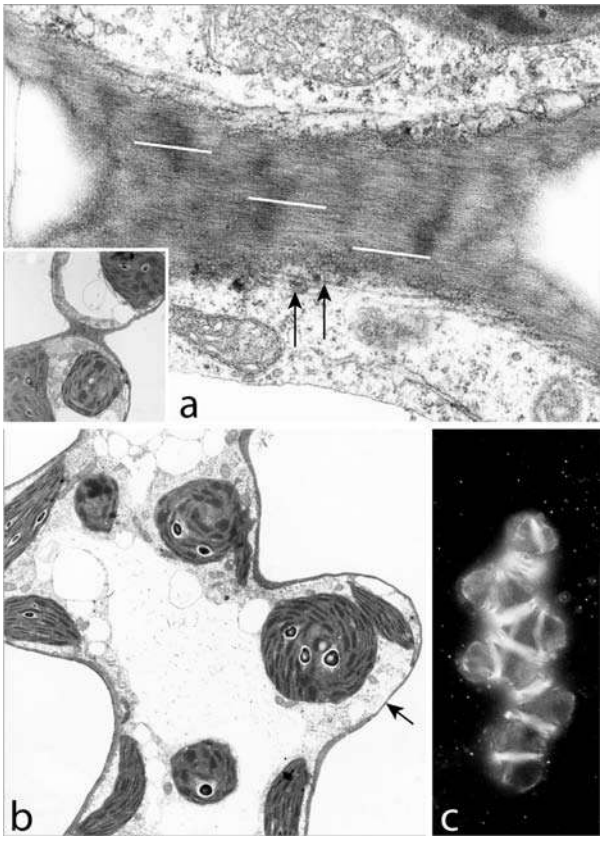

Figure 17.16 Morphogenesis of mesophyll cells in leaflets of *Adiantum capillis-veneris*. (a) Surface view of a wall thickening in a constricted region (inset) of a mesophyll cell. Orientation of cellulose microfibrils is indicated by the white lines. Microtubules (arrows) just beneath the plasmalemma are oriented parallel to the microfibrils. Magnification × 17 025, inset × 934. (b) Outward extension of a lobe of a mesophyll cell between regions of wall thickenings. The arrow indicates the thin wall of the lobe as compared with thicker wall regions on either side of it. Magnification × 2334. (c) A nearly mature mesophyll cell showing the relationship of rings of microtubules (white) to the cell lobes. Magnification × 532. From Panteris *et al.* (1993). Used by permission of Springer-Verlag Wien.

which have been observed in parallel arrangement with them (see Seagull, 1989).

Until recently, understanding of the control and integration of factors that lead to leaf development has been limited. However, during the past two decades workers have identified genes that affect dorsiventrality, blade formation, and cell and tissue characteristics of developing leaves (e.g., Waites and Hudson, 1995; Bowman, 2000) as well as pinna form, size, and number in compound leaves (Lu *et al.*, 1996; DeMason and Chawla, 2004), and many other aspects of leaf development (see below). In time, the application of genetics and its integration with the extensive knowledge of morphology, anatomy, and patterns of development will lead to solutions of many of the unsolved problems in leaf morphogenesis.

The role of genetics in leaf development

Extensive research over many years has led to the conclusion that auxin and polar auxin transport (by which auxin is delivered to developing regions of the plant) are essential, indeed crucial, in regulating the many aspects of plant development. Recent studies indicate that **PIN proteins**, which function as **auxin efflux transporters**, regulate the

development and location of auxin concentration gradients and auxin maxima, thus controlling the pattern of development of the venation system and many other aspects of leaf morphology (see also the section on leaf development in this chapter, and Fleming, 2004; Scarpella *et al*., 2006; Scheres and Xu, 2006).

Leaves are structurally and functionally complex organs. It is through gene expression that development of the innumerable characteristics of the leaf are controlled. A gene (e.g., the PIN gene) is expressed through the translation of encoded information into a protein (e.g., auxin) which, in turn, either singly or through interaction with other gene products, modulates both the initiation and differentiation of structure and the regulation of function. Some genes are expressed constantly in all living cells. Others are expressed only in some cells and at certain stages during development. Regulation of gene function allows cells to control the timing and location of gene expression within cells, tissue domains, or organs. For example, as hormones such as auxin move through the developing regions of the plant, they can act as signals activating or inhibiting gene action.

During the last decade studies of the effects of morphologic mutants in several plants, e.g., *Arabidopsis, Antirrhinum* (snap dragon), petunia, maize, rice, among others, compared with the wild type morphology, have allowed the identification of many genes and provided important information on their roles in plant differentiation and morphogenesis. Many studies have dealt with leaf development. For example, the *WUSCHEL* (*WUS*) gene is thought to integrate information that controls the activities of the shoot apical meristem (Wang and Li, 2008). Several studies suggest that, in *Arabidopsis*, the formation of leaf and bud primordia are controlled by an interaction of the *CLAVATA* (*CLV*) and *WUSCHEL* genes, with the position and timing of primordia initiation controlled by auxin (Wang and Li, 2008; see also Benkova *et al*., 2003). The *KNOX* (*KN*) genes, in particular, *KN1*, are also thought to have a major role in the formation and maintenance of apical meristems of the shoot and, possibly, in regulating the formation of compound leaves (Sinha, 1999).

In *Antirrhinum* the *PHANTASTICA* (*PHAN*) gene controls dorsiventrality in leaves. Mutations at this locus result in radially symmetrical leaves that, consequently, lack a blade (Sinha, 1999; see also Fleming, 2004). The leaf/length ratio in *Arabidopsis* is controlled by the *ROTUNDIFOLIA* gene (Tsukaya, 2006). Proliferation and expansion of cells that contribute to the length of the developing leaf are under control of the *ROT3* gene whereas leaf width is controlled by *ROT4*. Other genes are known that control margin characteristics and leaf flatness, etc. (Tsukaya, 2006). These are only a few examples of the multitude of genes that control the various aspects of leaf morphogenesis including primordium initiation, cell division rates, establishment of tissue domains, cell and tissue differentiation, and the identification of signal transduction cascades that connect gene expression to signaling events (Sinha, 1999). Gene control of the structure and function of cells, tissues, and organs is a very active and complex field that contributes highly

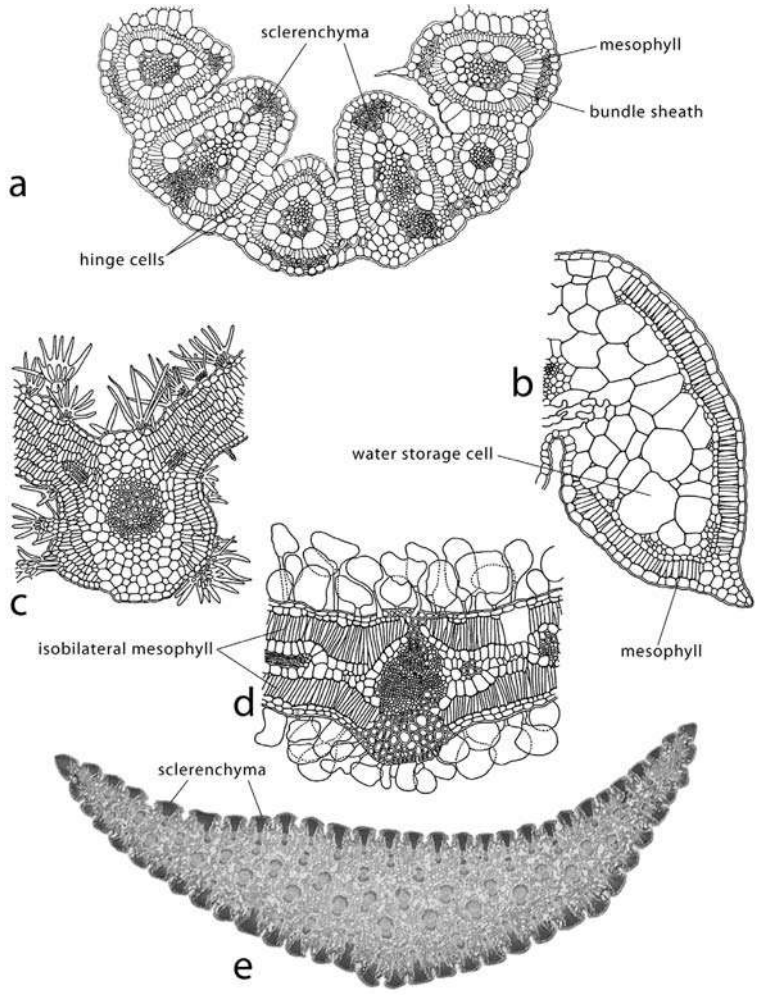

Figure 17.17 Drawings of sectional views of leaves of xeromorphic plants. (a) A leaf of the grass *Bouteloua breviseta*, with hinge cells and plates and strands of sclerenchyma. (b) Part of a leaf of the succulent plant *Salsola kali*. Note the large water storage cells. (c) The leaves of *Sphaeralcea incana* are characterized by a dense layer of branched epidermal trichomes and a mesophyll lacking differentiation into palisade and spongy regions. (d) Part of a leaf of *Atriplex canescens* covered by vesicular trichomes, and characterized by an isobilateral mesophyll. (e) Leaf of *Yucca*. The conspicuous strands of sclerenchyma within the ridges are bundle caps of peripheral vascular bundles. Stomata are located in the epidermis that lines the grooves. Magnification × 14. (a) From Shields (1951b). Used by permission of the International Society of Plant Morphologists. (b–d) Redrawn from Shields (1951a). Used by permission of the Botanical Society of America.

significant information on plant development. For more extensive and detailed information of this subject, please see Sinha (1999), Fleming (2004), Tsukaya (2006), and Wang and Li (2008), and references therein.

Variations in leaf form, structure, and arrangement

Although the basic anatomy and morphology of most leaves are directly related to the process of photosynthesis, the form of some specialized leaves is related to other functions. For example, cotyledons are specialized as food storage organs, bracts and bud scales function in protection and/or storage of photosynthate, and flower parts are related to the process of reproduction. Thus, leaves are highly diverse in gross morphology, and to a lesser extent in internal anatomy. This diversity is related not only to leaf function, but also to the environment in which leaves have evolved as well as to that in which they develop. For example, **xerophytes**, plants that have evolved in arid (xeric) regions (Fig. 17.17),

possess leaves that have structural features such as a heavily cutinized epidermis, sunken stomata, and sclerenchymatous hypodermal layers that contribute to a restriction of water loss. Others have water storage cells, dense coverings of trichomes or isobilateral mesophylls. Xerophytic grasses commonly have bulliform or hinge cells that facilitate the involution (rolling up) of leaves, and many species are characterized by plates or strands of sclerenchyma. Furthermore, because in arid regions light intensity tends to be very high, leaves are often, but not always, small and frequently thick (e.g., Groom *et al*., 1997; Burrows, 2001). On the other hand, **mesophytes**, plants that have evolved in regions of abundant rainfall and where light intensity is lower, have larger and thinner leaves, thinner cuticles, collenchyma more often than sclerenchyma as the supporting tissue in the blade, and stomata at the same level as the rest of the epidermal cells (Fig. 17.2a, b). The leaves of **hydrophytes**, aquatic plants, have reduced vascular systems, highly aerenchymatous mesophyll (Fig. 17.6), no or relatively small amounts of sclerenchyma, and an epidermis composed of thin-walled cells that often contain chloroplasts.

During development, the morphology of leaves on the same plant may vary depending on factors of the environment such as spectral quality and light intensity. For example, leaves that develop in conditions of low light intensity tend to be large and thin, and are called **shade leaves**, whereas those that develop in conditions of high light intensity are smaller and thicker, and called **sun leaves**. Experiments by Buisson and Lee (1993) on the effects of simulated canopy shade demonstrated that leaves of *Carica papaya* (papaya) grown under reduced irradiance were significantly thinner, with lower specific weight, had fewer stomata, produced more chlorophyll per unit area, and were characterized by a larger volume of air space in the mesophyll than leaves growing under conditions of high light intensity. In addition, under conditions of low light intensity and low red : far red light, leaf lobing was dramatically reduced. Change in spectral quality also resulted in a reduction in the ratio of chlorophyll a to b.

The leaves of **plagiotropic shoots** (shoots with all leaves oriented in essentially the same plane) are commonly **anisophyllous**, that is, at maturity the leaves on the upper side of the stem are smaller than those on the lower side. Anisophylly is considered an adaptation that facilitates light interception in environments of low light intensity since the smaller leaves and their orientation in relation to the light source minimize shading of the larger leaves on the lower side of the stem (see Dengler, 1991, 1999). Some dorsiventral shoots with distichous phyllotaxy provide a somewhat different variant in leaf arrangement reflected in the anatomy of the buds. In plants characterized by what Charlton (1993) calls the **rotated-lamina syndrome** (some woody species such as *Ulmus*, *Zelkova*, *Tilia*, *Corylus*, etc.), leaf primordia in the bud become oriented in more or less one plane with the upper surface of the laminae facing the axis bearing the bud rather than the axis on which they are borne (Fig. 17.18). Thus, as the leaves mature they occur in one plane on opposite sides of the shoot axis, an adaptation

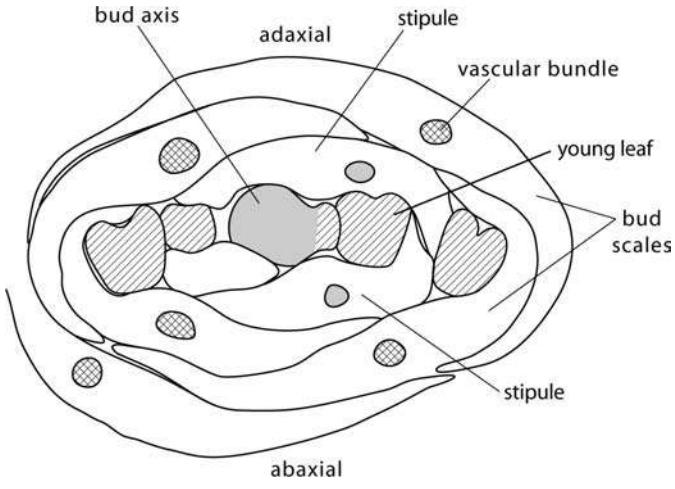

Figure 17.18 Transverse section of a vegetative bud of *Zelkova serrata* illustrating the "rotated-lamina syndrome." During development, the leaf primordia become oriented in one plane with their upper surfaces facing the axis bearing the bud rather than toward the bud axis. This orientation facilitates light reception of the mature leaves. Drawn from figure 34 in Charlton (1993). Used by permission of the National Research Council of Canada.

which facilitates light reception. For variations and other examples of the rotated-lamina syndrome, see Charlton (1997). The unusual tropical fern *Teratophyllum rotundifoliatum* provides another interesting example of the effect of low light intensity on leaf anatomy (see Nasrulhaq-Boyce and Duckett, 1991). The major part of the leaf lamina of *Teratophyllum* consists almost entirely of the upper and lower epidermis and the intervening vascular bundles. In its leaves, which essentially lack mesophyll, all epidermal cells contain chloroplasts. Those in the upper, lens-shaped epidermal cells are very large whereas those of the lower epidermis are small and numerous, and identical to those of the stomatal guard cells. The distribution and characteristcs of the chloroplasts and other aspects of anatomy appear to be adaptations that maximize light absorption in conditions of diffuse light of very low intensity (Nasrulhaq-Boyce and Duckett, 1991).

Another type of morphological variation is the acropetal progression of leaves of different morphology during shoot development that comprises what is called a **heteroblastic series**. Such a progression of leaf forms often accompanies development from embryo to juvenile and adult vegetative states and ultimately to the reproductive state. The first leaves to appear in the seedling of a plant that typically has compound leaves when mature may be simple (see Gerrath and Lacroix, 1997). Rarely, the reverse may occur: i.e., the first leaves may be compound and later ones simple. In woody plants, the first leaves that develop on a twig at the beginning of a growth period are bud scales followed later by foliage leaves. Leaves of intermediate morphology often develop between these two extremes. In the transition from a vegetative to a reproductive state, leaf form commonly changes from that of typical foliage leaves with a gradual reduction in size to that of bracts and floral appendages such as sepals and petals (Kerstetter and Poethig, 1998). Leaf form may also change with increasing age of the plant, and in some plants typical foliage leaves may be followed in succession by structures such as tendrils and spines. In addition to transitions in morphology, anatomical changes such as variation in

cuticle thickness, changes in epidermal cell shape and size, thickness of the leaf blade, size of bundle sheath cells, variation in the transverse area of veins, distance between veins, number of layers of palisade mesophyll cells, etc., may also characterize leaves in heteroblastic series (see Gould, 1993; Lawson and Poethig, 1995; BongardPierce *et al*., 1996).

Mechanisms that control heteroblastic development are not clearly understood, but it is apparent that morphogenetic stimuli lead to the formation by the apical meristem of leaf primordia that develop into leaves (and floral appendages) of different morphologies. This stimulus may be a hormone such as auxin or gibberellic acid, and one which is influenced by external factors such as temperature and/or photoperiod. Some workers have suggested that carbohydrate concentration might play a significant role in heteroblastic development (e.g., Sussex and Clutter, 1960). Ultimately, understanding of the molecular basis of the control of heteroblasty will be dependent on determining the genes that affect various aspects of leaf development (see Lawson and Poethig, 1995).

Structure in relation to function

Leaves are highly variable in both morphology and anatomy, varying in gross form from simple to compound, in thickness, whether laminate or tubular, in characteristics of lobing and lamina margins, in surface characteristics such as cuticle thickness, type and density of trichomes, position, distribution, and density of stomata, in the presence of dorsiventral or isobilateral mesophyll, presence of toxic compounds, presence of silica, presence or absence and distribution of sclerenchyma, etc. It is likely, therefore, that they have evolved in relation to both biotic and abiotic influences in the environment (see Beerling and Kelly, 1996; Gutschick, 1999; Press, 1999), and that many of these features are directly related to leaf function.

Photosynthesis and phloem loading

Many of the structural characteristics of leaves are directly related to the process of photosynthesis. All cells of the mesophyll contain chloroplasts, the sites of the process. According to Evans (1999), there are, typically, about 10 million chloroplasts in each square centimeter of leaf! It is well known that the great volume of intercellular space within the mesophyll and the presence in the epidermis of stomata facilitate exchange of O_2 and CO_2. The extensive surface area of exposed cell walls provides for efficient absorption of CO_2 into mesophyll cells where it is utilized in photosynthesis. Cell surfaces abutting on intercellular spaces are lined with a thin layer of "cuticle-like" material which makes them unwettable (Martin and Juniper, 1970). According to Romberger *et al*. (1993) it is essential that these surfaces be water repellent in

order to prevent the intercellular spaces from filling with water during periods of high humidity and, thus, negating their function in aeration.

The laminate form of many leaves and the orientation of the tubular palisade cells at right angles to the leaf surface are adaptations which enhance the penetration of light, the source of energy for the process of photosynthesis. In some plants upper epidermal cells with convex outer cell walls function like lenses, focusing light on the palisade mesophyll, as for example in *Medicago sativa* and *Oxalis* (Martin *et al*., 1989; Poulson and Vogelmann, 1990). The spongy mesophyll scatters the light which enhances its absorption (see Evans, 1999). This scattering effect is especially important because it increases the absorption of the green and yellow wavelengths. Although these wavelengths are the strongest part of the solar spectrum they would be poorly utilized in photosynthesis if it were not for this effect (P. Ray, personal communication). In some plants that grow in conditions of low light intensity the palisade mesophyll cells are cone-shaped with the widest part of the cells located just below the epidermis. In cells of this shape more of the peripherally located chloroplasts are exposed directly to light than in tubular palisade cells typical of plants that grow in conditions of higher light intensity (see Buisson and Lee, 1993), thus increasing the efficiency of light absorption.

It is apparent that the venation system provides pathways for transport of water and minerals (the primary xylem) and of photosynthate (the primary phloem). The presence of companion cells, some of which are transfer cells, vascular parenchyma cells (also called **intermediary cells**), and leaf sheath cells associated with sieve tube members facilitates **phloem loading**, the transport of photosynthate from the mesophyll into the sieve tube system. Plasmodesmata connecting the mesophyll cells with the bundle sheath cells provide for symplastic transport of photosynthate into the more central regions of the minor veins. In some monocotyledons, e.g. *Zea mays*, there are two types of phloem-loading cells, larger vascular parenchyma cells and smaller, more internal companion cells. Vascular parenchyma cells which are in contact with vessel members are connected to thick-walled sieve tube members by pore–plasmodesmata connections (Evert *et al*., 1978). They are able to retrieve sucrose from the vessels and transfer it to the thick-walled sieve tubes but are not thought to be involved in long-distance transport of photosynthate (Fritz *et al*., 1983). The thin-walled sieve tube members which function in long-distance transport are also connected to their associated companion cells by numerous pore–plasmodesmata connections, but are essentially isolated from other cells in the leaf by the very low frequency of interconnecting plasmodesmata (Evert *et al*., 1978).

It is interesting that in many species of seed plants, the minor vein system in which phloem loading and transport take place is characterized by vein endings that contain no sieve tube members. Lersten (1990) found that about a third of the vein endings in *Rudbeckia laciniata* lack a sieve tube, that only 10% have sieve tubes extending to the tip, and that the sieve tubes in about 60% stop at some intermediate point. In an even

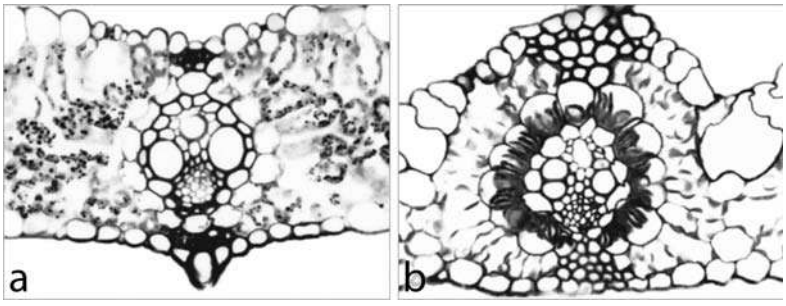

Figure 17.19 Transverse sections of grass leaves showing structural variation in C_3 and C_4 plants. (a) Leaf of *Panicum bisulcatum*, a C_3 plant. The bundle sheath is composed of cells with a few small chloroplasts, and lacks a clearly defined surrounding sheath of mesophyll cells. (b) Leaf of *Eragrostis speciosa*, a C_4 plant. The bundle sheath contains numerous, large chloroplasts, and is enclosed by a well-defined concentric layer of mesophyll cells. Magnification (a, b) × 160. See the text for more detail. Photographs provided by Professor N. G. Dengler.

more extreme case, Fisher (1989) observed that in *Cananga odorata* about 60% of the entire minor vein network lacks sieve tubes. He concluded that assimilate was transported from the mesophyll through lateral parenchymatous extensions from bundle sheaths, and then along the veins through the bundle sheaths, or vascular parenchyma cells until contact was made with a sieve tube member where phloem-loading could occur. This type of collection of assimilate from the mesophyll has been observed by other workers (e.g., Dengler and MacKay, 1975; Franceschi and Giaquinta, 1983b; Russin and Evert, 1984). For a more detailed discussion of phloem-loading in leaves, see Chapter 12 on the phloem.

Because photosynthesis and respiration require passageways for gaseous exchange between the external environment and the interior of the leaf (usually resulting in loss of water from the leaf), certain structural features that reduce water loss have evolved. These are especially apparent in xerophytes. Among these features are the presence of a thick water-impermeable cuticle, a hypodermis, abundant epidermal hairs, sunken stomata, and in some plants, the reduction in number and size of stomata. The latter adaptations are features of many C_4 plants.

Leaf structure of C_3 and C_4 plants

One of the most interesting structural features of leaves is the distinction between the bundle sheaths of C_3 and C_4 plants (Fig. 17.19). The bundle sheaths of C_3 plants (Fig. 17.19a) have few organelles and small chloroplasts, and appear empty at low magnifications. The mesophyll cells surrounding the bundle sheaths show no specific arrangement in relation to the sheath cells. In C_4 plants (Fig. 17.19b), the bundle

sheath cells are prominent, of relatively large size and have thick walls. They contain many large chloroplasts (larger than those in cells of the mesophyll) that often (but not always) are located adjacent to the tangential walls in contact with mesophyll cells. The immediately surrounding mesophyll cells are frequently arranged in an orderly array. Because of the prominence of the bundle sheath, its intensely green color, and the concentric layers formed by the sheath and immediately surrounding mesophyll cells, the term "Kranz" (wreath) was applied to this type of anatomy by the German botanist Haberlandt. Of course, such bundle sheaths appear as wreaths only in transverse sections of veins. In recent times, the term **kranz syndrome**, has been applied to the combination of anatomy and physiology reflected in the processes that incorporate both the C_4 (or Hatch–Slack) pathway and the Calvin cycle during the dark reactions of photosynthesis.

During the **Calvin cycle** in C_3 plants, characteristic of most angiosperms, the first product of CO_2 reduction is the three-carbon compound, 3-phosphoglyceric acid. Following a series of enzymatic reactions, photosynthate (glucose) is formed. By contrast, in C_4 plants utilizing the four-carbon or **Hatch–Slack pathway** in photosynthesis, which takes place in the mesophyll cells, the first product of CO_2 fixation is oxaloacetic acid. Following several intermediate reactions malate or aspartate is formed. The malate or aspartate then moves into the bundle sheaths where, in chloroplasts, it is decarboxylated to yield CO_2. This CO_2 is then utilized in the Calvin cycle with the ultimate synthesis of glucose. C_4 plants thus have two sources of CO_2, the Hatch–Slack pathway and the external atmosphere. Because C_4 plants utilize CO_2 more efficiently than C_3 plants they can maintain a photosynthetic rate comparable to that of C_3 plants with fewer and smaller stomata with a consequent reduction in water loss. This explains why many grasses which are C_4 plants can tolerate very dry conditions. It is not surprising, therefore, to note that many C_4 plants evolved in the tropics in conditions of high temperatures, high light intensity, and low availability of water (but see Press (1999) for a more detailed analysis of the functional significance of the C_4 pathway and some caveats). Recent papers by Nelson and Dengler (1992), Dengler *et al.* (1994, 1997), and Soros and Dengler (2001) present detailed discussions of the development of the vascular system in leaves of C_3 and C_4 plants as well as variations in photosynthetic pathways. Sinha and Kellogg (1996), Kellogg (1999), and Soros and Dengler (2001) discuss the evolution of the C_4 pathway.

Supporting structures in leaves

Certain structural features of leaves such as the hypodermis, sclerenchymatous ribs (Figs 17.9, 17.17e), bundle sheath extensions (Figs 17.5, 17.19b), and the system of veins as well as the hydrostatic pressure within the living cells function in providing support. In some mesophytic leaves, however, an important element of support is not

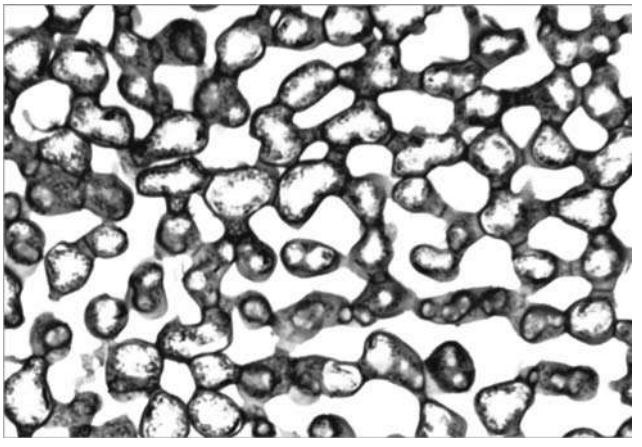

Figure 17.20 Spongy mesophyll as seen in paradermal section. Note the reticulate system of cells which provides support in the lower part of the leaf. Magnification × 247.

immediately apparent. When observed in **paradermal section** (sections cut parallel to the leaf surface), the cells of the spongy mesophyll are characterized by radiating extensions that abut on similar extensions of adjacent cells thus providing a structural net-like system that provides support in the lower part of the leaf (Fig. 17.20). This may be especially important in large, thin laminate leaves, contributing to the several aspects of support that prevent such leaves from collapsing on themselves. Characteristics of the petiole such as length, transverse shape, geometry, and stiffness (provided primarily by the presence of tracheary tissue, collenchyma, and sclerenchyma), and the propensity of many laminate leaves "to fold and curl into streamlined objects" reduce the drag forces and allow leaves to resist high wind velocities without damage (Niklas, 1999).

Transfusion tissue in conifers

In conifers and some other gymnosperms the vascular supply in leaves is associated with **transfusion tissue**, a specialized tissue of parenchyma cells intermixed with short, tracheid-like cells, the walls of which contain circular bordered pits (Fig. 17.21a, b). In *Pinus*, the transfusion tissue completely surrounds the vascular bundles (Fig. 17.21a), but varies in quantity and arrangement in other conifers. The vascular bundles and transfusion tissue are enclosed by an endodermis (Fig. 17.3). Since the early studies of Münch and Huber, it has been accepted that water and solutes are transported from the tracheids of the vascular bundles through the tracheid-like cells of the transfusion tissue to the leaf mesophyll, and that photosynthate is transported from the mesophyll by way of the transfusion parenchyma into the phloem of the vascular bundles. It is likely, therefore, that the parenchyma cells of the transfusion tissue function as transfer cells. Canny (1993) has suggested that because two-way transport of water and assimilates is characteristic of plants that lack transfusion tissue, this tissue of conifers might have several other significant functions, for example,

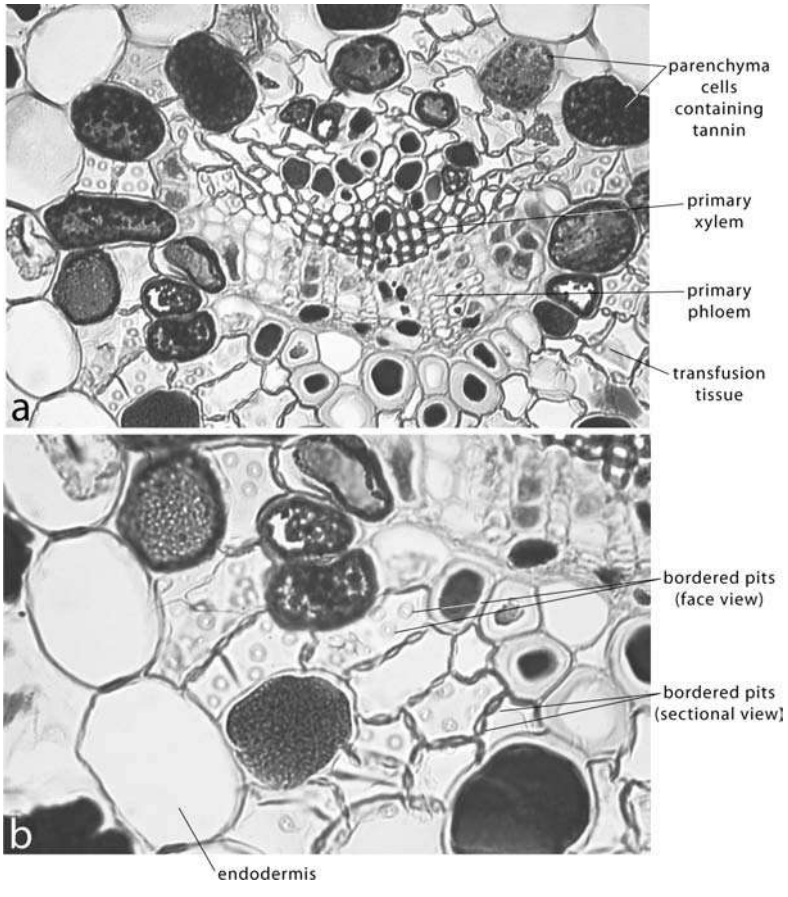

Figure 17.21 Transfusion tissue associated with the vascular bundle in a leaf of *Pinus monophylla*. (a) Note the tissue, surrounding the central vascular bundle, composed of large, tannin-filled parenchyma cells interspersed among smaller cells, the walls of which are characterized by circular bordered pits. Magnification × 312. (b) Enlargement of a region of transfusion tissue, showing the bordered pits in face and sectional views. Magnification × 459.

the concentration of solutes from the transpiration stream and the retrieval from the stream of selected solutes that are returned to the phloem through the transfer cells, or fowarded through the endodermis to the palisade. Unanswered are the means whereby water and photosynthate cross the endodermis.

Leaf abscission

Determinate plant structures such as leaves, leaflets (of compound leaves), flowers, flower petals, and fruit are shed from the plant at the end of their functional lifespans. In some plants, for example *Populus* (poplar), twigs and branches are also shed. This process of the shedding of plant parts is called **abscission**. It has been known for many years that abscission is controlled by the hormones auxin and ethylene, and that it is also closely correlated with environmental factors such as photoperiod, ozone, wounding and/or attack by pathogens, water stress, and senescence (see Taylor and Whitelaw, 2001). Recent studies indicate that the protein expansin may also play an important role in abscission through the process of wall loosening and cell expansion (Cho

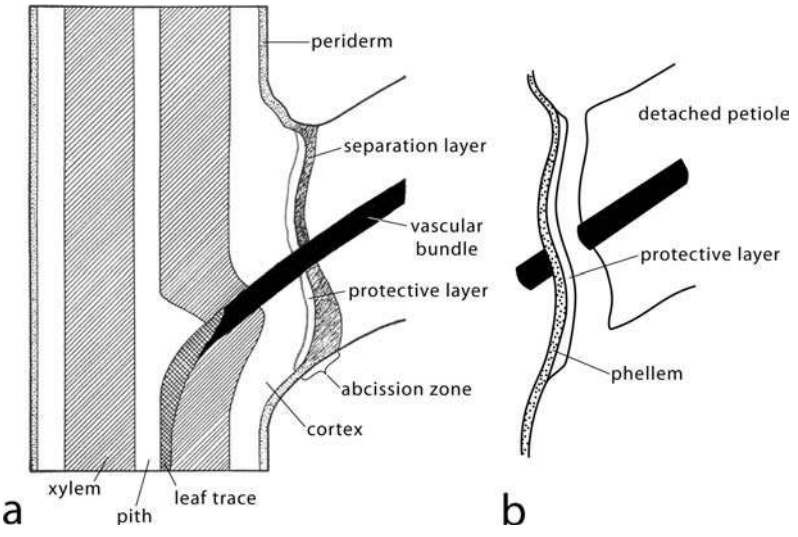

Figure 17.22 (a) Diagram illustrating the abscission zone of a leaf. Median longitudinal section. The abscission zone extends through the vascular bundle(s) in parenchyma cells. (b) Diagram showing the separation from the stem of the leaf of a woody plant. Note that at this stage, the protective layer is underlain by a layer of phellem which provides additional protection against water loss and the entry of pathogens.

and Cosgrove, 2000). Prior to the release of organs from the plant an **abscission zone** develops, characterized by two anatomically distinct layers, a separation layer and a protective layer (Fig. 17.22a). The effects of auxin and ethylene on cells of the developing **separation layer** have been described in detail by Osborne (1976) and Osborne and Sargent (1976a, 1976b). They found that, in *Sambucus nigra*, some cells increase in size in response to ethylene but not auxin, others in response to auxin but not ethylene and in some, growth occurred in response to both hormones. The results of research by numerous workers suggests, however, that in general, ethylene stimulates, and auxin restricts, cell growth in the separation layer. The balance of these two hormones is thought to provide a regulatory mechanism for the control of the size and shape of cells in the separation layer (see Taylor and Whitelaw, 2001). The actual separation of the leaf (Fig. 17.22b), or other organ, from the plant results from the loss of adhesion between cells caused by dissolution of the middle lamella through the action of hydrolytic enzymes such as polygalacturonase and cellulase (see Taylor *et al*., 1990; Taylor and Whitelaw, 2001). The separation layer consists of parenchyma tissue traversed by vascular bundles, the xylem of which may differ from that on either side of the layer. The metaxylem vessel members in the separation layer of *Acer pseudoplatanus*, for example, have pitted–scalariform, helical–scalariform and scalariform–pitted secondary wall thickenings (Fig. 17.23), but vessel members with pitted walls only on either side of the abscission zone (Andre *et al*., 1999). In woody plants, the tracheary tissue in the separation layer often consists of very short cells resulting in a weakened zone. Even so, in some plants, for example *Quercus*, leaves remain on the tree until the vascular strands (leaf traces) are broken by freezing.

The **protective layer**, which prevents water loss and the entrance of pathogens, forms behind the separation layer. The walls of the component cells become impregnated with suberin and wound gum, and

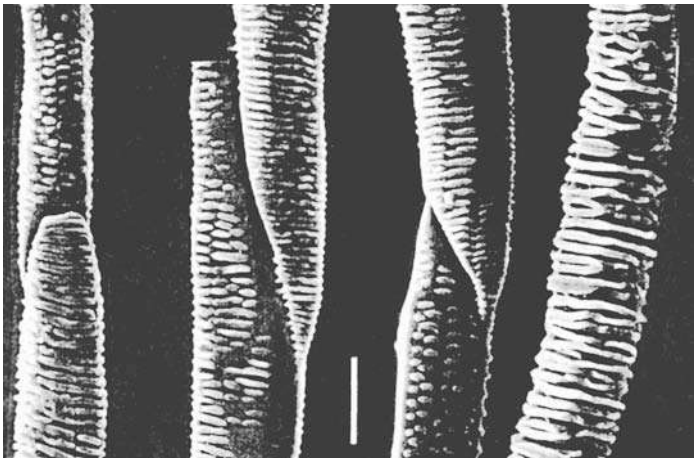

Figure 17.23 Scanning electron micrographs of vessel casts from the abscission zone of *Acer pseudoplatanus*. Bar = 50 μm. From Andre *et al.* (1999). Used by permission of the National Research Council of Canada.

the intercellular spaces are often filled with the same substances. In woody plants a layer of phellem (Fig. 17.22b) that enhances or replaces the function of the protective layer develops just before or immediately following separation.

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Chapter 18

Reproduction and the origin of the sporophyte

Perspective: the plant life cycle

Reproduction in higher plants is relatively complex, involving a life cycle consisting of two phases, a diploid sporophyte phase and a haploid gametophyte phase, comprising what is called an **alternation of generations**. The prominent bodies of angiosperm trees, shrubs, perennials, and annuals as well as those of gymnosperms, ferns, sphenophytes, and lycophytes are **sporophytes**, having developed from fertilized egg cells (zygotes). The gametes which fused to form the zygotes, however, were produced by **gametophytes**, very small plant bodies, parasitic on the sporophytes in seed plants, but somewhat larger and free-living in pteridophytes (except in heterosporous species in which gametophytes when mature remain, at least in part, within the walls of the spores from which they develop).

The sporophyte in pteridophytes is dominant, and although dependent initially for its nutrition on the gametophyte, soon becomes independent. The gametophyte is much reduced in size but is free-living and either autotrophic or saprophytic. In seed plants, the sporophyte is also dominant and initially dependent on the gametophyte, but soon becomes independent. The gametophyte is greatly reduced, however, and parasitic on the sporophyte. In angiosperms it is exceptionally small, consisting in many taxa of only seven cells and eight nuclei, and can be observed only with a microscope.

The life cycle of a vascular plant can be summarized as follows. The sporophyte produces specialized cells called **sporocytes** that undergo meiosis producing **haploid spores**. The spores germinate to form the gametophytes in which **gametes** are produced. The gametes fuse to form a **diploid zygote** from which the **embryo** (young sporophyte) develops.

In most pteridophytes, spores of only one size are produced. Plants of this type are described as being **homosporous**. Each spore has the potential to develop into a gametophyte that produces both egg cells and sperms. In contrast, the sporophytes of a few pteridophytes and all seed plants produce spores of two sizes, with different potentials, called microspores and megaspores. These plants are, thus, **heterosporous**.

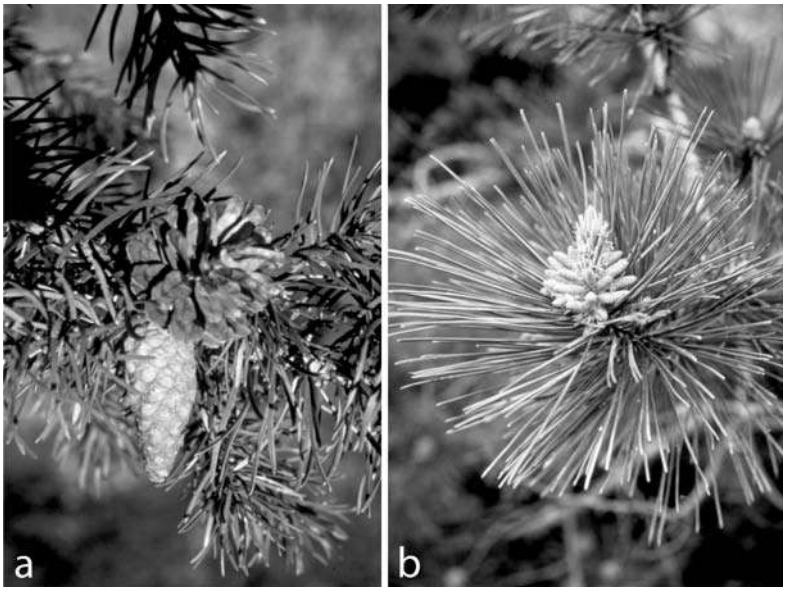

Figure 18.1 Female and male cones of *Pinus* (pine), the sites of development of ovules and microsporangia, respectively. (a) Megasporangiate cones of *Pinus banksiana* (jack pine) in which ovules are produced. (b) Microsporangiate cones of *Pinus resinosa* (red pine) in which microsporangia are produced.

Microspores develop into gametophytes that produce sperms, and **megaspores** develop into gametophytes that produce egg cells.

Reproduction in gymnosperms

Although reproduction in gymnosperms and angiosperms is basically similar, there are several major differences, including the location on the sporophyte of the ovules that contain the **megasporangia** (in which megaspores and, ultimately, egg cells are produced), and the location of the **microsporangia** (in which microspores and, ultimately, pollen grains and sperms develop). Other significant differences are the complexity of the gametophytes, mechanisms of pollination and fertilization, and nutrition of the developing embryo. In general, the structures involved in angiosperm reproduction, contained in the flower, are much reduced in comparison with those in gymnosperms. The ovules and microsporangia of extant gymnosperms are produced in female (**megasporangiate**) and male (**microsporangiate**) cones (or strobili) respectively (Fig. 18.1a, b). Exceptions are the ovules of *Ginkgo biloba* which are borne terminally, usually in pairs, on long stalks called peduncles, and the ovules of *Gnetum* which occur laterally on branched axes. Whereas we shall emphasize reproduction in conifers in this book, interesting research on *Ginkgo*, *Ephedra*, and *Gnetum* has been published recently (Friedman, 1990, 1994, 1998; Friedman and Gifford, 1997; Friedman and Carmichael, 1998). This research is especially important because of the demonstration of double fertilization in both *Gnetum* and *Ephedra*, and the light it throws on the phylogenetic relationship of these taxa to the angiosperms.

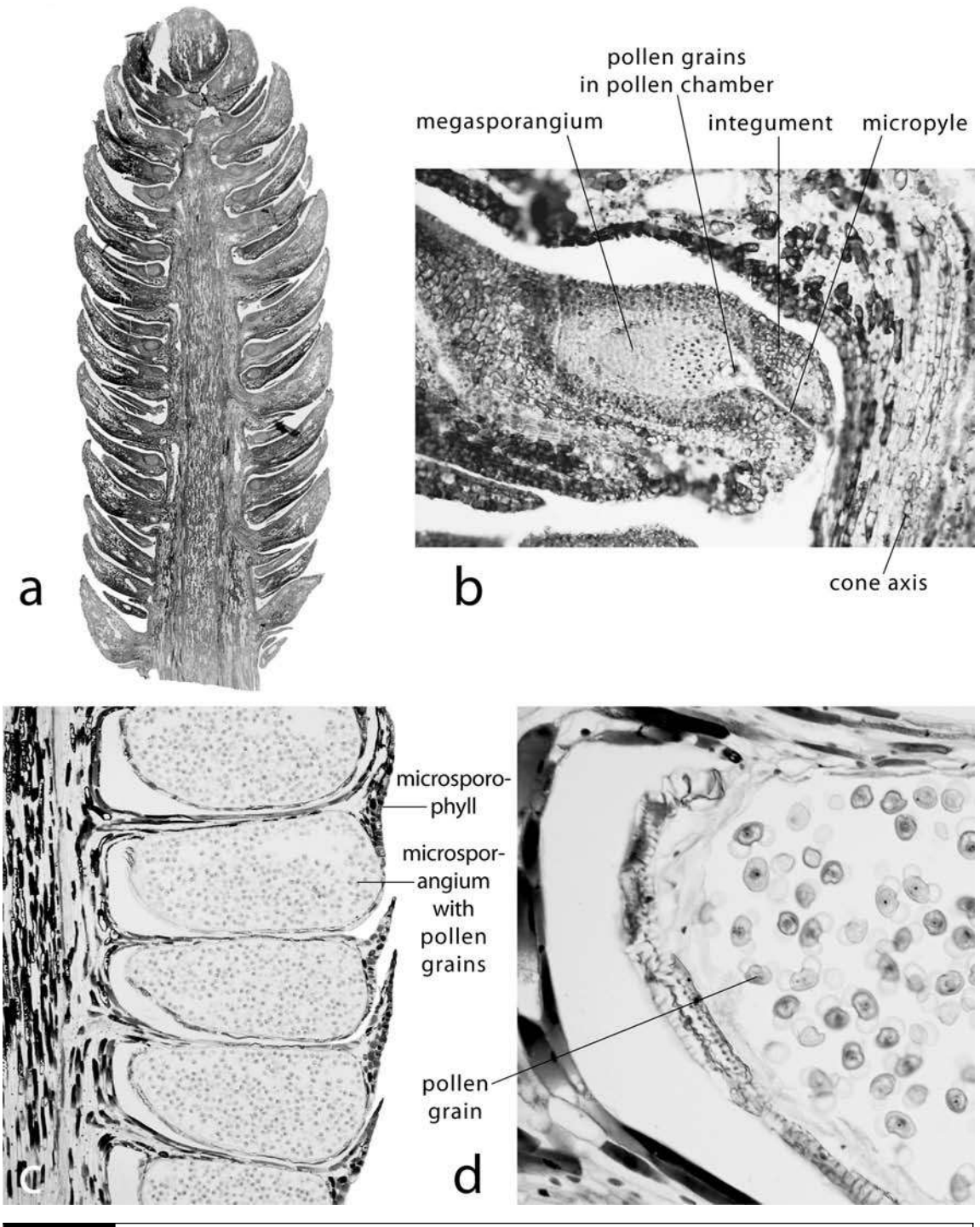

Figure 18.2 (a) Median longitudinal section of a female cone of *Pinus wallichiana* (Himalayan pine) showing bracts, ovuliferous scales, and adaxial ovules. Magnification × 5. (b) Enlargement of an ovule from (a) showing the integument and megasporangium. Note that the micropylar end of the ovule faces the cone axis; also the presence of pollen grains in the pollen chamber. Magnification × 74. Compare with Fig. 18.3a. (c) Median longitudinal section of part of a microsporangiate (male) cone of *Pinus* sp. showing microsporophylls bearing, abaxially, two microsporangia. Only one of the pair can be seen in this longitudinal section. Magnification × 28. (d) Enlargement of a part of a microsporangium from (c) illustrating the pollen grains which have developed from microspores. Magnification × 15.

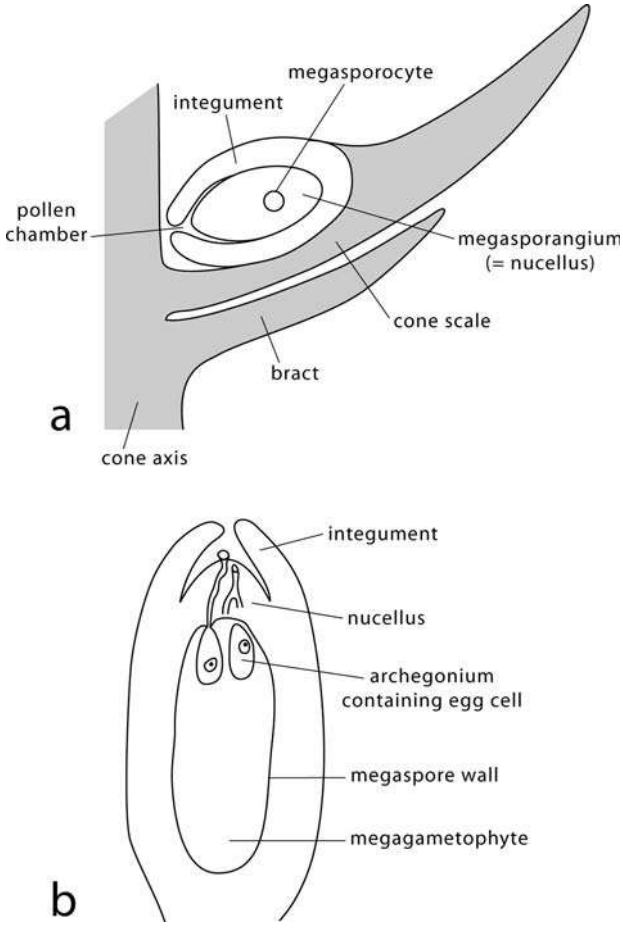

Figure 18.3 (a) Diagram illustrating the megasporocyte in the megasporangium of a conifer ovule. (b) Mature ovule containing a megagametophyte. Following meiosis three of the megaspores abort, and the remaining spore develops into the megagametophyte. Please see the text for a more detailed description.

In conifers, ovules are borne on the adaxial surface of **ovuliferous scales** (Fig. 18.2a, 18.3a) with the **micropylar end** of the ovules near to, and facing, the cone axis (Fig. 18.2b). Microsporangia are borne on the abaxial surface of **microsporophylls** (Fig. 18.2c). In conifers a multicellular megasporangium (called nucellus in older literature) and a single enclosing integument comprise the ovule. Meiosis occurs in the **megasporocyte** located within the megasporangium (Fig. 18.3a) resulting, typically, in a **linear tetrad of megaspores**, three of which abort, the remaining one developing into the **megagametophyte** (Fig. 18.3b). As the functional megaspore enlarges, the nucleus divides repeatedly, in some species, over a period of several months, accompanied by increase in the volume of cytoplasm and in the size of the developing gametophyte. During the following spring in, for example *Pinus virginiana*, walls develop between the many nuclei, and one or more **archegonia** develop near the micropylar end of the gametophyte, each containing a large egg cell (Fig. 18.3b). In gymnosperms archegonia vary in number from one to as many as 50. During its development and growth the megagametophyte derives nutrition symplastically via plasmodesmata from the enclosing megasporangial tissue. In the mature

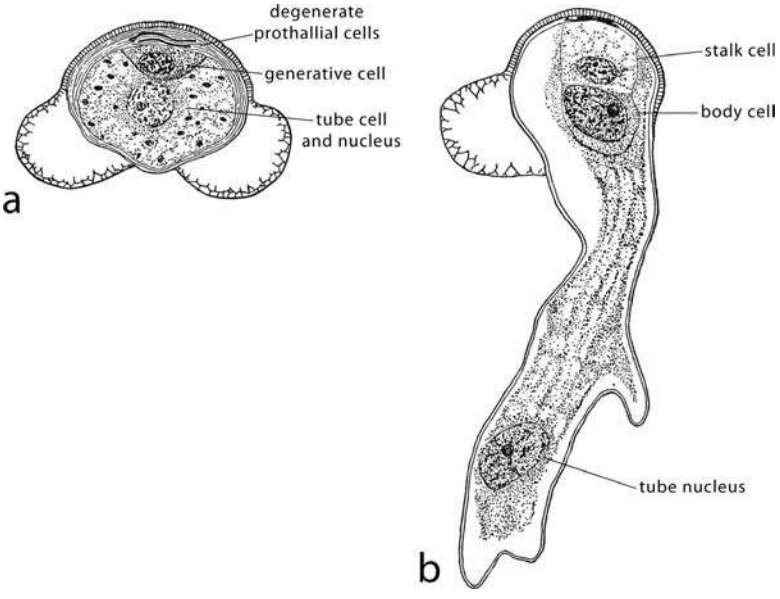

Figure 18.4 (a) A pollen grain of *Pinus* at the time of pollination. (b) Germinating pollen grain (male gametophyte). The stalk cell and body cell were derived from the generative cell. The body cell will divide to form two sperms. Note the branching of the pollen tube which in many conifer species becomes haustorial. From Coulter and Chamberlain (1917).

ovule (Fig. 18.3b) at the time of fertilization, the megagametophyte is enclosed by the enlarged **megaspore wall** and a layer of disintegrated and compressed sporangial tissue called the **tapetal wall**.

Following **microsporogenesis** (meiosis and spore development) microspores develop into pollen grains (Fig. 18.2d) which are immature male gametophytes. At the time of pollination each pollen grain contains two degenerate prothallial cells, a generative cell and a tube cell (Fig. 18.4a). The pollen grain, wind-dispersed, lands in a pollination droplet which retracts and draws the pollen grain through the micropyle and into contact with the surface of the megasporangium (Fig. 18.2b). Here it germinates producing a **pollen tube**, often branched (Fig. 18.4b), which enters megasporangial tissue where it functions as a **haustorium**. After a variable period of time, in different species, during which the megagametophyte develops to maturity (e.g., several months in *Picea abies* and over a year in several species of *Pinus*), the **generative cell** divides, forming a stalk cell and a body cell (Fig. 18.4b). At this stage, the pollen tube containing the body cell begins to grow, and the **body cell** divides to form two sperm nuclei. By secreting proteases (see Pettitt, 1985) the tube digests its way through gametophyte tissue and into contact with the egg cell where the tip bursts, releasing the sperm nuclei, one of which fuses with the egg nucleus, forming the zygote, the other disintegrating. In some gymnosperms, several egg cells may be fertilized with the result that several embryos will develop (Fig. 18.5a), a process called **polyembryony**. In many conifers, the **proembryo**, which represents an early stage in sporophyte development, becomes subdivided into several (usually four) embryos, a process called **cleavage polyembryony**. In either case, only one of the embryos continues its development (Fig. 18.5b), the others abort. During the growth and development of the embryo within the seed, the young sporophyte obtains

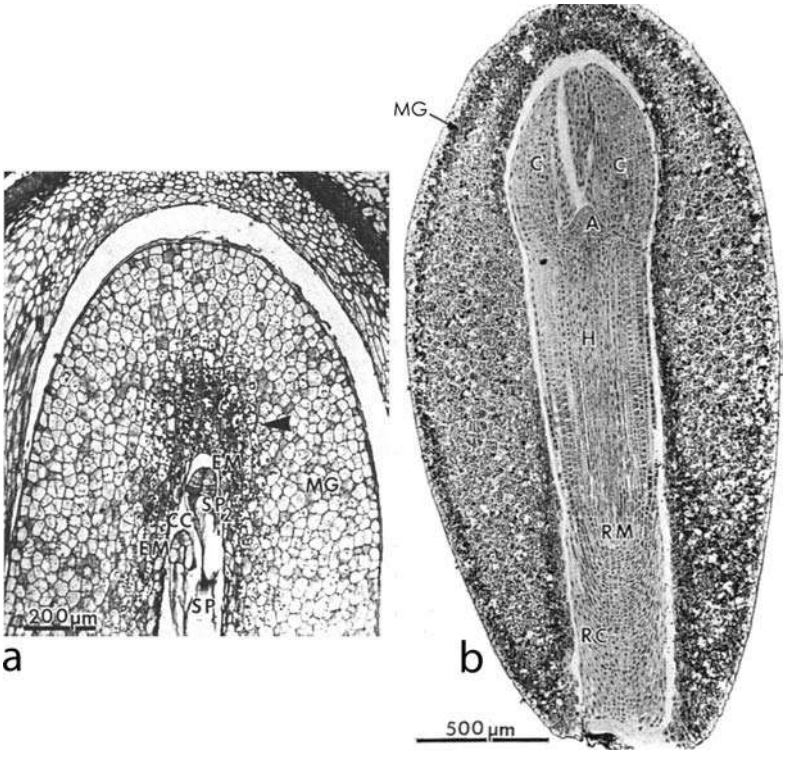

Figure 18.5 Conifer embryos. (a) Section through the ovule of *Picea glauca* (white spruce) showing the megagametophyte containing two proembryos, an example of polyembryony. MG, megagametophyte; EM, proembryo; SP, suspensor; CC, corrosion cavity; arrowhead indicates cells containing starch grains. (b) A mature embryo in the seed of *Picea laricio* (Corsican pine). A, apical meristem; C, cotyledon; H, hypocotyl; MG, megagametophyte; RM, root meristem; RC, root cap. From Krasowski and Owens (1993). Used by permission of the National Research Council of Canada.

nutrients from storage products, predominantly lipids and proteins (Krasowski and Owens, 1993), in the tissue of the megagametophyte in which it is enclosed. After release from the female cones the seeds may germinate, followed, ultimately, by development of independent sporophytes. For a detailed presentation of many aspects of reproduction and embryogeny in gymnosperms, see Doyle (1963), Singh (1978), Owens and Morris (1991), Romberger *et al.* (1993), Owens *et al.* (1998), Runions and Owens (1999a, 1999b), Bruns and Owens (2000), and Owens and Bruns (2000).

Reproduction in angiosperms

The **flower** (Fig. 18.6) is the site of sexual reproduction in angiosperms. Whereas it consists of fewer component parts than the cones of most gymnosperms, the parts, usually grouped in whorls, or shallow spirals, are more highly specialized, and each has evolved with a specific function. Evidence from the fossil record indicates that the various floral parts evolved from the leaves of their ancestors. The major evidence for this conclusion is the form and venation pattern of the sepals and petals and, to a lesser extent, carpels and stamens (see Stewart and Rothwell, 1993). The **sepals**, called collectively the **calyx**, and the lowermost whorl of floral parts, are the most leaf-like components of the flower. In many flowers they are green and photosynthetic. Following,

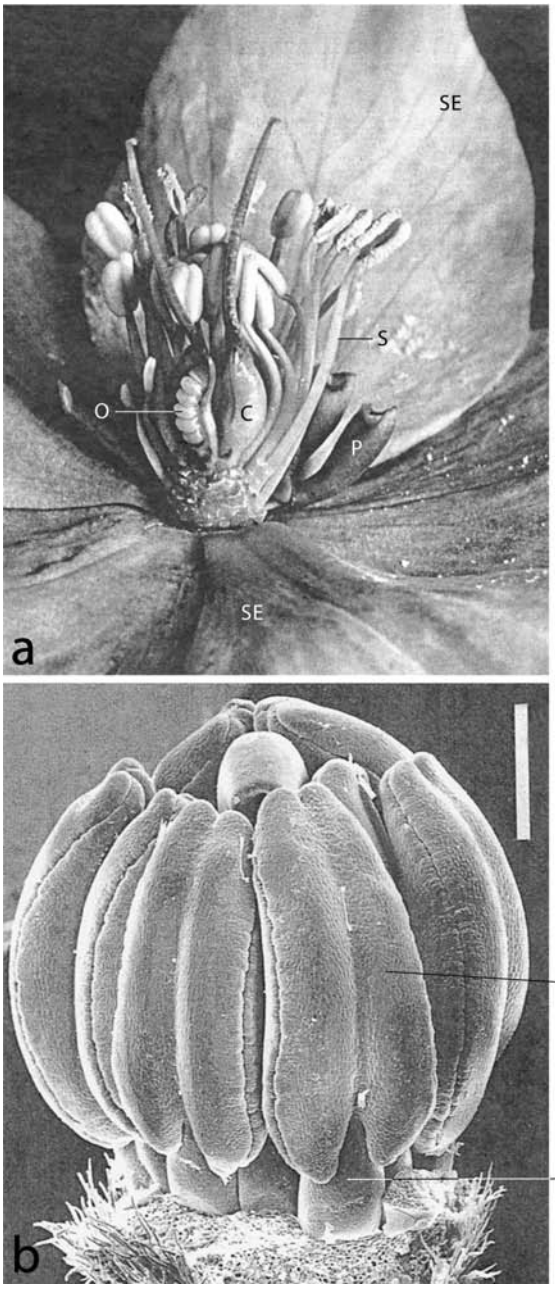

Figure 18.6 (a) The flower of *Helleborus*. This specimen has been dissected in order to show the separate floral components. The large leaf-like structures forming the basal whorl are sepals (SE), followed distally by petals (P) (in this taxon, highly modified), stamens (S) and carpels (simple pistils) (C). Part of the ovary wall of one carpel has been removed to show the ovules (O). (b) Stamens of *Senna artemisioides*. Note the broad filaments and large anthers which contrast with the slender filaments and smaller anthers of *Helleborus*. (a) From Jaeger (1961). Used by permission of Chambers Harrap Publishers Ltd. © Chambers Harrap Publishers 1961. (b) From Tucker (1997). Used by permission of the University of Chicago Press. © 1997 The University of Chicago. All rights reserved.

distally, are the **petals**, collectively called the **corolla** which with the calyx comprises the **perianth**. The petals typically are not photosynthetic, but in form and vasculature are usually, but not always, very leaf-like. They often contain brightly colored pigments and sometimes have specialized shapes that attract pollinators. The **stamens** (Fig. 18.6a, b) which comprise the next more distal whorl of floral parts may also be of foliar origin, but evidence from the fossil record in support of this conclusion is meager. Stamens consist of a **filament**, usually (but not

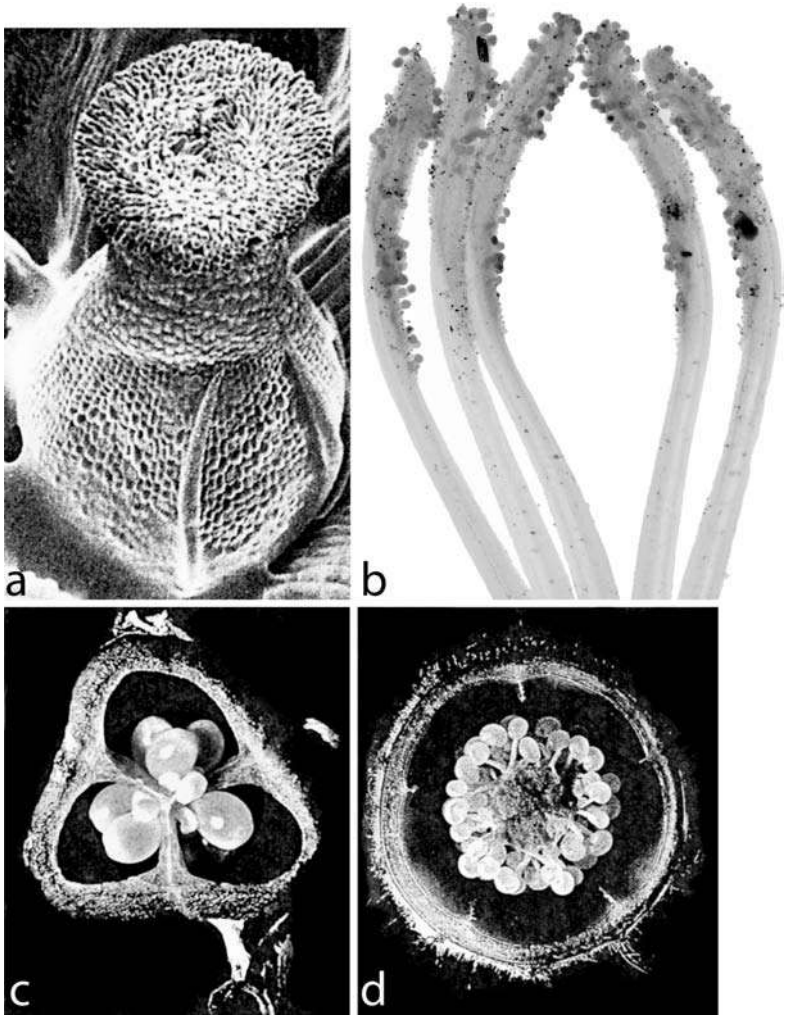

Figure 18.7 (a) The compound pistil of *Alyssum*. Note the short, broad style and prominent, papillate stigma. Magnification × 98. (b) The branched stigma of *Lilium grandiflorum* to which adhere numerous pollen grains, many of which have germinated. Magnification × 32. (c, d) Transverse sections through the ovaries of compound pistils. (c) A tricarpellate ovary of *Endymion* sp. with axile placentation. (d) A five-carpellate ovary of *Lychnis* sp. with free central placentation. Note loss of septa between the carpels. (a, c, d) From Jaeger (1961). Used by permission of Chambers Harrap Publishers Ltd. © Chambers Harrap Publishers 1961.

always) long and slender, which terminates in an **anther** that contains, typically, four microsporangia. Its major function is the production of pollen grains, which upon germination produce pollen tubes, each containing two sperms cells. The terminal whorl of floral parts is made up of the **carpels** (Fig. 18.6a). They are also considered to have a foliar origin, but the details of their evolution as well as the several hypotheses regarding their origin are highly controversial. Carpels consist of the **ovary**, containing the ovules (Figs 18.6a, 18.7c, d) which ultimately develop into **seeds**, and the **style** (lacking in some taxa), a usually slender apical extension of the ovary (Fig. 18.6a), terminated by the **stigma** (Fig. 18.7a, b). The stigma is the receptor of pollen and the structure upon which the pollen germinates. The parts of each floral whorl may remain separate or they may fuse during development. A single carpel is called a **simple pistil** (Fig. 18.6a) whereas fused carpels comprise a **compound pistil** (Fig. 18.7c, d). As the structure in which reproduction occurs in angiosperms, the flower has been modified during evolution

Figure 18.8 A flower of *Acer platanoides* (Norway maple) containing a prominent nectary surrounding the ovary and enclosing the bases of the stamen filaments. (b) Flowers of *Cornus sanguinea*, each with a nectary situated upon the inferior ovary and enclosing the base of the style. (a, b) From Jaeger (1961). Used by permission of Chambers Harrap Publishers Ltd. © Chambers Harrap Publishers 1961.

in several significant ways that attract pollinators such as insects and birds. One such innovation is the presence in most flowers of one or more nectaries (Fig. 18.8a, b), specialized secretory glands of diverse form that produce **nectar**, a liquid often containing a high concentration of sugar. Nectar is utilized as a food source by some insects and birds (especially hummingbirds). Nectaries commonly occur on the receptacle of the flower where they may surround the base of the pistil and even enclose the base of the stamen filaments as in *Acer* (Fig. 18.8a). In flowers with inferior ovaries, however, nectaries are usually located upon the ovary, and may surround the base of the style, as in *Cornus* (dogwood) (Fig. 18.8b). Bird-pollinated plants often produce copious quantities of nectar. It has been reported that the flowers of *Eucalyptus* produce so much nectar that they may overflow. A tree producing several hundred thousands of flowers would, therefore, provide a food supply for innumerable bird pollinators (Jaeger, 1961).

Meiosis occurs in two different parts of the flower, anthers and ovules. In anthers meiosis occurs in **microsporocytes** (sometimes called meiocytes) contained in microsporangia, producing microspores (Fig. 18.9a–c). Microspores develop into pollen grains (Fig. 18.9d, e) which upon germination develop into male gametophytes, commonly called **microgametophytes**. Each pollen grain consists of two cells, a generative cell and a tube nucleus (Fig. 18.9e). Upon germination, the generative cell nucleus divides to form two sperm cells (Fig. 18.10a, b) each comprising a nucleus and some surrounding cytoplasm. It was long assumed that the two sperm cells were essentially identical and that it was a matter of chance which one fused with the egg cell. Recent research has shown, however, that the sperm cells in some taxa differ in size and content of cytoplasmic organelles such as plastids and mitochondria, and that preferential fertilization may occur in species in which the sperm cells are different (Russell, 1984, 1985; Knox *et al*., 1993). Sperm cells of some other species, for example, *Nicotiana tabacum* (tobacco), are approximately the same size and have similar distributions of cytoplasmic organelles. Consequently, they are characterized as being isomorphic (Yu *et al*., 1992). Prior to fertilization,

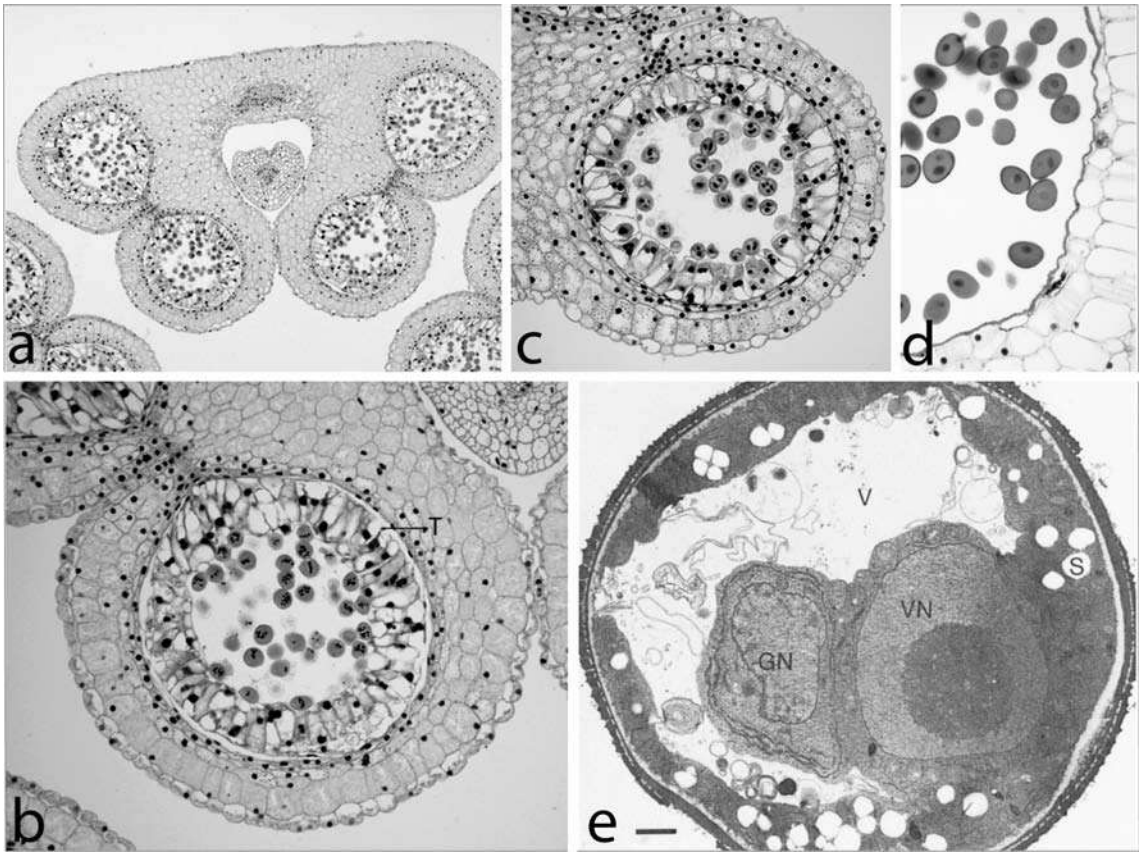

Figure 18.9 Microsporogenesis in *Lilium* sp. (a) A section through an anther with four microsporangia. Magnification × 29. (b) Microsporangium showing the tapetum (T) and the first meiotic division in microsporocytes. Magnification × 87. (c) Tetrads of microspores resulting from meiosis. Magnification × 76. (d) Mature pollen grains. Magnification × 94. (e) Transmission electron micrograph of a pollen grain illustrating the generative cell (GN) and the tube (vegetative) nucleus (VN). V, vacuole; S, starch. Bar = 1 μm. (e) From Polowick and Sawhney (1993). Used by permission of the National Research Council of Canada.

the two sperm cells are in contact with each other, and the leading sperm cell is intimately associated with the tube (vegetative) nucleus (Fig. 18.10a, b).

Meiosis also occurs in **megasporocytes**, one of which is contained in each of the developing ovules (Fig. 18.11). The megasporocyte is enclosed in a vegetative tissue, the **nucellus**, bounded by one or two ovular integuments. Most commonly, in angiosperms, as in conifers, meiosis results in the formation of a linear tetrad of megaspores, oriented in a plane parallel to the long axis of the ovule (Fig. 18.12a, b). Three of these spores degenerate and the remaining megaspore (Fig. 18.12c) develops into the female or **megagametophyte**, called in angiosperms the **embryo sac**. Three mitotic divisions within this cell result in eight nuclei (Fig. 18.12d–f). As these nuclear divisions are occurring, the original cell expands and elongates, and four of the nuclei migrate to each end of the developing embryo sac. At the **micropylar end** (the end of the embryo adjacent to the micropyle in the ovule) (Fig. 18.12g) one nucleus becomes at least partially enclosed by a cell wall and functions as the egg cell, while two others differentiate into **synergids**. These cells, in contact with the egg cell, are distinctive in possessing a **filiform apparatus** (Fig. 18.13), a much-branched system of haustoria that extends from the synergid walls into the surrounding

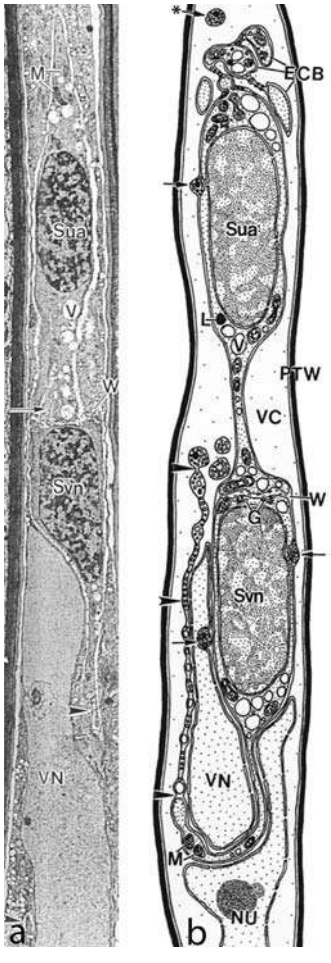

Figure 18.10 (a) Transmission electron micrograph of sperm cells and the vegetative nucleus (VN) in a pollen tube of *Nicotiana tabacum*. The two sperm cells travel in tandem down the pollen tube behind the vegetative nucleus. V, vacuole; M, mitochondrion; Sua, trailing sperm cell; Svn, leading sperm cell. Magnification × 3375. (b) A diagrammatic reconstruction of the male germ unit (sperm cells plus vegetative nucleus) in a pollen tube of *Nicotiana tabacum*. ECB, enucleated cytoplasmic bodies; L, lipid body; arrows and arrowheads, vesicle-containing bodies; W, region of contact between sperm cells; G, Golgi bodies; NU nucleolus; PTW, pollen tube wall; VN, tube nucleus; W, region of contact between sperm cells. From Yu *et al.* (1992). Used by permission of Springer-Verlag Wien.

cytoplasm (Jensen, 1965; Jensen and Fisher, 1968). The function of the filiform apparatus is unclear, but it may be a transfer structure, similar in function to the highly branched wall ingrowths of transfer cells. The egg cell and the two synergids may be homologous with the archegonia in the megagametophytes of gymnosperms. Three of the nuclei at the other end of the developing embryo sac, the **chalazal end**, differentiate, with associated cytoplasm, as **antipodal cells**. The remaining (fourth) nucleus at each end migrates to the center of the developing embryo sac. These two nuclei, the **polar nuclei**, and the cytoplasm remaining after wall formation around the antipodal cells, the synergids, and the egg cell, are contained within the **central cell**. The three antipodal cells, plus the central cell with its polar nuclei, two synergids and the egg cell comprise the mature female gametophyte (Fig. 18.12g). In **megagametogenesis** of the type just described the embryo sac develops from a single spore and, thus, is referred to as **monosporic**. This most common type of embryo sac development in angiosperms was first described in *Polygonum* and, consequently, was called the *Polygonum* type by Maheshwari (1950). There are several variations in embryo sac development, the next best known probably being the **tetrasporic type**, often designated as the *Fritillaria* type in which, following meiosis, there is no degeneration of megaspores, all four becoming incorporated into the embryo sac.

Following pollination, and upon germination of pollen grains on the stigma (Fig. 18.14a–c), pollen tubes will grow down through the style into the locules of the carpels and through the ovular micropyles. As a pollen tube approaches the embryo sac, one of the synergids begins

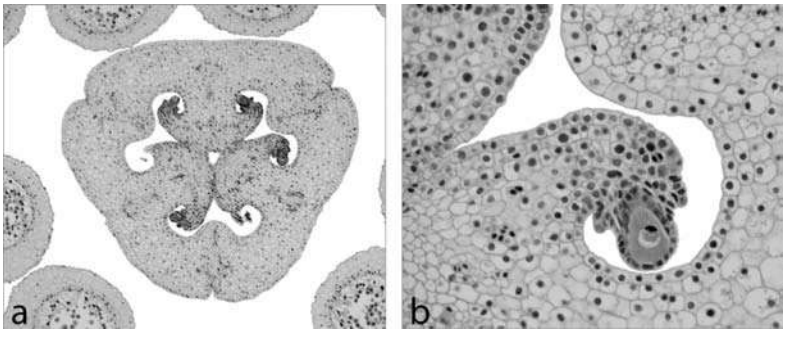

Figure 18.11 (a) Transverse section of a tricarpellate ovary of *Lilium* showing young ovules. Magnification × 26. (b) Enlargement of an immature ovule containing a megasporocyte. Note the immature integuments. Magnification × 116.

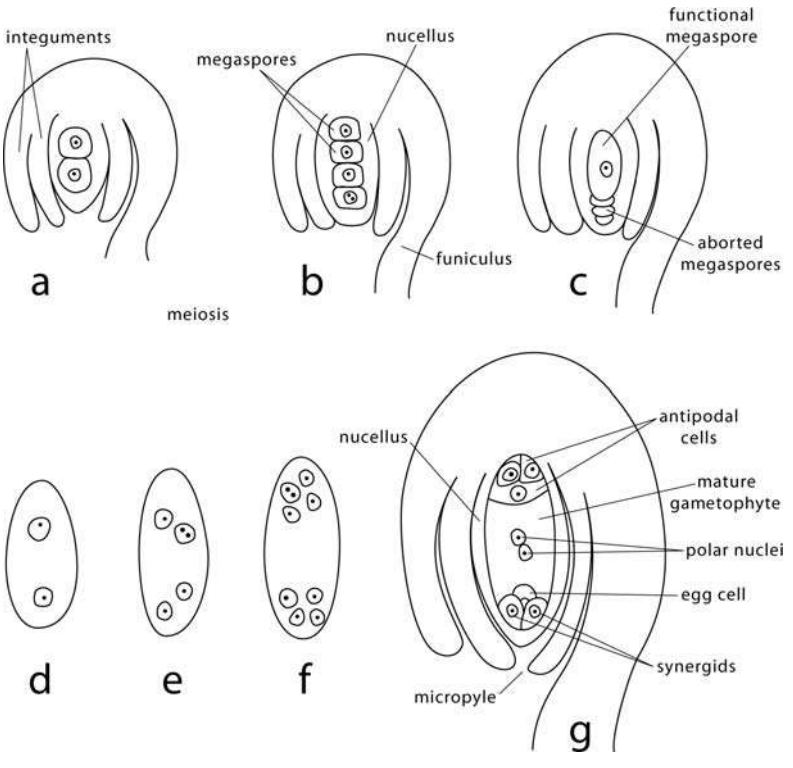

Figure 18.12 Diagrams representing stages in the development of the megagametophyte in *Lilium*. (a, b) Meiosis results in the formation of a linear tetrad of megaspores, three of which abort leaving the single functional megaspore (c). (d–f) A series of three mitotic divisions results in eight nuclei. (g) Three nuclei migrate to each end and two migrate to the center of the developing gametophyte. The three at the micropylar end develop into the egg cell and two synergids. Those at the opposite end (the chalazal end) differentiate as antipodal cells, and the central pair function as polar nuclei. For more detail, please see the text.

to deteriorate, in preparation for entrance of the tip of the pollen tube. Upon entry, the two sperm cells are released into the synergid, the plasma membrane of which has disintegrated (Jensen and Fisher, 1968).

The mechanism whereby non-motile sperm cells are transported down the pollen tube has been of great interest for many years. Recent studies have demonstrated that myosin, adsorbed to the surfaces of the sperm cells, interacts with microfibrils of F-actin promoting their transport down the pollen tube (Zhang and Russell, 1999). The possibility that microtubules associated with the sperm cells may also contribute to their mobility has been proposed recently (Heslop-Harrison and Heslop-Harrison, 1997), but the mechanism is unknown. Upon entry into the embryo sac (female gametophyte), the leading sperm cells of the pair (Fig. 18.10), associated with the tube nucleus, will fuse preferentially with the polar nuclei forming the triploid **endosperm nucleus**. The trailing sperm cell fuses preferentially with the egg cell (Zhang and Russell, 1999), forming the diploid **zygote**, completing the process of **double fertilization**. At this stage the ovule consists of the embryo sac, enclosed by the nucellus, and one or two integuments. It is attached to the wall of the carpel by a stalk, the **funiculus**. At least one primary vascular bundle, which differentiated from provascular tissue prior to formation of endosperm, serves the ovule. This strand, which enters the funiculus from vasculature in the carpel wall (or sometimes several strands and their branches), extends to the chalazal end of the ovule through the outer integument.

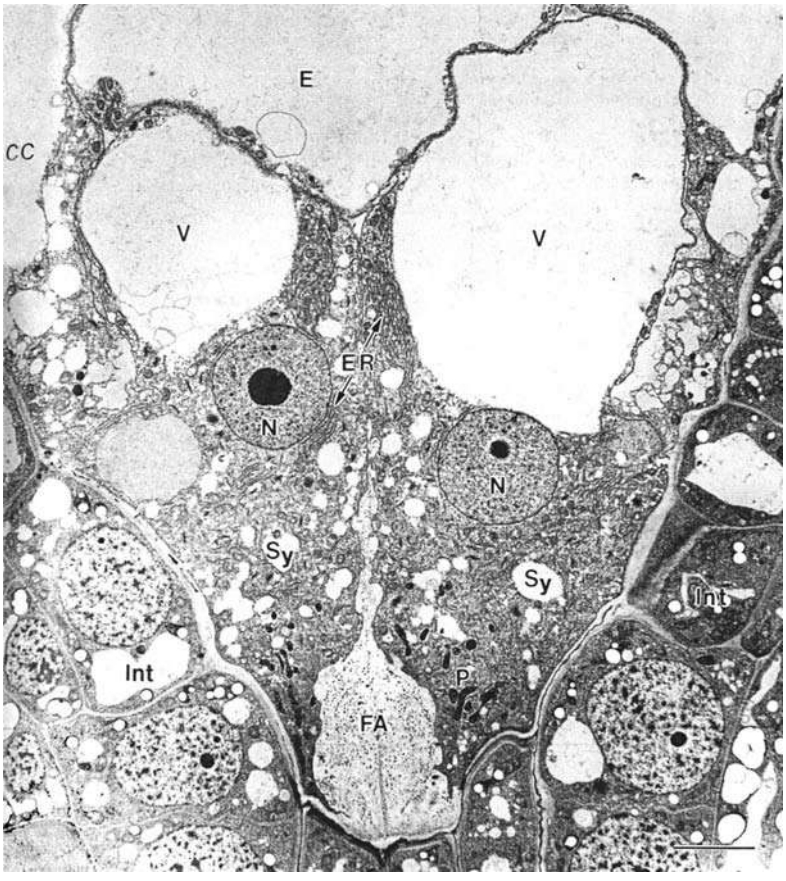

Figure 18.13 Transmission electron micrograph of the egg cell (E) and the two associated synergids (Sy) in the female gametophyte of *Nicotiana tabacum*. Extending from the filiform apparatus (FA) of one of the synergids into the surrounding cytoplasm of the gametophyte are much-branched haustoria, seen here as circular to irregularly shaped light areas. Int, cells of the integument; P, plastids; V, vacuole; N, nucleus; ER, endoplasmic reticulum. Bar = 5 μm. From Huang and Russell (1994). Used by permission of Springer-Verlag GmbH & Co. KG. © Springer-Verlag Berlin Heidelberg.

Development of the seed in angiosperms

In most taxa of dicotyledons, following double fertilization the endosperm begins a relatively rapid development with numerous free-nuclear divisions. As development continues, **nuclear domains** are defined by systems of microtubules which mark the sites of initial cell wall formation (Nguyen *et al*., 2001). Upon completion of wall formation the endosperm becomes a cellular tissue, enclosing the developing embryo (Fig. 18.15b–d), and becoming its direct source of nutrition. Transport of nutrients into the embryo sac and the endosperm from sporophyte tissues (e.g., from ovular integuments) is typically apoplastic, by way of transfer cells. Nutrient transfer between endosperm and embryo, however, can be either apoplastic, or symplastic through plasmodesmata (see Johansson and Walles, 1993a, 1993b).

The ovule and embryo sac increase in size concomitantly during this period. The first division of the zygote, usually transverse, but sometimes oblique, results in an apical and a basal cell. The **basal cell** is usually relatively large and highly vacuolate. Its progeny give rise to the suspensor which is attached to the micropylar end of the embryo sac (Fig. 18.15a). The **suspensor** is thought to function primarily as a

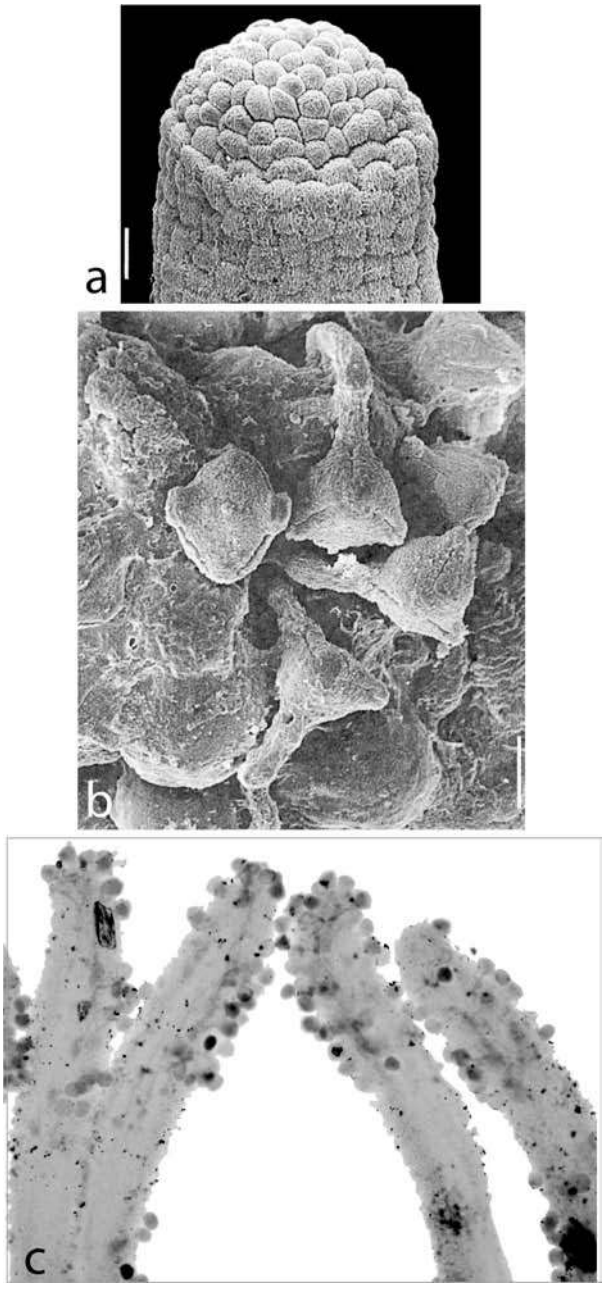

Figure 18.14 (a) The stigma of *Smyrnium perfoliatum*. Bar = 20 μm. (b) Germinated pollen grains on the stigma of *S. perfoliatum*. Individual cells of the stigma are obscured by a covering of exudate which facilitates adhesion of the pollen grains. Bar = 10 μm. (c) The branched stigma of *Lilium grandiflorum* to which many pollen grains adhere. Note the pollen tubes within the stigmatic arms. Magnification × 56. (a, b) From Weber (1994). Used by permission of the University of Chicago Press.

conduit for the translocation of nutrients from surrounding tissues to the developing embryo. Cells derived from divisions of the apical cell and its progeny form a globular mass of very small, densely cytoplasmic and meristematic cells called the **proembryo** (Fig. 18.15a). As development of the proembryo continues, it enlarges and elongates (Fig. 18.15b, c). At the same time protoderm and ground meristem differentiate, and a peripheral region that will become the cortex is delimited. A central region differentiates as provascular tissue, and

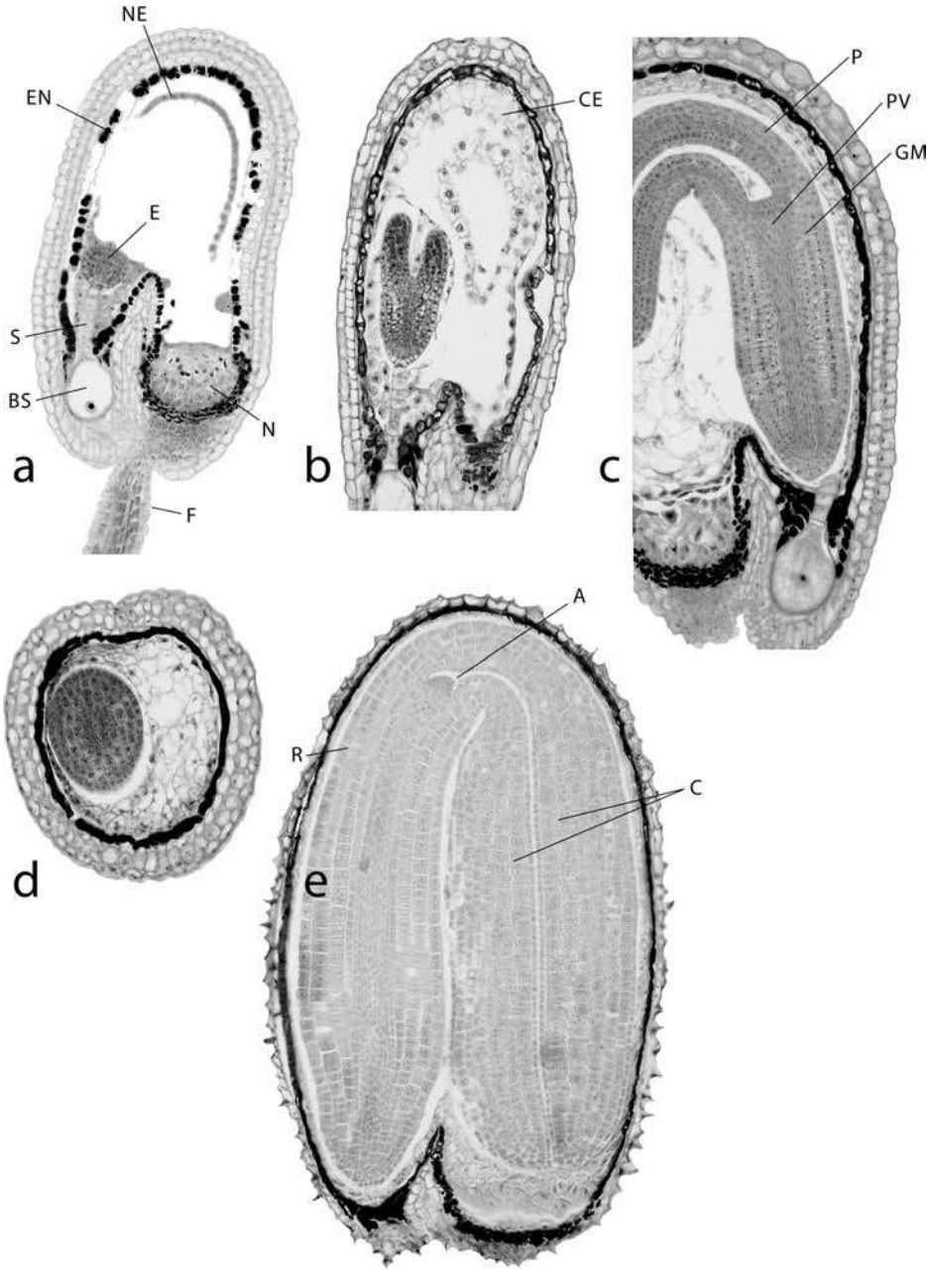

Figure 18.15 Sections of ovules of *Capsella bursa-pastoris* illustrating development of the embryo and endosperm. (a) Longitudinal section of a young, globular proembryo (E). Note the large, vacuolated, basal cell (BS) of the filamentous suspensor (S). EN, endothelium; N, nucellus; NE, nuclear endosperm; F, funiculus. (b) A young seed containing an embryo with developing cotyledons. Note the cellular endosperm (CE). (c) A young seed containing a nearly mature embryo with bent cotyledons. Protoderm (P), ground meristem (GM), and provascular tissue (PV) are conspicuous in the embryo at this stage. (d) Transverse section of an immature seed showing the radicle (young root) of the embryo enclosed by cellular endosperm. (e) A mature seed in which the embryo occupies most of the space within the seed coat. A, apical meristem of the shoot; C, cotyledons; R, radicle. Magnification (a–e) × 127.

ultimately extends into the **cotyledons**. Cotyledon primordia develop on either side of the distal end of the dome-shaped proembryo which, with continued cytokinesis, becomes expanded and in some taxa heart-shaped (Fig. 18.15b). An undifferentiated apical region between the cotyledon primordia becomes the apical meristem of the incipient shoot, and a similar region just above the suspensor differentiates as the apical meristem of the incipient root (Fig. 18.15c). As the embryo increases in size the endosperm decreases in volume, in many dicotyledons ultimately being entirely utilized by the growing embryo that fills the embryo sac (Fig. 18.15e).

Prior to seed dormancy, the embryo of dicotyledons consists of an **epicotyl**, bearing an apical meristem, and two cotyledons (rarely three or four as, for example, in *Degeneria*), the **hypocotyl**, and the **radicle**, or immature root (Fig. 18.15e). At this stage the suspensor has disintegrated. In many seeds photosynthate in the endosperm has been transferred symplastically to the cotyledons which have become much expanded and function as food storage organs (Fig. 18.15e). The early stages of embryogenesis in monocotyledons is essentially like that of dicotyledons. As development continues, however, the young embryo becomes elongate and columnar, lacking the heart-shaped stage of many dicotyledons. This columnar form is related to the presence of a single cotyledon which, with continued growth, becomes a dominant part of the embryo. Within the seed, the mature embryo may be curved or more or less straight. The embryo of members of the Gramineae (grasses) differs conspicuously from that of other monocotyledons (Fig. 18.16). The large cotyledon, called the **scutellum**, appears to be laterally attached to the axis of the embryo. In addition, the embryo consists of an **epicotyl**, consisting of the apical meristem and several leaf primordia enclosed in a sheath called the **coleoptile**, and a radicle (young root) enclosed in a sheath called the **coleorhiza**.

During development of the embryo other profound changes take place within the ovule as it develops into a seed (see Boesewinkel and Bouman, 1984; Bouman, 1984). In dicotyledons, the seed coat, or **testa**, develops from the integuments of the ovule, and at maturity is usually hard and dry. The number of integuments usually parallels that of the ovule although in some taxa the inner integument may disintegrate (as, for example, in *Cucurbita*). Thickness of the mature seed coat depends to some extent on the original thickness of the ovular integuments, but largely on developmental changes that occur as the seed matures including cell division and cell growth within the integuments. In general, cells of the integuments become more thick-walled and some differentiate into sclereids of several types. However, interspersed layers of aerenchyma and chlorenchyma also characterize the seed coats of some taxa. Typically, the seed coat is covered by a thick water-impermeable cuticle.

For more detail on the embryogeny of angiosperms, and references to the extensive literature on the subject, please see Maheshwari (1950), Bouman (1984), Romberger *et al*. (1993), and Jensen (1998) and references therein. For a recent discussion of research on the genetic control

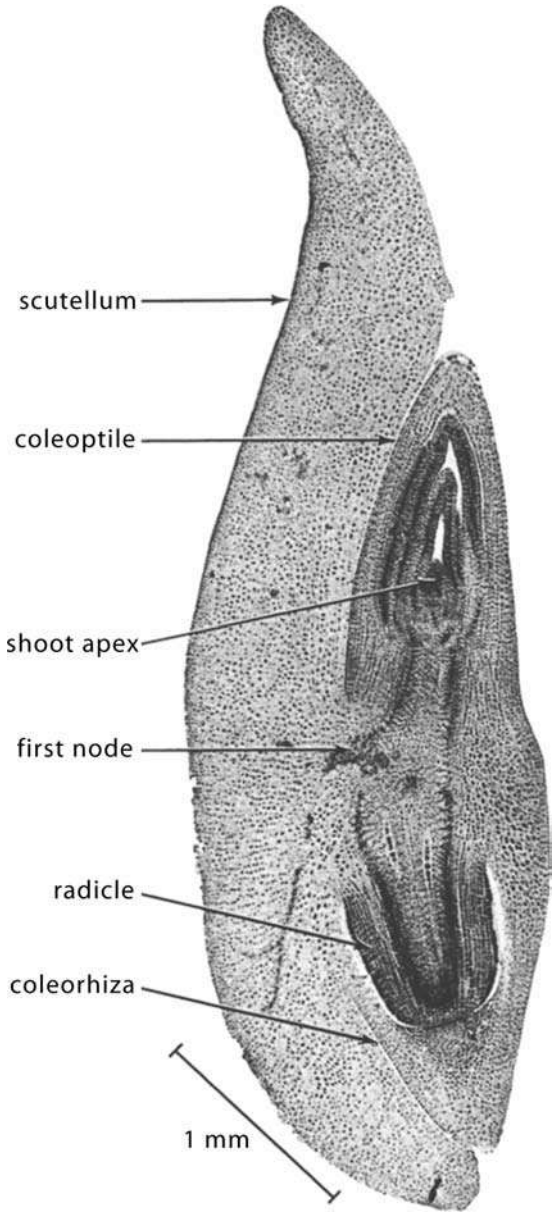

Figure 18.16 The embryo of *Zea mays*.

of fertilization see Faure and Dumas (2001) and for research on signal transduction and its role in plant reproduction, see Brownlee (1994).

Fruit development and the role of fruits in seed dispersal

Since seeds are contained in fruits, a primary means of their distribution is the distribution of the fruits. A **fruit** is a matured ovary and any attached floral parts such as the receptacle, calyx, or bracts. A **simple**

fruit is one that consists of a single carpel, or several fused carpels, without any attached floral parts. Examples are bean, tomato, and peach. Such fruits develop from **hypogynous** flowers in which the ovaries are superior. An **aggregate fruit** is one that consists of several to many separate carpels of a single flower such as strawberry or raspberry. A **multiple fruit** consists of the fused ovaries of several to many flowers such as mulberry or pineapple. If, in addition, these fruits are composed of floral parts other than the carpels they are termed **accessory fruits**. For example, an apple is a **simple accessory fruit** because it develops from an inferior ovary enclosed by the receptacle which becomes a part of the mature fruit. A strawberry is an **aggregate accessory fruit** consisting of an enlarged, fleshy receptacle in the surface of which many small ovaries are embedded. A mulberry is a **multiple accessory fruit** because, in addition to the ovaries of many flowers, it is also composed of the perianths and receptacles of these flowers.

At maturity, fruits may be fleshy or dry, and if the latter, dehiscent or indehiscent. The fruit wall, whether or not it develops from only the ovary wall or the ovary wall plus accessory parts, is termed **pericarp**. The pericarp may contain several histologically distinct layers: the outer layer, the **exocarp**, the middle layer, the **mesocarp**, and the inner layer, the **endocarp**. In fleshy fruits, all three layers, if they are distinct at any stage of development, may become fleshy, that is, composed of thin-walled parenchyma as in tomato. In this as well as in other berries, the septa between locules also become fleshy. In other taxa, the exocarp and mesocarp usually become the fleshy part of the pericarp, the endocarp maturing into a stony layer consisting entirely of sclereids as in drupes such as cherry and peach. Citrus fruits and members of the Cucurbitaceae, among many others, are characterized by an outer rind, usually consisting of the exocarp and at least part of the mesocarp. The inner fleshy tissue is usually derived from the endocarp, although mesocarp may also be involved in some taxa. In many cases, subdivisions of the pericarp are not clear. The rind, if soft as in citrus fruits, is usually composed of parenchyma and/or collenchyma and aerenchyma; if hard, as in cucurbits, of parenchyma, collenchyma, and sclerenchyma, often in layers. Vascularization of these fruits reflects that in the carpels of which the ovary is composed, although during fruit development branching of vascular bundles may occur. Prior to the completion of fruit development, the tracheary cells of the primary xylem in the vascular bundles are modified by enzymatic action, resulting in a thinning and softening of the cell walls. In the mature fruit, the vascular tissue is probably no longer functional.

Dry fruits are far more abundant than fleshy fruits. Among dehiscent dry fruits are **legumes** characteristic of members of the Leguminosae (bean family), **follicles** as in *Paeonia* (peony) and *Aquilegia* (columbine), and **capsules** as in *Papaver* (poppy) and *Koelreuteria* (golden rain tree). Legumes and follicles develop from single carpels whereas capsules usually develop from three or five carpels, but occasionally two as in the siliques of some members of the Cruciferae. When mature, the dry pericarp of these fruits consists usually of one or more outer

layers of thick-walled parenchyma cells, sometimes highly lignified, and at least one inner layer of sclerenchyma, but sclerenchyma may be absent. Dehiscence results from differential shrinkage in layers of the pericarp as the fruit becomes dry. It has been suggested that differential shrinkage, and ultimate dehiscence in some legumes is directly related to the difference in the angle of microfibrils in S2 wall layers of sclerenchyma cells in different regions of the pericarp.

Dehiscence occurs variably in different fruit types. For example, in legumes, derived from single carpels, dehiscence occurs along both sutures whereas in follicles, also derived from single carpels, dehiscence occurs along the dorsal suture only (i.e., the suture formed by fusion of carpel margins). Dehiscence in capsules varies, depending in large part on the type of placentation of the ovaries. If placentation is axile, the split may occur between the carpels along the septa (**septicidal dehiscence**) or in the outer walls of the carpels, opening the locules (**loculicidal dehiscence**). When dehiscence is septicidal the carpels usually pull away from the central column of the ovary. When placentation is parietal, dehiscence may occur between contiguous carpels, or midway between carpel margins. The capsules of some plants that produce very small seeds, such as *Papaver*, release their seeds through apical pores.

Among indehiscent dry fruits are the **achene** and **caryopsis**. The pericarp of each is fused to the seed coat, and each contains a single seed. The seed coat usually remains thin and parenchymatous and, in some taxa, essentially disintegrates prior to maturity of the fruit. Achenes are common in the Compositae and Ranunculaceae. Large, winged achenes (**samaras**) characterize *Acer*, *Fraxinus*, and *Ulmus* among others. The fruits of the Compositae as well as of *Fraxinus* and *Ulmus* are composed of two carpels, but only one seed develops. Those of the Ranunculaceae consist of a single one-seeded carpel. The caryopsis is characteristic of members of the Gramineae (grasses). Caryopses differ from achenes in that their pericarp is fused to the seed coat whereas in achenes the seed is free from the pericarp except at the site of attachment of the funiculus. The cellular composition of the pericarp of dry, indehiscent fruits is variable, but usually contains largely sclerenchyma (in achenes) and/or thick-walled, pitted parenchyma (in caryopses).

As noted above, dispersal of seeds is frequently the result of their being contained in fruits that are distributed by various means. Fleshy fruits are commonly eaten by animals, and their seeds pass unharmed through the digestive tract of the disperser. Some fruits dehisce suddenly, scattering seeds some distance from the parent plant. Others such as the achenes of composites which bear a pappus, and the winged samaras of maples, ashes, and elms, are wind-dispersed as are some very small fruits. Fruits may also be dispersed by water as, for example, the coconut.

Once released from dry, dehiscent fruits, many seeds also possess modifications such as wings, pappus-like attachments, and extensive hairs (e.g., cotton seeds) that facilitate wind dispersal. Seeds that can pass intact through the digestive system of animals are dispersed by

animal migration. Some seeds, upon being exposed to water, release a sticky substance such as mucilage. The adherence of such seeds to the coats of animals results in their distribution. The seeds of some plants, for example, the orchids, are so light and small that they are wind-dispersed. For more detail on the functional morphology of fruits, please see Weberling (1989).

Seed germination and development of the seedling

Following seed distribution and a period of dormancy, variably long in different taxa, seed germination occurs when conditions are favorable. The protective seed coat contains inhibitors that prevent germination during unfavorable conditions for seedling growth. The seed coat is also typically impermeable to water by virtue of its being covered by a thick cuticle. When the impermeability is removed by exposure to the elements, by bacterial or fungal activity, or being passed through the digestive tract of animals, water is absorbed, the inhibitors are neutralized, and oxygen enters the seed, the young sporophyte resumes its growth, and germination ensues. During germination, the young sporophyte begins a transition from dependence on its parent to existence as an independent entity.

At the beginning of the germination process the young sporophyte is composed primarily of the meristematic regions, protoderm, ground meristem, and provascular tissue, as well as apical meristems of the epicotyl and hypocotyl. If the cotyledons have become storage organs, they usually no longer contain meristematic tissues. If they remain thin and become photosynthetic upon germination, they usually maintain their meristematic potential.

During germination of dicotyledon seeds the radicle is often the first part of the young sporophyte to begin active growth. At the same time, provascular tissue begins to differentiate into functional xylem and phloem. The radicle may elongate initially by general cytokinesis and cell elongation throughout. Subsequently, in some dicotyledonous taxa characterized by **epigeous germination**, cytokinesis of great frequency in the basal region of the hypocotyl results in the development of a hook that extends upward, pulling the seed out of the soil. The epicotyl then expands, becomes free from the seed coat, and cytokinesis in the apical meristem followed by cell and tissue differentiation leads to the formation of the young shoot. As the young sporophyte continues its growth, the transitional tissue regions, ground meristem, provascular tissue, and protoderm, in both root and shoot systems differentiate, respectively, into pith (in some but not most roots), cortex, vascular tissues, and epidermis.

In many monocotyledons, whether germination is epigeous or **hypogeous** (cotyledons remaining below the soil), the young sporophyte is extracted from the seed (or fruit, in the case of grasses) by extension growth of the single cotyledon. In others, e.g., *Zea mays* and

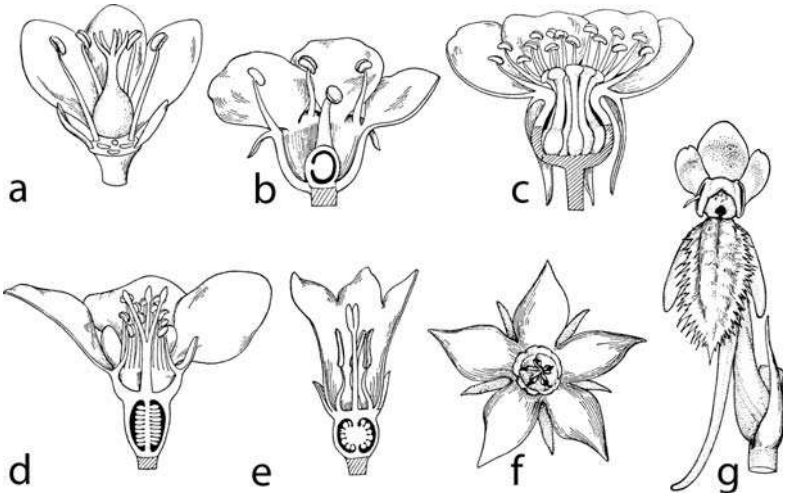

Figure 18.17 Diagrams of flowers showing diversity of form. See the text for descriptions. From Lawrence (1951). Reprinted by permission of Pearson Education, Inc., Upper Saddle River, NJ.

other members of the Gramineae, growth of the coleorhiza and coleoptile push through the enclosing pericarp followed by elongation of the hypocotyl and epicotyl which push through the enclosing sheaths. The cotyledon remains in the soil within the kernel, the radicle extends deeper within the soil, and the epicotyl extends upward above the soil.

Floral morphogenesis

Development of the flower has attracted the interest and energy of many botanists. Although flower form is highly diverse, certain morphological features are common to many taxa, for example, variation in the number of floral parts (Fig. 18.17a–c), whether the flower is **hypogynous** (Fig. 18.17a–c) or **epigynous** (Fig. 18.17d, e) (i.e., whether floral parts such as sepals and petals are attached below the ovary or upon it), whether organ "whorls" are free or fused to others (Fig. 18.17a–e), and whether flower symmetry is **radial** (Fig. 18.17f) or **zygomorphic** (i.e., bilaterally symmetrical) (Fig. 18.17g) (Tucker, 1997). Tucker notes, further, that whereas these characters may be stable in individual families there may be "intriguing divergences" such as "shifts in number of organ whorls, loss of some organs, and tendencies toward unisexuality."

Flowers are determinate structures and flowering in annuals terminates the vegetative growth of the plant. In perennials, however, new floral apices are formed repeatedly and flowering occurs throughout the life of the plant. Prior to **flower induction**, internodes of the vegetative shoot apex typically elongate, and numerous lateral buds may be initiated below the apical meristem. The floral meristem usually becomes much broader than in its vegetative state, and the rate of cell division increases. Genetic analyses have identified about 80 genes that function in multiple genetic pathways that control the transition from the vegetative to the floral state (Araki, 2001), a transition that

he describes as "the most dramatic phase change in plant development." The induction of the various floral components is initiated by one or several forms of signal transduction, factors in the external and internal environments such as photoperiod and temperature, and the production, often in the leaves, of various hormones and other chemical compounds which are transported, possibly through the phloem, to the apical meristems (see O'Neill, 1992; Lejeune *et al*., 1993; O'Neill *et al*., 1994; Bradley *et al*., 1996; Chang *et al*., 2001; Ruiz-Medrano *et al*., 2001; Hamano *et al*., 2002).

Tucker (1997) describes floral ontogeny as "a continuous succession of events, a cascade in which later events build on earlier ones." Among the many events that occur during floral morphogenesis are determination of the number, sites, and timing of initiation of floral parts of different types, the differentiation of form during which organ primordia become recognizable, increase in size and, in some taxa, fuse with adjacent primordia, and the development of specialized features often related to pollination such as nectaries, stigmatic papillae, specially shaped petals, etc. Research on the control by regulatory genes of floral patterning, the number and recognition of floral organs, and the development of these and other floral structures is destined to provide a much clearer understanding of the underlying mechanisms of floral morphogenesis (see Weigel, 1995; Frolich and Meyerowitz, 1997; Running and Hake, 2001).

The several floral parts are typically arranged in sequence beginning, at the base of the flower, with the sepals and continuing through petals, stamens, and carpels. Similarly, during ontogeny, initiation of the various floral components is typically acropetal, often with sepals appearing first, followed in sequence by petals, stamens, and carpels (Fig. 18.18a–e). However, this developmental sequence is highly variable and different sequences may characterize different species. Whereas the components of particular "whorls" may initially appear as separate entities, as they grow during development and contact those adjacent, they may fuse, as noted above, forming compound structures. In the flowers of more primitive angiosperms the floral parts commonly remain separate at maturity whereas in flowers of more evolutionarily advanced taxa the floral parts often fuse. Fusion of carpels (forming a pistil) and petals (forming a corolla) is especially common. Although fusion of plant parts has been observed for many years, the actual process whereby epidermal cells of the initially separate parts dedifferentiate following contact has only begun to be understood in the last few years. Siegel and Verbeke (1989), studying *Catharanthus roseus* (Madagascar periwinkle, often referred to by the synonym *Vinca rosea*), demonstrated that movement of unidentified "diffusible factors (morphogens)" between carpel primordia leads to a dedifferentiation of the epidermal cells and their redifferentiation into parenchyma cells in the contact zone. Although it has been widely accepted that fusion of floral parts in angiosperms occurs without transcellular cytoplasmic continuity, the presence of secondary plasmodesmata between fusing carpels has been demonstrated recently in *Vinca* (Van der Schoot *et al*.,

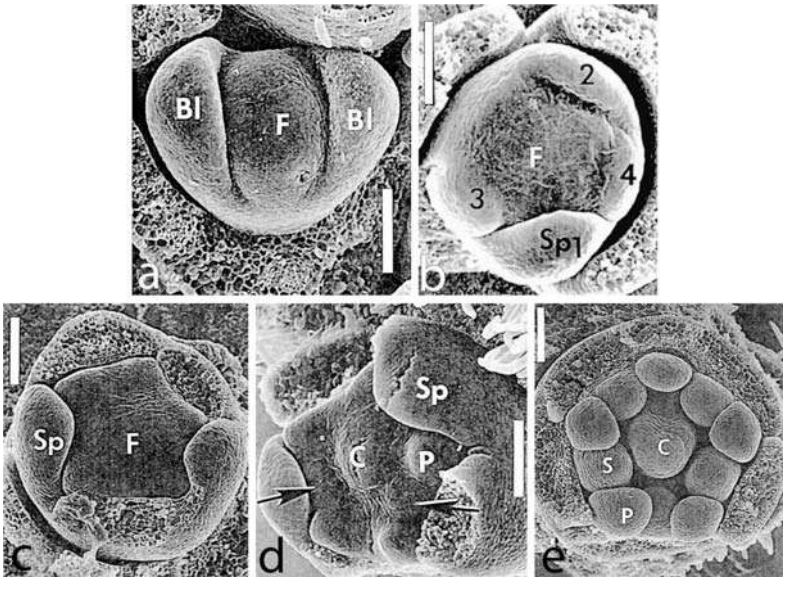

Figure 18.18 Early stages in the ontogeny of various floral organs of *Amherstia nobilis*, demonstrating the acropetal sequence of development from bracteoles to stamens. (a) A floral apex (F) with two opposite bracteole (B) primordia. (b) Bracteoles have been removed. Four of the five sepal primordia (Sp) have been initiated in a helical sequence. (c) Floral apex showing the last of the sepal primordia to be initiated. (d) The five petal primordia (P) have now appeared around the central carpel primordium (C). (e) The five petal primordia are prominent as is the carpel primordium. Stamen primordia (S) alternate with the petal primordia. Bars = 100 μm. From Tucker (1997). Used by permission of the University of Chicago Press.

1995). These workers suggested that these plasmodesmata might facilitate the transcellular movement of hormones or proteins essential for continued gynoecial development. Much is yet to be learned about the process of fusion of floral parts, the identity and specific activity of the diffusible factors mentioned above, the significance of the plasmodesmata that develop between the contiguous cells of carpel primordia during the development of the gynoecium, and whether or not what is becoming known in *Vinca* also characterizes other angiosperms.

One of the defining distinctions between gymnosperms and angiosperms is the presence of ovules on the abaxial surface of cone scales in gymnosperms (Figs 18.2, 18.3) and in enclosed carpels in angiosperms (Figs 18.6a, 18.7c, d). As has been shown by Tucker and Kantz (2001), however, young carpels containing ovules in some members of the legume family, Fabaceae, are open (Fig. 18.19) and become closed only during later stages of ontogeny. In their survey of the literature they found 44 species in 20 families with open, ovulate carpel primordia. They note that whereas open carpel primordia containing ovules are fairly uncommon in angiosperms, open carpel primordia without visible ovules have been reported in 180 taxa in 140 angiosperm

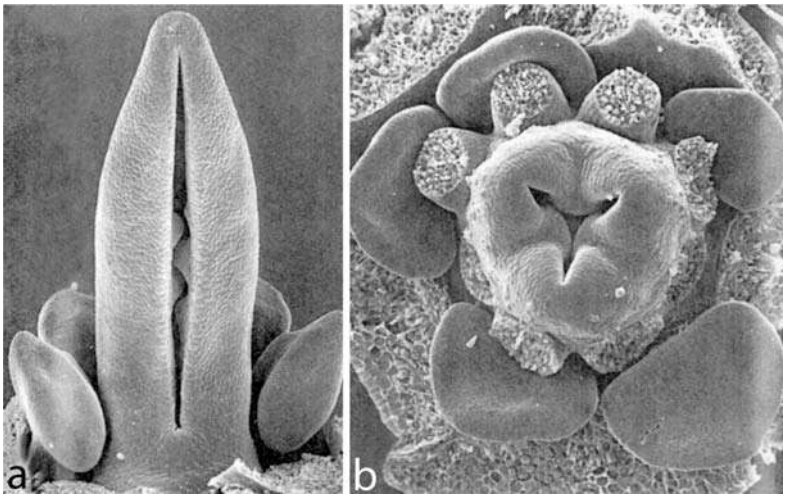

Figure 18.19 Open, ovulate carpels. (a) *Amherstia nobilis*. Outer floral parts have been removed. Magnification × 74. (b) View from above of the flower of *Koelreuteria elegans* showing a tricarpellate gynoecium before carpel closure. Sepals and stamens have been removed. Magnification × 96. From Tucker and Kantz (2001). Used by permission of the University of Chicago Press.

families. During the final stages of development and prior to maturity, carpel closure occurs in a variety of ways, including simple appression, interdigitation of epidermal cells, elimination of cuticles and fusion of the contacting cells, and cell divisions and reorientation of cells in the appressed tissues (Tucker and Kantz, 2001). Recently Endress and Igersheim (2000) have reported that, in most very primitive angiosperms (e.g., Amborellaceae, Cabombaceae, Nymphaeaceae, Trimeniaceae, Illiciaceae, Schisandraceae, and Chloranthaceae), carpel closure is accomplished "from the outside by secretion." Apparently, secretory cells or canals in the tissue on either side of the gap between carpel margins secrete a substance that fills the gap, thus closing the carpel.

Much of the material presented heretofore in this chapter is widely accepted, common knowledge among botanists. During the past decade, however, with the application of techniques of cellular and molecular biology, several important and exciting areas of research have produced information that is expanding our understanding of reproductive biology in plants. Among these areas are pollen–pistil interactions, including pollen adhesion, hydration and pollen tube growth, self-incompatibility, and the role of the cytoskeleton in various aspects of reproduction and embryogeny. We shall consider each of these in some detail.

Pollen–pistil interactions

The nature of the **stigmatic surface**, whether smooth or papillate, wet or dry, is important in the process of pollination (Figs 18.14a, 18.20a, b). A **wet stigmatic surface** is covered by exudates, secreted granulocrinously (i.e., by fusion of Golgi and/or ER vesicles with the plasma membrane of stigmatic cells; see Weber, 1994). In families such as the Solanaceae and Leguminosae, a wet surface facilitates the adhesion of pollen grains, and is known to be receptive to pollen in many species

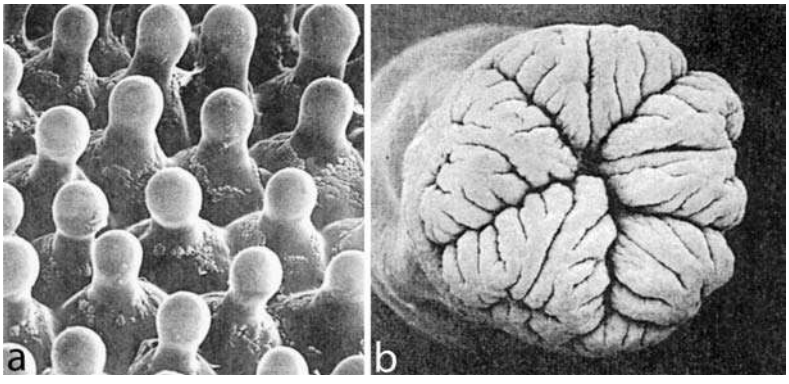

Figure 18.20 (a) Papillate epidermal cells of the stigma of *Primula* sp. (primrose). The epidermis is a glandular tissue that secretes a sugar-containing fluid that facilitates the adhesion of pollen grains to the stigma. It may also play a role in pollen hydration and germination. Magnification × 500. (b) The stigma of *Rhododendron intranervatum*, composed of five major lobes separated by grooves through which pollen tubes enter the stylar canal. Magnification × 20. (a) From Troughton and Donaldson (1972). Used by permission of the New Zealand Ministry of Research, Science and Technology. (b) From Palser *et al.* (1992). Used by permission of the National Research Council of Canada.

(Wheeler *et al.*, 2001). In families such as the Gramineae and Brassicaceae, however, characterized by **dry stigmatic surfaces**, adhesion of pollen is controlled by an interaction between the pollen coat and the stigmatic surface (Heslop-Harrison, 1979; Elleman and Dickinson, 1990, 1996; Elleman *et al.*, 1992; Wheeler *et al.*, 2001).

At the time of contact with a stigmatic surface, most pollen is highly dehydrated and must become hydrated in order to germinate. The exudate on the surface of wet stigmas facilitates pollen hydration as well as adhesion and germination (Figs 18.14b, 18.21a). On dry stigmas such as those of *Brassica oleracea*, Elleman and Dickinson (1990, 1996) have demonstrated that the coat of a pollen grain on a receptive stigma interacts with the subtending stigmatic surface cells eliciting an expansion of their outer wall layers and a "loosening of the wall matrix." Associated with these modifications of wall structure is uptake of water, a granulocrinous secretion (Elleman and Dickinson, 1990, 1996), and the extension of the pollen coat to form an adhesive "foot." Several proteins have been implicated in the adhesion of pollen grains in *Brassica* (e.g., Stephenson *et al.*, 1997). The presence of long-chain lipids (see Wheeler *et al.*, 2001) as well as proteins such as aquaporin (Ikeda *et al.*, 1997) in the stigmatic exudate play significant roles in regulating hydration. Proteins such as aquaporin are thought to form molecular "channels" in the plasma membrane, thus facilitating the transport of water from cells of the stigma onto the stigmatic surface and hydrating the pollen grains, or in self-incompatible taxa, transporting water away from the stigmatic surface, thus preventing hydration and germination of pollen (for more detail, see Ikeda *et al.*, 1997; Wheeler *et al.*, 2001). In contrast to that of many other families, grass pollen is transmitted

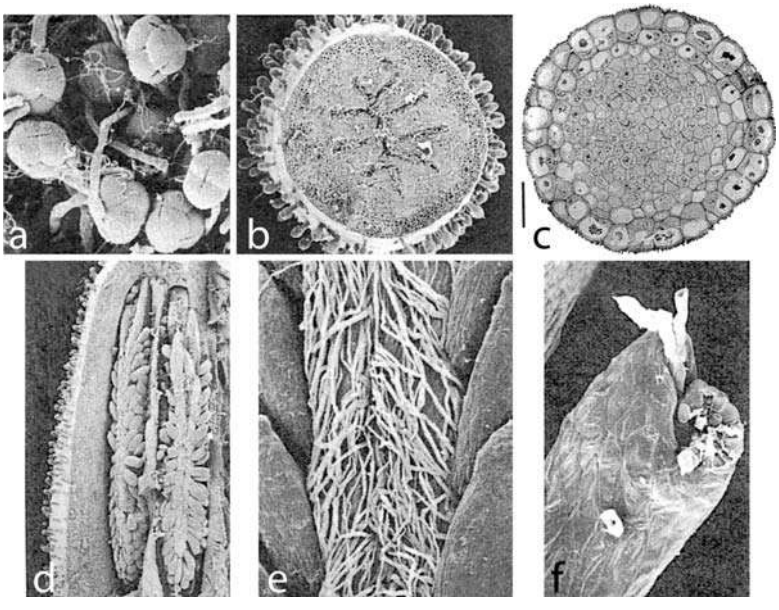

Figure 18.21 (a) Germinated pollen tetrads of *Rhododendron fortunei* on the stigmatic surface. Magnification × 158. (b) A transverse section of the style of *R. fortunei*, showing the multi-armed stylar canal containing pollen tubes. Magnification × 18. (c) A transverse section of the style of *Smyrnium perfoliatum* (Apicaceae) containing a solid core of transmitting tissue. Bar = 20 μm. (d) Two locules of an ovary of *R. fortunei* showing ovules attached to placentae. Numerous pollen tubes are visible on the placental surfaces. Magnification × 8. (e) Enlargement showing pollen tubes on the placental surface of *R. fortunei*. Magnification × 83. (f) Ovule of *R. intranervatum*. Two pollen tubes have entered the ovule through the micropylar end. Magnification × 464. (a, b, d–f) From Palser *et al.* (1992). Used by permission of the National Research Council of Canada. (c) From Weber (1994). Used by permission of the University of Chicago Press.

to the stigmatic surfaces in a hydrated condition, and can germinate and penetrate the stigma within less than 1 minute (J. Heslop-Harrison, 1979, 1987; Y. Heslop-Harrison, 2000). For more detail on pollen–pistil interactions and other interesting examples see Endress (1994).

Styles are characterized either by a hollow **stylar canal** (Fig. 18.21b) filled with exudate, composed of various combinations of polysaccharides, lipids, phenolics, pectins, and proteins, or a **central core** of specialized **transmitting tissue** (Fig. 18.21c). In the latter case, the transmitting tissue contains longitudinal, intercellular channels filled with secretions (Weber, 1994). In both types of styles, pollen tubes grow through the secretions toward the ovule. Upon germination the pollen tube penetrates the cuticle, grows through the stigma and into the stylar canal or transmitting tissue (Figs 18.14b, 18.21a, 18.22a, b). Some workers (e.g., Lush *et al.*, 1998, 2000; Wolters-Arts *et al.*, 1998) believe that the presence of triglycerides in the stigmatic exudate establishes a gradient of water that functions as a guidance cue for the growing pollen tube. Wang *et al.* (1993) and Cheung (1995) have proposed

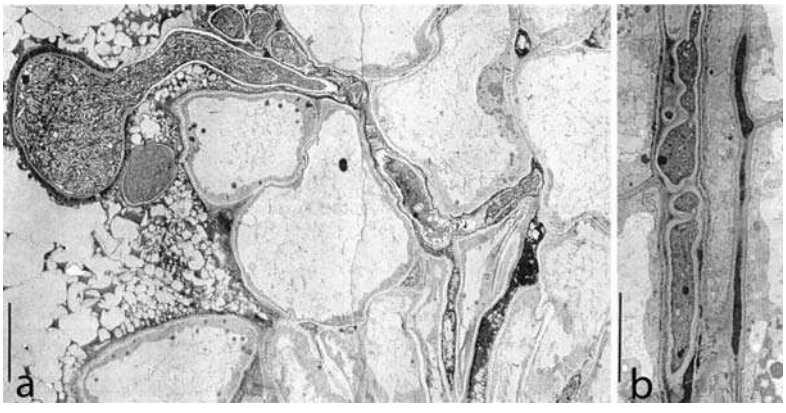

Figure 18.22 (a) A pollen tube penetrating the stylar transmitting tissue of *Smyrnium perfoliatum*. Bar = 10 μm. (b) Pollen tube in an exudate-filled intercellular canal of the stylar transmitting tissue. Bar = 5 μm. (a, b) From Weber (1994). Used by permission of the University of Chicago Press. © 1994 The University of Chicago. All rights reserved.

that proteins in the intercellular secretion in the transmitting tissue of solid styles provide directional cues. There is also evidence that, in some species, the embryo sac (female gametophyte) secretes substances that attract the pollen tube to the ovules (Ray *et al*., 1997; Hererro, 2000). In contrast to these proposals, Heslop-Harrison and Reger (1988) suggested that the direction of pollen tube growth resulted simply from the presence of longitudinal, intercellular channels between cells of the transmitting tissue; in other words, that the control of direction of pollen tube growth is physical, related directly to the structure of the tissue in the style. It seems that control of the direction of pollen tube growth is either multifaceted, or that it varies in different taxonomic groups. Further research will, no doubt, lead to clarification. Many pollen tubes may enter the locules of the carpels (Fig. 18.21d, e), and one or more will enter an ovule through the micropyle (Fig. 18.21f).

Self-incompatibility

Two types of pollen incompatibility have evolved in angiosperms. Pollen from a different species may be rejected because it is too dissimilar to that of the recipient species whereas pollen from the same plant or from the same species may be rejected because it is genetically too similar to that of the recipient, a mechanism referred to as **self-incompatibility**. This rejection by some plants of their own pollen was noticed by Darwin (1877) and described by him "as one of the most surprising facts I have ever observed." Self-incompatibility which forces cross-pollination and fertilization is important because it results in the maintenance of a high degree of heterozygosity in a species, and prevents the deleterious effect on progeny that often results from selfing. On the other hand, some taxa are regularly self-pollinating and self-fertilizing (see Lloyd and Schoen (1992) for a general discussion and more detail).

Between 30% and 50% of angiosperm species are self-incompatible (Wheeler *et al*., 2001). Rejection of pollen may occur at any of several stages in the reproductive process including hydration, germination, during growth of the pollen tube through the style, in the ovule, or

even post-fertilization in some species (Wheeler *et al*., 2001). Genetic studies during the 1980s and 1990s demonstrated that the incompatibility response in the Brassicaceae, Solanaceae, Papaveraceae, Rosaceae, and Scrophulariaceae is controlled by a single, multigene locus (see de Nettancourt, 2001; Dixit and Nasrallah, 2001) but in some other taxa, for example the Poaceae, by more than one "recognition locus" (Dixit and Nasrallah, 2001). When this so-called S (self-incompatibility) locus occurs in both pollen and pistil, the incompatibility response is initiated, preventing self-fertilization, often by inhibition of pollen germination or pollen tube growth. In members of the Solanaceae, the degradation of rRNA by cytotoxic proteins restricts the growth of the pollen tube through the style (Wheeler *et al*., 2001). In *Brassica* which has a dry stigma, it has been shown that self-incompatibility of pollen is related to the regulation of the transfer of water from the stigma to the pollen grains. These brief summaries of several of the self-incompatibility mechanisms in flowering plants are taken largely from Wheeler *et al*. (2001) and Dixit and Nasrallah (2001). The interested student should consult these references as well as Linskens (1988), Stephenson *et al*. (1997), and de Nettancourt (2001) for more detailed discussions of the genetic control of self-incompatibility and other aspects of pollen/pistil interactions as well as for comprehensive bibliographies.

Role of the cytoskeleton in pollen tube growth

Growth of the pollen tube through the stigma and style is one of the most dramatic examples of cell growth in the plant kingdom. In *Zea mays* (corn or maize) a pollen tube can extend through a 50 cm length of style in 24–36 hours at rates of about 0.5–0.7 cm per hour (Barnabas and Fridvalszky, 1984). It is not surprising, therefore, that the mechanism of pollen tube growth has long fascinated plant anatomists and other plant scientists.

Pollen tube growth which occurs only at the tip, is facilitated by, indeed is dependent on, the cytoskeleton (Mascarenhas, 1993; Taylor and Hepler, 1997; Geitmann *et al*., 2000; Vidali *et al*., 2001; Cai and Cresti, 2008; Cheung *et al*., 2008; Poulter *et al*., 2008). The sub-apical and more basal regions of the growing pollen tube contain endoplasmic reticulum and organelles such as mitochondria and Golgi bodies. In the sub-apical regions organelles move along the pollen tube flanks toward the tip of the tube, and just below the growing tip return toward the more basal regions through the center of the tube in the process known as cytoplasmic streaming. Some Golgi secretory vesicles follow a similar path (Bove *et al*., 2008) but many accumulate in the tip, whereas others return to the sub-apical and basal regions where they are incorporated into the membrane systems of the pollen tube (Cai and Cresti, 2008).

Actin microfilaments play a crucial role in pollen tube growth. Although microtubules are associated with the microfilaments, their

function is not yet clearly understood. Organelles as well as Golgi vesicles move along actin microfilaments through the mediation of myosin transport motors. In addition to the transport of Golgi vesicles to the growing tip of the pollen tube, growth is also dependent on the continual polymerization of new actin microfilaments by which their presence is maintained close to the tip, thus assuring a constant supply in the region of tip growth (Vidali and Hepler, 2001). It is also now well established that variations in the concentration of Ca^{2+} and H^{+} ions in the growing pollen tube tip influence the function of vesicle transport as well as other aspects of the growth process (Cheung and Wu, 2007).

Whereas movement along actin microfilaments seems to be the primary means of vesicle transport, some evidence suggests that vesicles and organelles can also move along microtubules (Wei *et al*., 2005; Cai and Cresti, 2008). Actin microfilaments occur in both central and peripheral regions of the pollen tubes. Microtubules, in contrast, have been observed primarily in the peripheral (commonly referred to as "cortical") region where they occur as single tubules or as bundles. In the peripheral region, single microtubules and microfilaments have been observed frequently oriented in parallel, and are possibly physically connected (Lancelle *et al*., 1987; Pierson and Cresti, 1992). Although the significance of their close association is not clear, it has been suggested that the microtubules might provide a rigid support for the system of actin microfilaments (Pierson and Cresti, 1992).

Just below the pollen tube tip, which contains solely secretory vesicles, there is a peripheral ring of short actin microfilaments called the **actin fringe** (Lovy-Wheeler *et al*., 2005). Whereas the accumulation of Golgi vesicles in the pollen tube tip probably results from trafficking along longitudinal actin microfilaments (Cardenas *et al*., 2008), it has been hypothesized that the ultimate movement of secretory vesicles to the plasma membrane, and determination of the sites of **exocytosis** (fusion of vesicles to the plasma membrane, and expulsion of cellulose synthase complexes and compounds required for cell wall synthesis), is controlled by microfilaments of the fringe (see Cai and Cresti, 2008). They have suggested also, however, that the vesicles might traffic through the fringe directly to the sites of exocytosis. As turgor pressure results in the extension of the thin-walled distal region of the pollen tube, Golgi vesicles fuse with the plasma membrane, providing not only compounds required for wall synthesis, but also new membrane that will be incorporated into the expanding plasma membrane of the growing pollen tube tip.

Research on pollen tube growth is an active area of interest because the molecular mechanisms which control pollen tube expansion are applicable to plant cell growth in general. This summary of some recent research and, often, hypothetical conclusions regarding the role of the cytoskeleton in pollen tube growth hardly scratches the surface of this important area. For an excellent, detailed, and analytical review of research in this area during the past 20 years, please see Cai and Cresti (2008).

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Glossary

This glossary is based on that of Esau, K. (1977) *Anatomy of Seed Plants*, 2nd edn. Some terms have been added, some deleted, and the definitions of some have been modified to reflect recent research and/or the usage in this book. Used by permission of John Wiley and Sons, New York.

abaxial Directed away from the axis. Opposite of *adaxial*.

abscission The shedding of leaves, flowers, fruit, or other plant parts, usually after formation of an *abscission zone*.

abscission layer In abscission zone, layer of cells the disjunction or breakdown of which causes the shedding of a plant part. Other term: *separation layer*.

abscission zone Zone at base of leaf, flower, fruit, or other plant part that contains an *abscission* (or *separation) layer* and a *protective layer*, both involved in the abscission of the plant part.

accessory bud A bud located above or on either side of the main *axillary bud*.

accessory cell See *subsidiary cell*.

accessory parts in fruit Parts not derived from the ovary but associated with it in fruit.

accessory transfusion tissue *Transfusion tissue* located within the mesophyll rather than associated with vascular bundle. In leaves of certain gymnosperms.

acicular crystal Needle-shaped crystal.

acropetal development (or differentiation) Produced or becoming differentiated in a succession toward the apex of an organ. The opposite of *basipetal development* but means the same as *basifugal development*.

actin filament See *microfilament*.

actin fringe A peripheral ring of short, actin microfilaments just below the growing pollen tube tip, thought to control the movement of Golgi vesicles to sites of exocytosis.

actinomorphic Having a flower that can be divided in two equal parts in more than one longitudinal plane, i.e., a radially symmetrical or *regular flower*. Opposite of *zygomorphic*.

actinostele *Protostele* with star-shaped outline in transverse section.

adaxial Directed toward the axis. Opposite of *abaxial*.

adaxial meristem Meristematic tissue on the adaxial side of a young leaf that contributes to the increase in thickness of the petiole and midrib.

adenosine triphosphate The major source of usable chemical energy in metabolism; commonly abbreviated as ATP.

adnation In a flower, union of members of different whorls, as stamens and petals.

adventitious Of structures, arising not at their usual sites, e.g., roots originating on stems or leaves instead of on other roots, or buds developing on leaves or roots instead of in leaf axils on shoots.

aerenchyma Parenchyma tissue containing particularly large intercellular spaces of *schizogenous*, *lysigenous*, or *rhexigenous* origin.

aggregate fruit A fruit developing from a single *gynoecium* (single flower) composed of separate carpels, as the strawberry or raspberry fruits.

aggregate ray In secondary vascular tissues, a group of small rays arranged so as to appear to be one large ray.

albedo White tissue of the rind in citrus fruit.

albuminous cells In gymnosperm phloem, certain ray and phloem–parenchyma cells spatially and functionally associated with the sieve elements, thus resembling the companion cells of angiosperms but usually not originating from the same precursory cells as the sieve elements. Also called *Strasburger cells*.

albuminous seed A seed that contains endosperm in mature state.

aleurone grains Granules of protein present in seeds, usually restricted to the outermost layer, the *aleurone layer* of the endosperm. (*Protein bodies* is the preferred term for aleurone grains.)

aleurone layer Outermost layer of endosperm in cereals and many other taxa which contains protein bodies and enzymes concerned with endosperm digestion.

aliform paratracheal parenchyma In secondary xylem, vasicentric groups of axial parenchyma cells having tangential wing-like extensions as seen in transverse sections. See also *paratracheal parenchyma* and *vasicentric paratracheal parenchyma*.

alternation of generations A reproductive cycle in which the haploid ($1n$) phase, the gametophyte, produces gametes which fuse to form a zygote (diploid; $2n$) which develops into a sporophyte. Meiosis in the sporophyte results in the production of haploid spores which germinate, forming new gametophytes.

alternate pitting In tracheary elements, pits in diagonal rows.

amoeboid tapetum In anther locules, tapetum assuming amoeboid form when it disintegrates during pollen wall development.

amphicribral vascular bundle Concentric vascular bundle in which the phloem surrounds the xylem.

amphiphloic siphonostele A stele in which the vascular system appears as a tube and has phloem both external and internal to the xylem.

amphivasal vascular bundle Concentric vascular bundle in which the xylem surrounds the phloem.

amyloplast A colorless *plastid* (*leucoplast*) that forms starch grains.

analogous Having the same function as, but a different phylogenetic origin from, another entity.

anastomosis Type of structure in which cells or strands of cells are interconnected with one another as, for example, the veins in a leaf.

anatomy The study of structure.

androecium Collective term for the stamens in a flower of an angiosperm; part of the flower in which male gametogenesis is initiated or also carried to completion.

angiosperm A member of a group of plants the seed (or seeds) of which are borne within a matured ovary (fruit).

angstrom A unit of length equal to one-tenth of a millimicrometer (mμ), or one-tenth of a nanometer (nm). Symbol A or Å.

angular collenchyma A form of collenchyma in which the primary wall thickening is most prominent in the angles where several cells are joined.

anisocytic stoma A stomatal complex in which three subsidiary cells, one distinctly smaller than the other two, surround the stoma.

anisotropic Having different properties along different axes; optical anisotropy causes polarization and double refraction of light.

annual ring In secondary xylem, growth ring formed during one season. The term is deprecated because more than one growth ring may be formed during a single year.

annular cell wall thickening In tracheary elements of the xylem, secondary wall deposited in the form of rings.

anomalous secondary growth A term of convenience referring to types of secondary growth that differ from the more familiar ones.

anomocytic stoma A stoma without subsidiary cells.

anther The pollen-bearing part of the stamen.

anthesis The time of full expansion of the flower, from development of a receptive stigma to fertilization.

anthocyanin A water-soluble blue, purple, or red flavonoid pigment occurring in the cell sap.

anticlinal Having the orientation of the cell wall or plane of cell division perpendicular to the nearest surface. Opposite of *periclinal*.

antipodals Three or more cells located at the chalazal end of the mature embryo sac in angiosperms.

aperture in pollen grain A depressed region in the wall in which thick intine is covered by thin exine; the pollen tube emerges through the aperture.

apex (pl. apices) Tip, topmost part, pointed end of anything. In shoot or root the tip containing the apical meristem.

apical cell The single cell that occupies the distal position in the shoot or root apex of many pteridophytes (and is usually interpreted as the initial cell from which other cells and tissues are derived).

apical meristem A group of meristematic cells at the apex of the root or shoot which by cell division produce the precursors of the primary tissues of the root and shoot; may be *vegetative*, initiating vegetative tissues and organs, or *reproductive*, initiating reproductive tissues and organs.

apocarpy Condition in the flower characterized by lack of union of carpels (free carpels).

apomixis Vegetative reproduction without meiosis or fusion of gametes.

apoplast The interconnected system of plant cell walls. Compare with *symplast*.

apoplastic loading The direct transfer of photosynthate into sieve tube members from the apoplast (cell walls) of surrounding parenchyma cells or companion cells.

apotracheal parenchyma In secondary xylem, axial parenchyma typically lacking contact with vessel members. Includes *boundary* (or *terminal*), *banded*, and *diffuse* apotracheal parenchyma.

apposition Growth of the cell wall by successive depositions of wall material, layer upon layer. Opposite of *intussusception*.

areole A small area of mesophyll in a leaf delimited by intersecting veins.

aril A fleshy outgrowth enveloping the seed and usually arising at the base of the ovule.

articulated laticifer A system of uniseriate cells produced by the apical meristem, with common walls intact or partly or entirely removed and containing latex; anastomosing or non-anastomosing.

aspirated pit In gymnosperm wood, bordered pit in which the pit membrane is laterally displaced with the torus covering the aperture.

astrosclereid A branched sclereid.
atactostele A stele in which the vascular bundles appear, in transverse section, to be scattered within the ground tissue.
ATP See *adenosine triphosphate*.
auxin A plant hormone that controls many aspects of development.
auxin efflux transporter A protein that facilitates the transfer of auxin from one cell to another.
axial parenchyma Parenchyma cells in the axial system of secondary vascular tissues, as contrasted with ray parenchyma cells in the radial system.
axial system All vascular cells derived from the fusiform cambial initials and oriented with their longest dimension parallel to the main axis of the stem or root.
axial tracheid Tracheid in the axial system of secondary xylem, as contrasted with ray tracheid.
axil The upper angle between a stem and a twig or a leaf.
axillary bud Bud in the axil of a leaf.
axillary meristem Meristem located in the axil of a leaf and giving rise to an axillary bud.

banded apotracheal parenchyma In secondary xylem, axial parenchyma in concentric bands as seen in transverse section, typically lacking contact with vessel members. See also *apotracheal parenchyma*.
bark A non-technical term applied collectively to all tissues outside the vascular cambium or the xylem; in older trees it may be divided into dead outer bark and living inner bark which consists of secondary phloem. See also *rhytidome*.
bars of Sanio See *crassulae*.
basifugal development See *acropetal development*.
basipetal development Produced or becoming differentiated in a succession toward the base of an organ. The opposite of *acropetal* and *basifugal development*.
bast fiber Originally phloem fiber; now any extraxylary fiber.
bicollateral vascular bundle A vascular bundle with primary phloem along the inner and outer surfaces of the primary xylem.
bifacial leaf A leaf with palisade parenchyma on one side of the blade and spongy parenchyma on the other. A *dorsiventral leaf*. Conceived ontogenetically, a leaf that develops continuously from the original leaf primordium apex and includes tissues from both adaxial and abaxial sides of the primordium. Compare with *unifacial* leaf.
bilateral symmetry Of a flower, having two corresponding or complementary sides and which, thus, can be divided by a single longitudinal plane through the floral axis into two halves that are mirror images of one another. Contrasted with *radial symmetry*.
biseriate ray A vascular ray two cells wide.
blind pit A pit without a complementary pit in an adjacent wall.
bordered pit A pit in which the secondary wall arches over the pit membrane except in the region of the *pit aperture*.
bordered pit-pair Two bordered pits opposite each other in adjacent cell walls.
boundary apotracheal parenchyma In secondary xylem, axial parenchyma cells occurring either singly or in a layer at the end or the beginning of a season's growth. Also called *terminal apotracheal parenchyma*.

brachysclereid A short, roughly isodiametric sclereid, resembling a parenchyma cell in shape. Also called a *stone cell*.

branch gap In the nodal region of a non-seed plant stem, a region of parenchyma in the primary vascular cylinder through which branch traces extend toward a lateral branch. It may be confluent with a subtending *leaf gap*.

branch traces Vascular bundles connecting the primary vascular system of the branch and that of the main stem.

bulliform cell An enlarged epidermal cell present with other similar cells in longitudinal rows in leaves of grasses; thought to function in the rolling and unrolling of leaves.

bundle cap Sclerenchyma or collenchyma appearing in transverse section like a cap on the outer surface of a vascular bundle.

bundle sheath Layer or layers of cells enclosing a vascular bundle in a leaf; may consist of parenchyma or sclerenchyma.

bundle sheath extension A plate of tissue extending from a bundle sheath to the epidermis in a leaf. May be present on one or on both sides of the bundle and may consist of parenchyma or sclerenchyma.

callose A polysaccharide, β-1,3-glucan, yielding glucose on hydrolysis. Common wall constituent in the sieve areas of sieve elements; also develops rapidly in reaction to injury in sieve elements and parenchyma cells.

callus A tissue composed of large thin-walled cells developing as a result of injury, as in wound-healing or grafting, and in tissue culture.

calyptrogen In the root apex, meristem giving rise to the root cap.

calyx The sepals collectively, which with the corolla comprise the perianth.

cambial initials Cells in the *vascular cambium* or *phellogen* which through periclinal divisions contribute cells toward the inside or toward the outside of the axis; in the vascular cambium classified as either *fusiform initials* (source of axial cells of secondary phloem or secondary xylem) and *ray initials* (source of ray cells).

cambium A meristem with products of periclinal divisions commonly contributed in two directions and arranged in radial files. The term is preferably applied only to the two lateral meristems, the *vascular cambium* and the *cork cambium*, or *phellogen*.

carpel Leaf-like organ in angiosperms enclosing one or more ovules; a constituent of the *gynoecium*, the female part of the flower.

carrier proteins Proteins that facilitate the movement into and out of cells across the plasma membrane.

caruncle A fleshy protuberance near the hilum of a seed.

Casparian band (Casparian strip in older literature) A band-like wall formation within primary walls that contains suberin and lignin; typical of endodermal and exodermal cells in roots in which it occurs in the radial and transverse walls.

cataphylls Leaves inserted at low levels of the plant or shoot, as bud scales, rhizome scales, and others. Contrasted with *hypsophylls*.

cauline Belonging to the stem or arising from it.

caulis Stem.

cell A structural and physiological unit of a living organism. The plant cell consists of protoplast and cell wall; in non-living state, of cell wall only.

cell plate A partition appearing at telophase between the two nuclei formed during mitosis (and some meioses) and indicating the early stage of the

division of a cell (*cytokinesis*) by means of a new cell wall; is formed in the *phragmoplast*.

cell wall A more or less rigid membrane enclosing the protoplast of a cell and, in higher plants, composed of cellulose and other organic and inorganic substances.

cellulose A polysaccharide, β-1,4-glucan, the main component of cell walls in most plants; consists of long chain-like molecules, the basic units of which are anhydrous glucose residues of the formula $C_6H_{10}O_5$.

cellulose synthase An enzyme that is required for the synthesis of cellulose.

cellulose synthase complex A cluster of cellulose synthase proteins. See *rosette*.

central cylinder A term of convenience applied to the vascular tissues and associated ground tissue in the stem and root. Refers to the same part of the stem and root that is designated as *stele*.

central mother cells Large vacuolated cells in the subsurface position in the apical meristem of the shoot in gymnosperms.

centric mesophyll A modification of isobilateral mesophyll in which the adaxial and abaxial palisade layers form a continuous layer; found in narrow or cylindrical leaves.

centrifugal development Produced or developing successively farther away from the center.

centripetal development Produced or developing successively closer to the center.

chalaza Region in the ovule where the integuments and the nucellus merge with the *funiculus*.

chimera A plant consisting of a combination of tissues of different genetic composition. In a periclinal chimera, cells of different composition are arranged in periclinal layers.

chlorenchyma Parenchyma tissue containing chloroplasts; leaf mesophyll and other green parenchyma.

chlorophyll The green pigment of plant cells required for photosynthesis.

chloroplast A chlorophyll-containing *plastid* with thylakoids organized into grana, and embedded in a stroma.

chromoplast A *plastid* containing pigments other than chlorophyll, usually yellow and orange carotenoid pigments.

cicatrice The scar left by a wound or by the separation of one plant part from another (as a leaf from a stem) and characterized by substances protecting the exposed surface.

circular bordered pit A circular pit with an overarching border; usually forms a pit-pair with a pit in a contiguous cell wall.

cisterna (pl. **cisternae**) A flattened, sac-like membranous compartment as in endoplasmic reticulum, a Golgi body, or a thylakoid.

cladophyll A branch resembling a foliage leaf.

closed venation Leaf venation characterized by anastomosing veins.

closing layer One of the compact layers of cells formed in alternation with the loose filling tissue (*complementary cells*) in a lenticel.

coenocyte A multinucleate organism or a multinucleate component of an organism; sometimes applied to multinucleate cells in seed plants.

cohesion In a flower, union of members of the same whorl, as sepals with sepals and petals with petals.

coleoptile The sheath enclosing the *epicotyl* of the grass embryo; sometimes interpreted as the first leaf of the epicotyl.

coleorhiza The sheath enclosing the *radicle* of the grass embryo.
collateral vascular bundle A bundle with phloem on only one side of the xylem, usually the abaxial side.
collenchyma A living, supporting tissue composed of generally elongate cells with unevenly thickened non-lignified primary walls. Common in the peripheral regions of stems and leaves.
colleter A multicellular appendage or a multicellular trichome producing a sticky secretion. Found on buds of many woody species.
columella The central part of a root cap in which the cells are arranged in longitudinal files.
commissural vascular bundle A small bundle interconnecting larger parallel bundles as in leaves of grasses.
companion cell A parenchyma cell in the phloem of an angiosperm associated with a sieve tube member and originating jointly with the latter from the same mother cell; some have the structure of a *transfer cell*.
compitum A region in the style of a syncarpous gynoecium where stylar canals are joined into one cavity.
complementary cells Cells of the loose tissue formed by the lenticel phellogen toward the outside; may or may not be suberized.
complementary tissue Loose tissue between closing layers in a lenticel. See *filling tissue*.
complete flower A flower having all types of floral parts: sepals, petals, stamens, and carpels, or tepals, stamens, and carpels.
compound laticifer Term sometimes applied to articulated laticifer.
compound middle lamella A collective term applied to two primary walls and the middle lamella; usually used when the true middle lamella is not distinguishable from the primary walls.
compound sieve plate A sieve plate composed of several sieve areas.
compression wood The reaction wood in conifers which is formed on the lower sides of branches and leaning or crooked stems and characterized by dense structure, strong lignification, and certain other features. See also *reaction wood* and *tension wood*.
concentric vascular bundle A vascular bundle with either the phloem surrounding the xylem (*amphicribral*) or the xylem surrounding the phloem (*amphivasal*).
conducting tissue See *vascular tissue*.
confluent paratracheal parenchyma In secondary xylem, coalesced aliform groups of axial parenchyma cells forming irregular tangential or diagonal bands, as seen in transverse section. See also *paratracheal parenchyma* and *aliform paratracheal parenchyma*.
conjunctive tissue Secondary parenchyma tissue interspersed with vascular tissue where the latter does not form a solid cylinder, as in monocotyledons and in dicotyledons with anomalous secondary growth.
connate Condition in which parts of the same whorl in a flower are united, as petals united into a corolla tube. See also *cohesion*.
connective The tissue between the two lobes of an anther.
contact cell An axial parenchyma or a ray cell physically as well as physiologically associated with a tracheary element. Analogous to a companion cell in the phloem. Also a cell next to a stoma.
contractile root A root that undergoes contraction at some time during its development and thereby effects a change in position of the shoot with regard to the ground level.

convergent evolution The independent evolution of similar structures in species that are unrelated or very distantly related; frequently characteristic of organisms living in similar environments.
coordinated growth Growth of cells in a manner that involves no separation of walls, as opposed to *intrusive growth*; also called *symplastic growth*.
copal A resinous substance that exudes from various tropical trees and hardens in air into roundish or irregular pieces. May be colorless, yellow, red, or brown.
cork See *phellem*.
cork cambium See *phellogen*.
cork cell A phellem cell derived from the phellogen, non-living at maturity, and having suberized walls; protective in function because the walls are highly impervious to water.
corolla A collective term for the petals of a flower.
corolla tube The tube-like part of a corolla resulting from congenital or ontogenetic union of petals.
corpus The core in an apical meristem covered by the *tunica*.
cortex The primary ground tissue region between the vascular system and the epidermis in stem and root. The term is also used with reference to the peripheral region of a cell protoplast.
cotyledon The leaf or leaves of an embryo within a seed.
crassulae (sing. **crassula**) Thickenings of intercellular material and primary wall along the upper and lower margins of a bordered pit-pair in the tracheids of gymnosperms; also called *bars of Sanio*.
cristae (sing. **crista**) Crest-like infoldings of the inner membrane in a mitochondrion.
cross-field A term of convenience for the rectangle formed by the walls of a ray cell against an axial tracheid, as seen in radial section of the secondary xylem of conifers.
crystalloid A protein crystal that is less angular than a mineral crystal and swells in water.
cuticle A layer consisting of cutin and waxes located on the outer walls of epidermal cells.
cutin A complex fatty substance that impregnates cell walls in some plant tissues including the epidermis and which comprises a layer called the cuticle on the outer surface of cell walls.
cutinization The process of impregnation with cutin.
cyclosis The streaming of cytoplasm in a cell.
cystolith A concretion of calcium carbonate on an outgrowth of a cell wall. Occurs in a cell called a *lithocyst*.
cytokinin A plant hormone that can both promote and inhibit cell division.
cytokinesis The process of division of a cell as distinguished from the division of the nucleus, or *karyokinesis*.
cytological zonation Presence of regions in the apical meristem, or other parts of shoot and root apices, having distinctive cytological characteristics that form the basis for a subdivision into distinguishable tissue regions.
cytology The study of cell structure and function.
cytoplasm In a strict sense, the visibly least differentiated part of the protoplasm of a cell that constitutes the groundmass enclosing all other components of the protoplast. Also called *hyaloplasm*.
cytoskeleton A dynamic, living, filamentous system in the protoplast composed of microtubules and microfilaments.

decussate Arrangement of leaves in pairs that alternate with each other at right angles.

dedifferentiation A reversal in differentiation of a cell or tissue which is assumed to occur when a more or less completely differentiated cell resumes meristematic activity.

dehiscence The opening of a structure such as an anther or a fruit, allowing the release of reproductive structures contained therein.

dermal tissue system The outer covering tissue of a plant, epidermis, or periderm.

dermatogen The meristem forming the epidermis and arising from independent apical initials. One of the three histogens, *plerome*, *periblem*, and *dermatogen*, according to Hanstein.

desmotubule Tubule connecting the two endoplasmic reticulum cisternae located at the two opposite ends of a plasmodesma.

determinate growth Growth of limited duration such as that of leaves, flowers, and other lateral appendages.

development The change in form and complexity of an organism or part of an organism from its inception to maturity; combined with growth.

diacytic stoma A stomatal complex in which one pair of subsidiary cells, with their common walls at right angles to the long axis of the guard cell, surrounds the stoma.

diarch Arrangement of primary xylem in the root; having two protoxylem strands, or two protoxylem poles.

dichotomous venation A venation pattern in which the veins repeatedly branch into equal parts.

dictyosome A membranous cell organelle composed of stacked cisternae each producing secretory vesicles at the periphery; a *Golgi body*.

dictyostele A stele in which large overlapping leaf gaps dissect the primary vascular system into anastomosing strands, each with the phloem surrounding the xylem.

differentiation The physiological and morphological changes that occur in a cell, tissue, organ, or organism during development from a meristematic, or juvenile, stage to a mature, or adult, stage. Usually associated with an increase in specialization.

diffuse apotracheal parenchyma Axial parenchyma in secondary xylem occurring as single cells or as strands distributed irregularly within the tissue.

diffuse porous wood Secondary xylem in which vessels of one predominant size are distributed fairly uniformly throughout a growth layer; or with the vessels decreasing in size very slightly from early to late wood.

distal Farthest from the point of origin or attachment. Opposite of *proximal*. Often used in plant anatomy to mean in the direction of the apical meristem.

distichous Arrangement of leaves in two vertical rows; any two-ranked arrangement.

dorsiventral leaf Type of leaf possessing distinct upper and lower sides. Term derived from the reference to the abaxial and adaxial sides of a leaf as dorsal and ventral, respectively.

double fertilization The fusion of egg and sperm (resulting in a $2n$ fertilized egg, the zygote) and the fusion of the second male gamete with the polar nuclei (resulting in a $3n$ primary endosperm nucleus). A unique characteristic of angiosperms.

druse A globular, compound structure composed of calcium oxalate crystals.
duct An elongated space formed by separation of cells from one another (schizogenous origin), by dissolution of cells (lysigenous origin), or by a combination of the two processes; usually concerned with secretion.

early wood The wood (secondary xylem) formed in the first part of a growth layer and characterized by a lower density and larger cells than the late wood. Also called *spring wood*.
eccrinous secretion A secretion that leaves the cell as individual molecules passing through the plasmalemma and cell wall. Compare with *granulocrinous secretion*.
ectophloic siphonostele A stele composed of primary xylem and external primary phloem enclosing a pith.
ectoplast See **plasmalemma**.
egg apparatus The egg cell and two synergids located at the micropylar end of the female gametophyte (or embryo sac) in angiosperms.
elaioplast A leucoplast (a type of plastid) which functions as an oil-storage organelle.
elaiosome An outgrowth on a seed or a fruit which stores oil and serves as food for ants.
embryo sac The female gametophyte of angiosperms.
embryogeny (or **embryogenesis**) The process whereby the embryo develops.
enation A term applied to outgrowths of the stem that are considered to be primitive leaves. See also *microphyll*.
enation theory A theory that regards microphylls as simple enations in contrast to megaphylls which are considered to have evolved from branch systems.
endarch order of maturation Xylem which during development is characterized by centrifugal maturation of cells; that is, the oldest, mature elements (protoxylem) are closest to the center of the axis.
endocarp The innermost layer or layers of the pericarp.
endodermis A specialized, single layer of cells enclosing the vascular regions of roots and some stems, the cells of which are characterized by the presence of Casparian bands in the transverse and radial anticlinal walls.
endogenous Arising from a deep-seated tissue, as a lateral root.
endomembrane system Collective term for the membrane continuum of a cell consisting of plasmalemma, tonoplast, endoplasmic reticulum, Golgi bodies, and the nuclear envelope.
endoplasmic reticulum (often abbreviated as **ER**) A complex, three-dimensional system of membranes forming tubular or flattened compartments (cisternae) that permeate the cytoplasm. The cisternae appear like paired membranes in sectional profiles. The membranes may be coated with ribosomes (rough ER) or be free, or nearly free, of ribosomes (smooth ER).
endosperm A tissue of stored food in the embryo sac of angiosperms formed following fusion of a sperm cell and two polar nuclei. The endosperm provides nutrition for the developing embryo.
endothecium A wall layer in an anther, usually with secondary wall thickenings.
endothelium See *integumentary tapetum*.
enucleate Lacking a nucleus.

epiblast A small structure opposite the scutellum present in the embryo of some grasses.
epicotyl The young shoot of the embryo or seedling above the cotyledonary node, consisting of an axis and leaf primordia. See also *plumule*.
epidermis The outer layer of cells of the primary body of a plant.
epigeal Type of seed germination in which the cotyledon or cotyledons are raised above the surface of the substrate. Opposite of *hypogeal*.
epigynous Borne on or arising from the ovary; used of floral parts (petals, sepals, and stamens) when the ovary is inferior and the flower is not perigynous.
epipetalous stamen A stamen adnate to the corolla.
epithelium A layer of cells, often secretory in function, covering a free surface or lining a cavity.
epithem Mesophyll of a hydathode, a water-secreting structure of leaves.
ergastic substances Passive products of a protoplast; storage or waste products which may be synthesized within a protoplast or transported from other cells.
eukaryote A cell, or an organism containing cells, characterized by a membrane-bound nucleus, genetic material organized into chromosomes, and membrane-bound cytoplasmic organelles.
eustele A stele, lacking leaf gaps, in which the primary vascular tissue comprises axial vascular bundles and leaf traces arranged around a pith. Characteristic of gymnosperms and angiosperms.
exalbuminous seed A seed without endosperm in the mature state.
exarch primary xylem Xylem which during development is characterized by centripetal maturation of cells; that is, the oldest, mature cells are farthest from the center of the axis. Typical of roots of most vascular plants as well as the stems of many pteridophytes.
exine The outer wall of a spore or a pollen grain.
exocarp The outermost layer or layers of the pericarp.
exocytosis Fusion of Golgi vesicles with the plasma membrane and expulsion of cellulose synthase and other compounds required for cell wall synthesis.
exodermis The outer layer, one or more cells in depth, of the cortex in some roots. The cells often are characterized by Casparian bands in radial and transverse walls and suberin lamellae covered by a cellulosic layer forming the inner part of the tangential walls.
exogenous Originating in a superficial tissue.
expansin A protein that controls wall loosening by uncoupling the molecular strands comprising the polysaccharide network of the wall.
external phloem Primary phloem located externally to, and in contact with, the primary xylem.
extrafloral nectary Nectary occurring on a plant part other than a flower.
extraxylary fibers Fibers in various tissue regions other than the xylem.

false annual ring One of two or more growth layers formed during a growing season; usually the result of severe drought, forest fire, or extreme temperature fluctuations.
fascicle A bundle.
fascicular cambium Vascular cambium that develops within a vascular bundle.
fertilization The fusion of two gametes, especially of their nuclei, resulting in the formation of a diploid ($2n$) zygote.

fiber An elongated, usually tapering, thick-walled cell of the primary and/or secondary xylem. The cell may, but does not always, have a living protoplast at maturity; the cell wall is often lignified.
fiber-tracheid A fiber-like tracheid in the secondary xylem; commonly thick-walled, with pointed ends, and bordered pits that have lenticular to slit-like apertures that extend beyond the pit cavities.
Fibonacci series A mathematical series, 1, 2, 3, 5, 8, 13, 21, etc., in which each value is the sum of the two values that precede it. These fractions are used to characterize phyllotaxy (leaf arrangement). The series is named after Leonardo Fibonacci of Pisa (*c.*1170–*c.*1250) who formulated the relationship.
fibril Submicroscopic thread-like structure.
fibrous root system A root system composed of many (often adventitious) roots of similar length and thickness that emanate from the base of a stem. Characteristic of grasses and other monocotyledons.
filament A fine, thread-like structure; also the stalk supporting the anther in a stamen.
file meristem See *rib meristem*.
filiform Thread-like.
filiform apparatus A complex of slender cell wall invaginations in a *synergid* similar to those in *transfer cells*.
filling tissue Loose tissue formed to the outside by the lenticel phellogen; may or may not have cells with suberized cell walls. Also called *complementary tissue*.
floral tube A tube or cup formed by the united bases of sepals, petals, and stamens, often in perigynous and epigynous flowers.
florigen A hormone that promotes flowering.
flower The reproductive structure of angiosperms.
follicle A dry, dehiscent, many-seeded fruit derived from one carpel and splitting along one suture.
fossil The remains or traces of an organism preserved in sediments of Earth's crust.
free nuclear division Nuclear division that occurs without cell wall formation as in the early stages of development of endosperm in certain taxa.
frond The compound leaf of a fern or cycad; any large, highly divided leaf.
fruit In angiosperms, a mature, ripened ovary or fused cluster of ovaries, and any associated floral parts.
fundamental system See *ground tissue system*.
fundamental tissue The ground tissue in which other tissue systems are embedded.
funiculus The stalk of an ovule.
fusiform initials Cells in the vascular cambium from which, by cell division, the cells of the axial system of the secondary vascular tissues are derived.

gametangium (pl. **gametangia**) A structure in which gametes develop.
gamete A haploid reproductive cell.
gametophyte The haploid, gamete-producing phase in plants that have an alternation of generations.
gelatinous fiber A fiber with little or no lignification and in which part of the secondary wall has a gelatinous appearance.

generative cell The cell of the male gametophyte in gymnosperms which divides to form the stalk and body cells; in angiosperms, the cell of the male gametophyte (pollen grain) which divides to form two sperms (male gametes).
genotype The genetic constitution of an organism; contrasted with *phenotype*.
germination The resumption of growth by the embryo in a seed; also the beginning of growth of a spore, pollen grain, bud, or other structure.
gibberellins Growth hormones that influence, among other aspects of plant development, the elongation of stems.
gland A multicellular secretory structure.
glandular hair A trichome having a unicellular or multicellular head composed of secretory cells; usually borne on a stalk of non-glandular cells.
gluten Amorphous protein occurring in the starchy endosperm of cereals.
glyoxysome A *microbody* containing enzymes necessary for converting fats into carbohydrates.
Golgi body See *dictyosome*.
graft A union of two plants, a part of one of which, the scion, is inserted into the root or stem of the other, the stock.
grana (sing. **granum**) Stacks of disk-shaped cisternae, the *thylakoids*, which contain chlorophylls and carotenoids; sites of the light reactions in photosynthesis.
granulocrinous secretion Release from the protoplast of a secretion carried in a vesicle by its fusion with the plasmalemma. Compare with *eccrinous secretion*.
gravitropism The response of roots and shoots to gravity. Roots are positively gravitropic, thus grow downward. Shoots are negatively gravitropic, thus grow upward.
ground meristem A transitional meristematic tissue, derived from the apical meristem, which gives rise to the ground tissues.
ground tissue system Primary tissues derived from the ground meristem; comprised primarily of parenchyma and collenchyma. Also called the *fundamental system*.
growth layer A layer of secondary xylem or secondary phloem produced by the vascular cambium. See also *annual ring*.
guard cells A pair of cells flanking the stomatal pore and causing, by changes in turgor pressure, the opening or closing of the pore.
guttation Exudation from leaves of water derived from the xylem.
gymnosperm A seed plant, the seeds of which are unenclosed; well-known living taxa include conifers, cycads, and *Ginkgo*.
gynoecium Collective term for the carpels in an angiosperm flower.

half-bordered pit-pair A pit-pair consisting of a bordered and a simple pit.
haplocheilic stomatal complex Structural arrangement in which development of subsidiary cells is perigene, that is, they arise independently of the guard cells. Characteristic of some gymnosperms.
hardwood Term applied to the wood of dicotyledons.
haustorium A specialized projection from a cell or tissue that functions as a penetrating and absorbing structure.
heartwood Non-living, inner layers of secondary xylem that no longer function in transport. The vessels in such wood are typically infiltrated by *tyloses*, and contain waste metabolites, often giving the wood a dark color.

helical cell wall thickening In tracheary elements, secondary wall deposited on the primary or secondary wall as a continuous helix.

hemicellulose A polysaccharide more soluble and less ordered than cellulose; a common component of cell walls.

heterocellular ray A ray in secondary vascular tissues composed of cells of more than one form: in dicotyledons, of procumbent and upright cells; in conifers, of parenchyma cells and ray tracheids.

heterogeneous ray tissue system System of rays in secondary vascular tissues consisting of only heterocellular rays or both homocellular and heterocellular rays.

heterosporous Producing two kinds of spores, *microspores* and *megaspores*.

hilum (1) The central part of a starch grain around which the layers of starch are deposited concentrically. (2) The scar left on a seed by the detached *funiculus*.

histogen Hanstein's term for a meristem in the shoot or root tip that forms a definite tissue system in the plant body. Three histogens were recognized: *dermatogen*, *periblem*, and *plerome*.

histogen concept Hanstein's concept stating that the three primary tissue systems in the plant body (the epidermis, the cortex, and the vascular system with associated ground tissue) originate from distinct meristems, the histogens.

homocellular ray A ray in secondary vascular tissues composed of cells of one form only: in dicotyledons, of procumbent, or upright cells; in conifers, of parenchyma cells only.

homogeneous ray tissue system System of rays in secondary vascular tissues consisting of only homocellular rays.

homologous Having the same phylogenetic, or evolutionary, origin but not necessarily the same structure and/or function.

hormone A chemical substance produced in one part of an organism and transported to another part in which it has a specific effect.

hyaloplasm See *cytoplasm*.

hydathode A secretory structure, often in the margin of a leaf, by which water is released through an epidermal pore.

hydrolysis The disassembly of large molecules by the addition of water.

hydromorphic Having the structural features of hydrophytes, plants that live in moist or aquatic environments.

hydrophyte A plant that requires a large supply of water and may grow partly or entirely submerged in water.

hypha (pl. **hyphae**) A single tubular filament of a fungus which with others comprise the *mycelium*.

hypocotyl Axial region of an embryo or seedling located between the cotyledon or cotyledons and the radicle.

hypodermis A layer or layers of cells beneath the epidermis distinct from the underlying ground tissue cells.

hypogeal Seed germination in which the cotyledon or cotyledons remain beneath the surface of the ground. Opposite of *epigeal*.

hypogyny Floral condition in which the sepals, petals, and stamens are attached to the receptacle below the ovary.

hypophysis The uppermost cell of the suspensor from which part of the root and root cap in the embryo of angiosperms are derived.

hypsophylls Floral bracts.

idioblast A cell in a tissue that markedly differs in form, size, or contents from other cells in the same tissue.
imperfect flower A flower lacking either stamens or carpels.
indehiscent Of a fruit, remaining closed at maturity, e.g., a *samara*.
indeterminate growth Unrestricted growth in which an apical meristem will remain active during growing seasons over many years.
inferior ovary Condition in which the calyx is completely or partly fused to the ovary, and other floral parts appear to arise from above or upon the ovary, that is, they are *epigynous*.
initial A cell in a meristem that by division gives rise to two cells, one of which remains in the meristem, the other of which is added to the plant body.
integument Outer cell layer enveloping the nucellus of the angiosperm ovule and from which the seed coat differentiates.
integumentary tapetum The deeply staining innermost integumentary epidermis lining the embryo sac in some taxa and apparently assisting in the nutrition of the embryo. Also called *endothelium*.
intercalary growth Growth by cell division some distance from the meristem in which the dividing cells originated as, for example, in a leaf petiole or in the internodes of a stem.
intercalary meristem Meristematic tissue derived from the apical meristem located some distance from it and often intercalated between tissues that are no longer meristematic.
intercellular space A space between two or more cells in a tissue.
interfascicular cambium Vascular cambium that differentiates between vascular bundles in the interfascicular parenchyma.
internal phloem Primary phloem located to the inside of, and in contact with, primary xylem.
internode The part of the stem between two successive nodes.
intervascular pitting The pitting between tracheids or vessel members.
intine The inner wall layer of a pollen grain or spore.
intrusive growth A type of growth in which a growing cell intrudes between other cells that separate from each other along the middle lamella.
intussusception Growth of a cell wall by interpolation of new wall material within previously formed wall.
irregular flower A flower in which one or more members of at least one whorl of the perianth differ in form from other members of the same whorl. An irregular flower cannot be divided in two equal halves in more than one plane.
isobilateral mesophyll A mesophyll in which palisade parenchyma occurs beneath the epidermis on both lower and upper sides of the leaf.
isobilateral leaf A leaf in which the palisade parenchyma occurs beneath both the upper and lower epidermis.
isodiametric Regular in form, with all diameters of the same length.
isogamy Sexual reproduction in which the gametes are identical (or very similar) in size.
isomorphic Identical (or very similar) in form.
isotropic Having the same properties along all axes. Optically isotropic material does not affect the light.

karyokinesis Division of a nucleus as distinguished from the division of the cell, or *cytokinesis*.

kranz anatomy The arrangement of mesophyll cells around a conspicuous bundle sheath forming a wreath-like structure in leaves of C_4 plants.

lacuna (pl. **lacunae**) The air space between cells; also the parenchymatous region in an increment of secondary xylem above and often partially enclosing a leaf trace. Lacuna, in the latter sense, is *not* synonymous with leaf gap. See also *multilacunar node*, *trilacunar node*, *two-trace unilacunar node*, and *unilacunar node*.

lacunar collenchyma Collenchyma tissue characterized by intercellular spaces and cell wall thickenings facing the spaces.

lamella A thin plate or layer.

lamellar collenchyma Collenchyma tissue comprised of cells with wall thickenings deposited between the corners of the cells.

lamina The leaf blade; also used to refer to a thin cell wall layer.

late wood The secondary xylem formed in the outer part of a growth layer; denser and composed of smaller cells than the early wood. Also called *summer wood*.

lateral meristem A meristem located parallel to the surface of an axis such as the *vascular cambium* and the *phellogen* or *cork cambium*.

latex (pl. **latices**) A fluid contained in laticifers; consists of a variety of organic and inorganic substances often including rubber.

laticifer A cell or a system of cells containing *latex*.

leaf buttress A lateral protrusion below the apical meristem constituting the initial stage in the development of a leaf primordium.

leaf gap A region of parenchyma in the primary vascular system (*siphonostele* or *dictyostele*) of many ferns opposite a diverging leaf trace.

leaf sheath The lower part of a leaf that invests the stem more or less completely.

leaf trace A vascular bundle which extends into a leaf from its connection with another vascular bundle in the primary vascular system of the stem.

lenticel A specialized region in the periderm containing intercellular spaces which allow an interchange of O_2 and CO_2 between the inner tissues of the plant and the external atmosphere.

leucoplast A colorless plastid; often a site of starch formation.

libriform fiber A xylem fiber commonly with thick walls and highly reduced bordered pits which often appear simple; a major component of secondary xylem in dicotyledons.

lignification Impregnation with lignin.

lignin A component of many cell walls which increases their rigidity and resistance to compression; a polymer of high carbon content derived from phenylpropane.

lithocyst A cell containing a *cystolith*.

locule The cavity within a sporangium containing the spores or pollen grains, or within an ovule containing the ovules.

lumen In a non-living cell, the space enclosed by the cell wall.

lutoids Vesicles, also called vacuoles, in laticifers bound by a single membrane and containing hydrolytic enzymes capable of degrading most of the organic compounds in the laticifer.

lycophytes (**Lycophyta**) A group of primitive vascular pteridophytes which includes extant taxa such as *Lycopodium* and *Selaginella* and their extinct relatives.
lysigenous Of an intercellular space, originating by a dissolution of cells.
lysis A process of disintegration or degradation.
lysosome An organelle bound by a single membrane and containing acid hydrolytic enzymes capable of breaking down proteins and other organic macromolecules.

maceration The artificial separation of cells of a tissue by causing a disintegration of the middle lamella.
macrofibril An aggregation of cellulose microfibrils, usually visible with the light microscope.
macrosclereid Elongated, rod-like sclereid with unevenly distributed secondary wall thickenings.
marginal meristem A meristem on the margin of a leaf primordium which gives rise to the blade.
matrix A medium in which something is embedded, e.g., the cell wall matrix in which cellulose microfibrils are embedded.
medulla An archaic synonym for *pith*.
medullary bundles Vascular bundles located in the pith.
medullary rays A rarely used synonym for *vascular rays*, referring to the broad regions of secondary parenchyma between elongate masses of secondary tracheary tissues in the stems of some vines and other plants with anomalous structure.
megagametophyte Female gametophyte in heterosporous plants; the embryo sac within the ovule in angiosperms.
megaphyll Usually a large leaf with a complex venation; the leaf trace is associated with a leaf gap. These characters contrast with those of a *microphyll*.
megasporangium A sporangium in which megaspores are produced; the *nucellus* in the ovule of angiosperms.
megaspore A haploid spore which develops into a female gametophyte in heterosporous plants.
megaspore mother cell See *megasporocyte*.
megasporocyte A diploid cell that undergoes meiosis and produces four haploid megaspores. Also called *megaspore mother cell*.
megasporophyll A leaf-like organ which bears a megasporangium.
meristem A region of undifferentiated tissue from which, by cell division, new cells are produced.
mesarch order of maturation Development of the primary xylem in a vascular bundle in which metaxylem differentiates in all directions from centrally located protoxylem.
mesocarp The middle layer of the ovary wall, or pericarp, of a mature fruit.
mesocotyl The internode between the scutellar node and the coleoptile in the embryo and seedling of members of the Poaceae.
mesogene Stomatal development in which neighboring or subsidiary cells and guard cells have a common origin. May also be referred to as *mesogenous*.
mesomorphic Having the structural features of *mesophytes*.

mesoperigene Stomatal development in which at least one subsidiary cell is related by origin to the guard cells, the others are not. May also be referred to as *mesoperigenous*.

mesophyll The photosynthetic parenchyma of a leaf blade located between the two epidermal layers.

mesophytes Plants that require an environment containing moderate levels of soil moisture and a moist atmosphere, in contrast to *xerophytes* which thrive in dry conditions and *hydrophytes* which often live in water or soil that remains very wet.

mestome sheath The inner, thick-walled, endodermis-like sheath of two sheaths that enclose the vascular bundles in the leaves of some grasses.

metaphloem Part of the primary phloem which differentiates after the protophloem and before the secondary phloem, if any of the latter is formed in a given taxon.

metaxylem Part of the primary xylem which differentiates after the protoxylem, and usually after cessation of elongation in associated tissues.

micelle A region in a cellulose microfibril in which the cellulose molecules are arranged in a crystalline lattice structure.

microbody Organelle bound by a single membrane and containing various enzymes. *Peroxisomes* and *glyoxysomes* are microbodies.

microfibril A slender strand of cellulose molecules which, with the matrix, are the major components of the cell wall.

microfilament A long, thin, protein (actin) filament, about 8 nm in diameter frequently associated with microtubules and the endoplasmic reticulum (ER); facilitates cytoplasmic streaming and, through interaction with myosin, organelle movement.

microgametophyte The male gametophyte of a heterosporous plant; the pollen grain in a seed plant.

micrometer A unit of measurement commonly used to measure cellular and subcellular structures. 1/1000 millimeter; 10^{-6} m. Also called a *micron*. The symbol for micrometer is μm.

micron See *micrometer*.

microphyll Small leaf, usually containing a single vascular bundle; not associated with a leaf gap. Characteristic of plants containing protosteles. See also *enation*.

micropyle The opening in the integuments of an ovule of seed plants through which the pollen grains or pollen tubes usually enter.

microsporangium The sporangium in which microspores are formed; the anther locule and its walls in angiosperms.

microspore A haploid spore that develops into a male gametophyte in heterosporous plants.

microspore mother cell See *microsporocyte*.

microsporocyte A diploid cell that undergoes meiosis and forms four haploid microspores. Also called *microspore mother cell*.

microsporophyll Leaf-like organ that bears microsporangia; in angiosperms, modified into the stamen.

microtubules Slender tubes of indeterminate length, usually straight, with a diameter of about 25 nm. They are composed of protein subunits (dimers of alpha and beta tubulin) forming a circle of 13 when observed in transverse section. They occur in the periphery of the protoplast, are closely associated with cellulose microfibrils and also make up the meiotic and mitotic spindles and the phragmoplast.

middle lamella A layer of intercellular material, chiefly pectic substances, which cements together the primary walls of contiguous cells.
mitochondrion (pl. **mitochondria**) A double membrane-bound cell organelle concerned with respiration in eukaryotic cells; the major source of ATP in non-photosynthetic cells.
monocotyledon One of the two major groups of angiosperms, differing from dicotyledons in having embryos with only one cotyledon.
monosaccharide A simple sugar, e.g., a 5-carbon or 6-carbon sugar.
morphogenesis The development of form; the sum of the various processes of development and differentiation of tissues and organs.
morphology The study of form and its development.
mucilage cell A cell containing mucilages or gums or similar carbohydrate material characterized by the property of swelling in water.
mucilage duct A duct containing mucilage or gum, or similar carbohydrate material.
multilacunar node A node characterized by five or more leaf traces that supply a single leaf. Typically, associated with each leaf trace, and through which each leaf trace passes, is a parenchymatous region in the first-formed increment of secondary xylem, called a *lacuna*.
multiperforate perforation plate In a vessel member of the xylem, a perforation plate that has more than one perforation.
multiple epidermis A tissue two or more cell layers deep derived from the protoderm; only the outermost layer differentiates as a typical epidermis.
multiple fruit A fruit composed of several matured ovaries each produced in a separate flower as, for example, the pineapple.
multiseriate ray A ray in secondary vascular tissues that is several to many cells wide.
mycelium All of the *hyphae* which, collectively, comprise the body of a fungus.
mycorrhiza (pl. **mycorrhizae**) The symbiotic association of a fungus and the roots of a vascular plant; may be ectotrophic wherein hyphae invest the root of the host or endotrophic wherein hyphae are located within the root cells; mycorrhizae enhance the water and mineral absorption capability of plants.

nacré wall See *nacreous wall*.
nacreous wall A non-lignified wall that is often found in sieve elements and resembles a secondary wall when it attains considerable thickness; the designation is based on the glistening appearance of the wall. Also called *nacré wall*.
nanometer One millionth of a millimeter; 10^{-9} m. A nanometer is equal to 10 angstroms (Å or A). The symbol for nanometer is nm.
nectary A multicellular glandular structure which secretes nectar, a liquid containing organic substances including sugar. Nectaries occur in flowers (*floral nectary*) and on vegetative plant parts (*extrafloral nectary*).
netted venation See *reticulate venation*.
nodal diaphragm A septum of tissue at the node of a stem extending across the otherwise hollow pith region.
node That part of the stem at which one or more leaves are attached; not sharply delimited anatomically.
nodules Enlargements on roots of plants, particularly in the Fabaceae, inhabited by nitrogen-fixing bacteria.

non-articulated laticifer A simple laticifer consisting of a single, commonly multinucleate, usually branched, tube which originated from a single cell through cell growth; contains *latex*.
nucellus The inner part of an ovule in which the embryo sac develops. Considered to be equivalent to the *megasporangium*.
nuclear envelope The double membrane enclosing the cell nucleus.
nucleolus A spherical body, composed mainly of RNA and protein, present in the nucleus of eukaryotic cells, one or more to a nucleus; site of synthesis of ribosomes.
nucleus An organelle in a eukaryotic cell bound by a double membrane and containing the chromosomes, nucleoli, and nucleoplasm.

ontogeny The development of an organism, organ, tissue, or cell from inception to maturity.
open venation Leaf venation in which large veins end freely in the mesophyll instead of being connected by anastomoses with other veins.
opposite pitting Pits in tracheary elements disposed in horizontal pairs or in short horizontal rows.
organ A distinct and visibly differentiated part of a plant such as a root, stem, leaf, or part of a flower.
organelle A distinct body within the cytoplasm of a cell, specialized in function.
orthostichy A vertical or nearly vertical line along which is attached a series of leaves or scales on an axis of a shoot or shoot-like organ; may be identical to the steepest parastichy in a phyllotactic system.
osteosclereid A bone-shaped sclereid having a columnar middle part and enlargements at both ends.
ovary The lower part of a carpel (simple pistil) or of a gynoecium composed of united carpels (compound pistil) containing the ovules, and which will develop into a fruit or part of a fruit.
ovule Structure in a seed plant enclosing the female gametophyte and composed of the nucellus, one or two integuments, and a funiculus (ovular stalk); differentiates into the seed.
ovuliferous scale In conifers, the appendage of a cone to which the ovule is attached.

paedomorphosis Delay in evolutionary advance in some characteristics as compared with others resulting in a combination of juvenile and advanced characteristics in the same cell, tissue, or organ.
palisade mesophyll Leaf mesophyll characterized by elongated cells with their long axes perpendicular to the surface of the leaf and in contact with the epidermis; may occur only in the adaxial part of a leaf blade or in both adaxial and abaxial regions (*isobilateral mesophyll*). May function in part in the transmission of light into the inner part of the leaf.
palisade parenchyma The mesophyll immediately beneath the upper epidermis of leaves, usually tubular in form. In leaves with *isobilateral mesophyll*, palisade parenchyma occurs in both upper and lower regions.
paracytic stoma A stomatal complex in which one or more subsidiary cells flank the stoma parallel to the long axes of the guard cells.
paradermal Parallel to the epidermis. Refers specifically to a section made parallel to the surface of a flat organ such as a leaf.

parallel evolution Evolutionary process that results in similar structures and functions in two or more evolutionary lines. See also *convergent evolution*.

parallel venation Arrangement in which main veins in a leaf blade are approximately parallel to one another, although converging at the base and apex of the leaf. Also called *striate venation*.

parastichy A helix along which is attached a series of leaf primordia in a shoot apex, or leaves or scales along the axis of a mature shoot. Compare *orthostichy*.

paratracheal parenchyma Axial parenchyma in secondary xylem associated with vessels. Includes *aliform*, *confluent*, and *vasicentric* patterns.

paraveinal mesophyll Mesophyll in a leaf blade that forms a sheet of tissue parallel to the venation system, often in the same plane as the veins.

parenchyma A tissue composed of parenchyma cells.

parenchyma cell A living cell in which various physiological and biochemical processes occur, usually thin-walled and of variable size and form. Parenchyma cells comprise the ground tissue of plant organs.

parthenocarpy The development of fruit without fertilization; the fruits are usually seedless.

passage cell A cell in an endodermis that remains thin-walled when other cells in the same tissue region develop thick secondary walls. *Casparian bands* are deposited within the transverse and radial walls of the passage cell and contiguous cells.

pectic substances A group of complex carbohydrates, derivatives of polygalacturonic acid, which occur in plant cell walls; major constituents of the *middle lamella*.

pedicel The stalk of an individual flower in an inflorescence.

peduncle The stalk of a solitary flower or of an inflorescence.

peltate trichome A trichome consisting of a discoid plate of cells borne on a stalk or attached directly to the basal foot cell.

perennial A plant that continues to produce reproductive structures for three or more years.

perfect flower A flower having both carpels and stamens.

perforation plate Part of a wall of a vessel member that is perforated.

perianth Petals and sepals of a flower considered together.

periblem The meristem which gives rise to the cortex. One of the three histogens, *plerome*, *periblem*, and *dermatogen*, according to Hanstein.

pericarp The wall of a fruit which develops from the ovary wall.

periclinal Having the orientation of cell wall or the plane of cell division parallel with the nearest surface of an organ. Opposite of *anticlinal*.

pericycle The tissue region located between the primary vascular tissues and the endodermis.

periderm Secondary protective tissue that replaces the epidermis in stems and roots, rarely in other organs; consists of *phellem* (cork), *phellogen* (cork cambium), and *phelloderm*.

perigene Stomatal development in which neighboring or subsidiary cells and guard cells have separate origins. May also be referred to as *perigenous*.

perigyny The arrangement of floral parts in which the sepals, petals, and stamens are attached to a cup-shaped extension of the receptacle, but appear to be attached to the ovary.

perisperm Storage tissue in a seed similar to endosperm but derived from the nucellus.

peroxisome A cell organelle of the *microbody* type that is involved in glycolic acid metabolism associated with photosynthesis.
petal A flower part, often colored, which with other petals comprises the corolla.
petiole The stalk of a leaf.
petiolule The stalk of a leaflet.
phellem (cork) An outer protective tissue of roots and stems composed of non-living cells with suberized walls and formed centrifugally by the phellogen (cork cambium) as part of the periderm.
phelloderm A tissue resembling cortical parenchyma produced centripetally by the phellogen (cork cambium) as part of the periderm of stems and roots in seed plants.
phellogen (cork cambium) A lateral meristem which gives rise to the periderm which consists of phellem and phelloderm.
phelloid cell A cell within the phellem but distinct from other cells in this tissue in lacking suberin in its walls.
phenotype The physical appearance of an organism which results from interaction between its *genotype* (genetic constitution) and the environment.
phloem The food-conducting tissue of vascular plants which is composed of sieve elements, various kinds of parenchyma cells, fibers, and sclereids.
phloem loading The process by which photosynthate is transferred into sieve cells or sieve tube members.
photoperiodism Response to the duration and timing of day and night expressed in certain aspects of growth, development, and flowering in plants.
photorespiration The light-dependent production of glycolic acid in chloroplasts and its subsequent oxidation in peroxisomes.
photosynthates The carbohydrates produced during the process of photosynthesis.
photosynthesis The process by which carbohydrates are formed from carbon dioxide and water in the presence of chlorophyll, using light energy.
phragmoplast A subcellular structure composed of microtubules that arises between daughter nuclei at telophase and within which the cell plate forms during cell division; appears initially as spindle-shaped, but later spreads laterally in the form of a ring.
phragmosome A layer of cytoplasm formed across the cell where the nucleus becomes located and divides. The equatorial plane of the phragmoplast coincides with the plane of the cytoplasmic layer (phragmosome).
phyllode A flat, expanded petiole or stem replacing the leaf blade in photosynthetic function.
phyllotaxy (or **phyllotaxis**) The arrangement of leaves on a stem; the mathematical principles of such arrangement. See also *Fibonacci series*.
phylogeny Evolutionary history of a species or large taxon.
phytochrome A pigment occurring in the cytoplasm and serving as a photoreceptor for red and far-red light; involved in timing certain processes such as dormancy, leaf formation, flowering, and seed germination.
PIN proteins Proteins that function as auxin efflux transporters which transfer auxin from cells in one region to cells in another.
pinocytosis A process of uptake of a substance by invagination of the plasmalemma.

pistil The ovary, style, and stigma of a flower. May be simple, consisting of a single carpel, or compound, consisting of several fused carpels.

pistillate Of a flower, having one or more carpels but no functional stamens.

pit A depression in the cell wall where the primary wall is not covered by secondary wall.

pit aperture An opening into the pit from the interior of the cell. If a *pit canal* is present in a bordered pit, two apertures are recognized, the inner, from the cell lumen into the canal, and the outer, from the canal into the pit cavity.

pit canal The passage from the cell lumen to the chamber or cavity of a bordered pit. See also *pit aperture*.

pit cavity The space within a pit from pit membrane to the cell lumen or to the outer pit aperture if a *pit canal* is present.

pit membrane The part of the intercellular layer (middle lamella) and primary walls that separate the pit cavities of a pit-pair.

pit-pair Two opposite pits in the walls of contiguous cells plus the pit membrane.

pith Ground tissue in the center of a stem or root.

placenta The part of the ovary walls to which ovules or seeds are attached.

placentation The arrangement of ovules in an ovary.

plasma membrane See *plasmalemma*.

plasmalemma Single membrane enclosing the protoplast. A type of unit membrane. Also called *plasma membrane* or *ectoplast*.

plasmodesma (pl. **plasmodesmata**) Highly specialized regions of endoplasmic reticulum that extend through cell walls and connect the protoplasts of adjacent cells.

plastid An organelle with a double membrane in the cytoplasm of many eukaryotes. May be the site of photosynthesis (chloroplast) or starch storage (amyloplast), or contain yellow or orange pigments (chromoplast).

plastochron The time interval between the inception of two successive repetitive events, as the origin of leaf primordia.

plate meristem A meristematic tissue consisting of parallel layers of cells which divide only anticlinally with reference to the wide surface of the tissue. Characteristic of ground meristem of plant parts that assume a flat form, as a leaf.

plerome The meristem forming the core of the axis composed of the primary vascular tissues and associated ground tissue, such as pith and interfascicular regions. One of the three histogens, *plerome*, *periblem*, and *dermatogen*, according to Hanstein.

plumule Embryonic shoot above the cotyledon or cotyledons in an embryo. See also *epicotyl*.

polar nuclei The two centrally located nuclei in an embryo sac which fuse with a male nucleus forming the triploid endosperm nucleus.

polar auxin transport The basipetal movement of auxin from sites of synthesis in the shoot apex to sites of activity. Pathways of auxin transport are provascular strands and the vascular cambium and its immature derivatives.

pollen A collective term for pollen grains.

pollen grain In seed plants a microspore included in an elaborately structured wall and which contains an immature or mature *microgametophyte*.

pollen mother cell See *microsporocyte*.

pollen sac A locule in an anther containing the pollen grains.
pollen tube A tubular cell extension formed by the germinating pollen grain; carries the male gametes into the ovule.
pollination In angiosperms, the transfer of pollen from the anther to the stigma; in gymnosperms, the transfer of pollen from the male cones to the immature ovules.
polyarch Primary xylem column of the root characterized by many protoxylem strands.
polyderm A type of protective tissue in which layers of parenchyma cells with suberized walls alternate with layers of parenchyma cells having non-suberized walls.
polyembryony Development of more than one embryo in a single seed.
polymer A large molecule composed of many similar molecular subunits.
polymerization Chemical union of monomers, such as glucose or nucleotides, resulting in the formation of polymers such as starch, cellulose, or nucleic acid.
polyribosomes Aggregates of ribosomes involved in protein synthesis.
polysaccharide A carbohydrate composed of many monosaccharide units joined in a chain, such as starch or cellulose.
pore A term of convenience for a vessel member as seen in transverse section of secondary xylem.
pore multiple (or **cluster**) A group of two or more pores (vessels in cross-sections of secondary xylem) crowded together and usually flattened along the surfaces of contact.
porous wood Secondary xylem containing vessels.
P-protein Phloem protein; found in cells of the phloem of seed plants, most commonly in sieve elements. Formerly called slime.
preprophase band A ring-like band of microtubules delimiting the equatorial plane of the future mitotic spindle in cells preparing to divide.
primary body The part of the plant, or the entire plant if no secondary growth occurs, that arises from the embryo and the apical meristems and their derivative meristematic tissues.
primary growth Growth resulting from activity of apical meristems of roots and shoots and their derivative meristems.
primary peripheral thickening meristem The meristem in many large monocotyledons, proximal to the apical meristem, responsible for increase in thickness of the stem.
primary phloem Phloem tissue derived from the provascular tissue during primary growth and differentiation of a vascular plant. *Protophloem* differentiates first, followed by *metaphloem*.
primary pit field A thin region in a primary wall traversed by plasmodesmata. Usually the site of development of pits in the secondary wall.
primary root The root that develops from the radicle in the embryo. If development of this root continues it becomes a tap root.
primary tissues Tissues derived from the apical meristem and the transitional tissue regions, protoderm, ground meristem, and provascular tissue; contrasting with secondary tissues derived from lateral meristems such as the vascular cambium and the phellogen.
primary vascular tissues The xylem and phloem that differentiate from provascular tissue during primary growth and differentiation of a vascular plant.

primary wall The wall layer that develops during cell growth as opposed to the secondary wall that develops after cell expansion has ceased.

primary xylem Xylem tissue that differentiates from provascular tissue during primary growth and differentiation of a vascular plant. *Protoxylem* differentiates first, followed by *metaxylem*.

primordium (pl. **primordia**) A cell or organ in an early stage of differentiation, e.g., a sclereid primordium, or a leaf primordium.

procambium See *provascular tissue*.

procumbent ray cell In secondary vascular tissues, a ray cell having its longest axis oriented radially.

proembryo An early development stage of an embryo before the main body of the embryo and the suspensor become distinct.

prokaryotes Single cells, or organisms consisting of cells lacking membrane-bound nuclei and membrane-bound organelles, e.g., bacteria, blue-green algae, mycoplasmas. See *eukaryote*.

promeristem The initiating cells and their most recent derivatives in an apical meristem.

prop roots Adventitious roots that develop on the stem above the soil level and which serve as additional support for the plant axis.

prophyll The first leaf, or one of two first leaves, on a lateral shoot.

proplastid A plastid in its earliest stages of development.

protective layer In the abscission zone, a layer of cells that, because of substances impregnating its walls, has a protective function in the scar formed by abscission of a leaf or other plant part.

protein bodies See *aleurone grains*.

prothallial cell Sterile (vegetative) cell or cells in the microspores of gymnosperms and the microgametophytes of other non-angiospermous vascular plants.

protoderm A single-layered meristematic tissue region that gives rise to the epidermis.

protophloem The first-formed cells of the primary phloem in a plant organ.

protoplasm Living substance of cells, excluding their organelles.

protoplast The organized living unit of a single cell excluding the cell wall.

protostele The simplest type of stele, containing a solid column of vascular tissue, with the phloem peripheral to the xylem.

protoxylem The first formed cells of the primary xylem in a plant organ.

protoxylem lacuna A space surrounded by parenchyma cells in the protoxylem of a vascular bundle; often develops when protoxylem elements are stretched and torn resulting from elongation growth.

protoxylem poles Term of convenience for loci of protoxylem strands as seen in transverse section.

provascular tissue The transitional tissue region, partly meristematic, from which the primary vascular tissue differentiates.

proximal Situated near the point of origin or attachment. Opposite of *distal*. Often used in plant anatomy to mean in a direction away from the apical meristem, i.e., toward the base of the plant.

pteridophyte Any plant that lacks seeds and that is characterized by free-sporing reproduction, such as ferns and other relatively primitive taxa.

pulvinus An enlargement at the base of the petiole of a leaf, or petiolule of a leaflet; has a role in the movements of a leaf or leaflet.

quantasomes Granules located on the inner surface of chloroplast lamellae; thought to be involved in the reactions in photosynthesis requiring light.
quiescent center A region in the apical meristem of roots which is relatively inactive in cell division; considered to be a region that has some control in root development.

rachis The petiole of a fern frond, or main axis of a compound leaf.
radial section A longitudinal section cut along a radius of a stem or root; in secondary xylem or phloem, a section cut parallel to a vascular ray.
radial seriation Arrangement of units, such as cells, in an orderly sequence in a radial direction; characteristic of cambial derivatives.
radial symmetry Of a flower, having parts that can be divided equally in more than one longitudinal plane passing through the floral axis. Contrasted with *bilateral symmetry*.
radicle The embryonic root.
ramified Branched.
ramiform pit A pit with a *pit canal* that branches.
raphe A ridge along the body of the seed formed by the part of the funiculus that is adnate to the ovule.
raphides Needle-shaped crystals which commonly occur in bundles.
ray A sheet of tissue, variable in height and width, formed by a ray initial in the vascular cambium and which extends radially in the secondary xylem and secondary phloem.
ray cell initials Meristematic cells in a ray initial from which ray cells are derived.
ray initial A cluster of meristematic cells in the vascular cambium that gives rise to a ray.
ray tracheid Non-living, radially oriented cells with walls containing circular-bordered pits that occur in the rays of the secondary xylem of several conifer and angiosperm families as well as in the extinct progymnosperm *Archaeopteris*.
reaction wood Wood with abnormal anatomical characteristics formed in parts of leaning or crooked stems and on the lower (conifers) or upper (dicotyledons) sides of branches. See also *compression wood* and *tension wood*.
receptacle The part of the flower stalk that bears the floral organs.
regular flower See *actinomorphic*; *radial symmetry*.
residual meristem A meristematic region in the shoot apex, below the apical meristem in some taxa, in which provascular strands develop.
resin duct A duct of schizogenous origin lined with resin-secreting cells (epithelial cells) and containing resin.
reticulate cell wall thickening In tracheary elements of the xylem, secondary cell wall deposits on the primary wall in an anastomosing or net-like pattern.
reticulate perforation plate In vessel members of the xylem, a multiperforate perforation plate in which the bars delimiting the perforations form a reticulum.
reticulate sieve plate A compound sieve plate with sieve areas arranged so that the wall between forms a net-like pattern.
reticulate venation A pattern of venation in a leaf blade in which the veins form an anastomosing system, the whole resembling a net. Also called *netted venation*.

retting Freeing fiber bundles from other tissues by utilizing the action of microorganisms causing, in a suitable moist environment, the disintegration of the thin-walled cells surrounding the fibers.
rhexigenous As applied to an intercellular space, originating by rupture of cells.
rhizodermis The epidermis of roots.
rhytidome The part of the bark consisting of intersecting regions of internal periderm between which are regions of cortex and/or non-functional secondary phloem.
rib meristem A meristem in which the cells divide perpendicular to the longitudinal axis of an organ and produce a complex of parallel, vertical files of cells; particularly common in ground meristem of organs that are of cylindrical form. Also called *file meristem*.
ribonucleic acid Nucleic acid formed on chromosomal DNA and involved in protein synthesis. Commonly abbreviated as RNA.
ribosome A cell component composed of protein and RNA; the site of protein synthesis.
ring porous wood Secondary xylem in which the vessels (pores) of the early wood are distinctly larger than those of the late wood, forming a well-defined zone or ring as seen in transverse section.
RNA See *ribonucleic acid*.
root cap A sheath of cells covering the apical meristem of the root.
root hair A tubular trichome on the root epidermis that is an extension of a single epidermal cell; occurs in the zone of maturation and facilitates absorption.
rosette A cluster of at least three cellulose synthase proteins required for the synthesis of cellulose. The synthesis of cellulose in primary and secondary walls require different sets of cellulose synthase proteins.

samara Simple, dry, one- or two-seeded indehiscent fruit; characterized by wing-like outgrowths of the pericarp.
sapwood Outer part of the wood of the stem (or trunk) in which active conduction takes place; usually lighter in color than the heartwood.
scalariform cell wall thickening In tracheary elements, secondary wall depositions on the primary wall in a ladder-like pattern. Similar, in some taxa, to a helix of low pitch with the coils interconnected at intervals.
scalariform perforation plate In a vessel member, a type of multiperforate end wall in which elongated perforations are arranged more or less parallel to one another so that the cell wall bars between them form a ladder-like pattern.
scalariform pitting In tracheary elements, elongated pits arranged parallel to one another so as to form a ladder-like pattern.
scalariform–reticulate cell wall thickening In tracheary elements, secondary wall thickening intermediate between scalariform and reticulate wall thickening.
scalariform sieve plate A compound sieve plate with elongated sieve areas arranged parallel to one another in a ladder-like pattern.
schizogenous Of an intercellular space, originating by separation of cell walls along the middle lamella.
schizo-lysigenous Of an intercellular space, originating by a combination of two processes, separation and degradation of cell walls.

scion See *graft*.
sclereids Sclerenchyma cells, varied in form, but (with a few exceptions) not very elongate, and having thick, lignified secondary walls with many simple pits.
sclerenchyma A tissue composed of sclerenchyma cells, also a collective term for sclerenchyma cells in the primary plant body; includes fibers, fiber-sclereids, and sclereids.
sclerenchyma cell A cell of variable form and size and having more or less thick, often lignified, secondary walls; belongs to the category of supporting cells and may or may not be devoid of a protoplast at maturity.
sclerification The process of becoming changed into sclerenchyma, i.e., the development of secondary walls, with or without subsequent lignification.
scutellum (pl. **scutella**) The single cotyledon in a grass embryo, specialized for the absorption of the endosperm.
secondary body The part of the plant body that is added to the primary body by the activity of the lateral meristems, vascular cambium, and phellogen; consists of secondary vascular tissues and periderm.
secondary cell wall The inner layer of the wall deposited upon the primary wall after cell growth (increase in size) has ceased.
secondary growth In gymnosperms, most dicotyledons, and some monocotyledons, a type of growth characterized by an increase in thickness of the stem and root, and resulting from formation of secondary tissues by the vascular cambium. Commonly supplemented by activity of the cork cambium (*phellogen*) forming periderm.
secondary phloem Phloem tissue formed by the vascular cambium during secondary growth in a vascular plant.
secondary plant body See *secondary body*.
secondary tissues Tissues produced by the vascular cambium and phellogen during secondary growth.
secondary vascular tissues Vascular tissues (both xylem and phloem) formed by the vascular cambium during secondary growth in a vascular plant.
secondary wall See *secondary cell wall*.
secondary xylem Xylem tissue formed by the vascular cambium during secondary growth in a vascular plant.
secretory cavity A space lysigenous in origin and containing a secretion derived from the cells that broke down in the formation of the cavity.
secretory cell A living cell specialized with regard to secretion of one or more, often organic, substances.
secretory duct A duct schizogenous in origin and containing a secretion derived from the cells (epithelial cells) lining the duct. See *epithelium*.
secretory hair See *glandular hair*.
secretory structure Any of a great variety of structures, simple or complex, external or internal, that produce a secretion.
seed coat The outer coat of the seed derived from the integument or integuments of the ovule. Also called *testa*.
sepal A unit of the calyx.
separation layer See *abscission layer*.
septate fiber A fiber with thin transverse walls (septa) that are formed after the cell develops a secondary wall.
septum (pl. **septa**) A partition.
sessile Of a leaf, lacking a petiole; of a flower or a fruit, lacking a pedicel.

sexine The outer layer of the exine of a pollen grain; the sculptured part of the exine.

sheath A sheet-like structure enclosing or encircling another; applied to the tubular or enrolled part of an organ, such as a leaf sheath, and to a tissue layer surrounding a complex of other tissues, as a bundle sheath enclosing a vascular bundle.

sheathing base A leaf base that encircles the stem.

sieve area A specialized region of a sieve element containing pores commonly lined with callose and through which traverse protoplasmic strands that connect the protoplasts of contiguous sieve elements.

sieve cell A sieve element that has sieve areas, usually with sieve pores of small diameter, on all walls; there are no end wall sieve plates. Typical of gymnosperms and seedless vascular plants.

sieve elements Cells in the phloem tissue concerned primarily with conduction of photosynthate and hormones; *sieve cells* and *sieve tube members*.

sieve plate The part of the cell wall (usually the end walls) of a sieve element bearing one or more highly differentiated sieve areas typical of angiosperms.

sieve tube A series of sieve tube members arranged end to end and interconnected through sieve plates.

sieve tube element See *sieve tube member*.

sieve tube member One of a series of cell components of a sieve tube. Characterized by sieve plates on the end walls and less highly differentiated lateral sieve areas. Also called *sieve tube element*.

signaling pathways Paths along which move hormones and sensory inputs from the external environment.

signal transduction Transmssion of, and response to, environmental stimuli such as hormones, CO_2, blue light, water availability and plant pathogens.

silica cell Cell filled with silica, as in the epidermis of many grasses.

simple perforation plate A perforation plate of a vessel member with a single perforation.

simple pit A pit in a secondary wall which lacks an overhanging border.

simple pit-pair A pair of opposing simple pits in the walls of contiguous cells.

simple sieve plate A sieve plate composed of one sieve area.

siphonostele A stele in which the vascular system is in the form of a cylinder enclosing the pith.

slime Archaic term for *P-protein*.

slime body An aggregation of *P-protein*.

slime plug An accumulation of *P-protein* on a sieve area, usually with extensions into the sieve pores.

softwood The wood of conifers.

solitary pore A vessel, as seen in transverse section, in the secondary xylem surrounded by cells other than vessel members.

specialized Of organisms, having special adaptations to a particular habitat or mode of life; of cells or tissues, having distinctive functions.

spenophytes (**Spenophyta**) A group of primitive vascular pteridophytes which includes the extant taxon *Equisetum* and its extinct relatives.

sperm The male gamete.

spherosomes Single membrane-bound bodies in the cytoplasm containing lipids.

spindle fibers Microtubules aggregated in a spindle-shaped complex extending from pole to pole in cells with a dividing nucleus.

spongy parenchyma Leaf mesophyll parenchyma with conspicuous intercellular spaces and containing chloroplasts.
sporangium (pl. **sporangia**) A hollow structure (unicellular or multicellular) in which spores develop.
spore A reproductive cell, resulting from meiosis, from which, through mitoses, a haploid (1*n*) *gametophyte* develops.
sporophyll A leaf or leaf-like organ that bears sporangia.
sporophyte The diploid (2*n*) phase which produces spores in a life cycle characterized by an *alternation of generations*.
sporopollenin The substance composing the outer wall, or exine, of pollen grains and spores; a cyclic alcohol highly resistant to decay.
spring wood See *early wood*.
stamen Floral organ which produces the pollen and is usually composed of anther and filament. Collectively the stamens constitute the *androecium*.
staminate Of a flower, having stamens but lacking functional carpels.
starch An insoluble carbohydrate, the chief food storage substance of plants, composed of numerous glucose units.
stele A morphologic unit of the plant axis (stems and roots) comprising the primary vascular system and associated ground tissue (pericycle, interfascicular regions, and, in some concepts, the pith).
stellate Star-shaped.
stigma The region of the carpel, usually at the apex of the style, that serves as a surface upon which the pollen germinates.
stock See *graft*.
stoma (pl. **stomata**) An opening in the epidermis of leaves and stems bordered by two guard cells and functioning in gas exchange. Also called *stomate*.
stomatal apparatus See *stomatal complex*.
stomatal complex Stoma and associated epidermal cells (*subsidiary cells*) that may be ontogenetically and/or physiologically related to the guard cells. Also called *stomatal apparatus*.
stomatal crypt A depression in a leaf, the epidermis of which bears one or more stomata.
stomate See *stoma*.
stomium A fissure or pore in an anther lobe through which pollen is released. Its formation is a type of dehiscence.
stone cell See *brachysclereid*.
storied cambium Vascular cambium in which the fusiform and ray initials are arranged in horizontal rows as seen in tangential sections. Also called *stratified cambium*.
storied wood Wood in which the axial cells and rays are arranged in horizontal rows as seen in tangential section. In some taxa, the rays alone may be storied. Also called *stratified wood*.
Strasburger cells Marginal ray cells in the secondary phloem of conifers that have a function similar to that of companion cells in angiosperms, but which typically are not related developmentally to the sieve cells.
stratified cambium See *storied cambium*.
stratified wood See *storied wood*.
striate venation See *parallel venation*.
strobilus An axis bearing numerous sporophylls or ovule-bearing structures (scale-like in conifers); characteristic of gymnosperms, lycophytes, and sphenophytes.

stroma The ground substance of plastids.
style An extension of the ovary, usually columnar, through which the pollen tube grows.
suberin Fatty substance in the cell walls of cork (phellem) cells and in the Casparian band of endodermal and exodermal cells.
suberin lamella A thin layer of suberin deposited on the primary wall in cells of an endodermis or exodermis; may subsequently be covered by a cellulosic layer (secondary wall).
suberization Impregnation of the cell wall with suberin or deposition of a suberin lamella on a cell wall.
submarginal initials Meristematic cells beneath the protoderm along the margins of a developing leaf lamina that contribute cells to the interior tissue of the leaf.
subsidiary cell An epidermal cell associated with a stoma, sometimes developmentally related to the guard cells, and usually morphologically distinguishable from epidermal cells composing the groundmass of the tissue.
summer wood See *late wood*.
superior ovary See *hypogyny*.
suspensor An extension at the base of the embryo that anchors the embryo in the embryo sac and pushes it into the endosperm.
symbiosis A living in close association of two (or more) dissimilar organisms; included are parasitism in which the relationship is harmful to one of the organisms, and mutualism in which the relationship is beneficial to both.
symplast The living protoplasts of all cells in an organism, or a region of an organism, and the plasmodesmata by which they are connected.
symplastic growth Growth in which cells in a developing tissue grow in a coordinated manner and in which there is no intrusion of some cells between others or slippage between contiguous cells.
symplastic loading The transfer of photosynthate into companion cells and sieve tube members through plasmodesmata.
sympodium A vascular bundle of the stem and the associated leaf traces.
syncarpy A condition in a flower characterized by a fusion of carpels.
syndetocheilic Stomatal type of gymnosperms in which the subsidiary cells or their precursors are derived from the same protodermal cell as the guard cell mother cell.
synergids Two cells in the micropylar end of the embryo sac associated with the egg cell in angiosperms.
syngamy The process by which two haploid cells (gametes) fuse forming a zygote; fertilization.

tangential section A longitudinal section cut at right angles to a radius of a cylindrical structure such as a stem or root. A tangential section of secondary wood or secondary phloem is cut at right angles to the rays.
tannins A heterogeneous group of phenol derivatives; amorphous, strongly astringent substances widely distributed in plants, and used in tanning, dyeing, and preparation of ink.
tapetum A layer of cells in an anther lining the locule and absorbed as the pollen grains mature. In the ovule, an integumentary epidermis next to the embryo sac. Also called *endothelium*.
tap root The first or primary root of a plant; a continuation of the radicle of the embryo.

tap root system A root system based on the tap root which may have branches of various orders.

taxon (pl. **taxa**) Any one of the categories (species, genus, family, etc.) into which living organisms are classified.

telome One of the distal branches of a dichotomously branched axis in a primitive vascular plant.

telome theory A theory that regards the telomes as basic units from which the diverse types of leaves and sporophylls of a vascular plant have evolved.

template A pattern or mold guiding the formation of a negative or a complement. A term applied in biology to DNA duplication.

tension wood Reaction wood in dicotyledons, formed on the upper sides of branches and leaning or crooked stems; characterized by lack of lignification and often by high content of gelatinous fibers. See also *compression wood* and *reaction wood*.

tepal A member of a floral perianth that is not differentiated into calyx and corolla.

terminal apotracheal parenchyma See *boundary apotracheal parenchyma*.

testa The seed coat.

tetrarch The primary xylem of the root with four protoxylem strands (or poles).

thylakoids Sac-like membranous structures (cisternae) in a chloroplast combined into stacks (grana) and present singly in the stroma as interconnections between grana.

tissue A group of cells organized into a structural and functional unit. Component cells may be alike (simple tissue) or diverse (complex tissue).

tissue system A tissue or tissues in a plant or plant organ structurally and functionally organized into a unit. Commonly three tissue systems are recognized: *dermal*, *vascular*, and *fundamental* (ground tissue system).

tonoplast The cytoplasmic membrane (a unit membrane) bounding the vacuole. Also called the *vacuolar membrane*.

torus (pl. **tori**) The central, thickened part of the pit membrane in a bordered pit; consists of middle lamella and two primary walls. Typical of bordered pits in conifers and some other gymnosperms.

trabecula (pl. **trabeculae**) A rod-like extension of cell wall material across the lumen of a cell.

tracheary element A water-conducting cell, tracheid, or vessel member.

tracheid An elongate tracheary element of the xylem with tapered or rounded ends, and having no perforations, as contrasted with a vessel member; may occur in primary and in secondary xylem.

trafficking The intra-cell movement of cytoplasmic organelles such as mitochondria and Golgi bodies.

transection See *transverse section*.

transfer cell A parenchyma cell with wall ingrowths that increase the surface of the plasmalemma which lines the wall surface. Specialized for short-distance, apoplastic transfer of solutes.

transfusion tissue In gymnosperm leaves, a tissue surrounding or otherwise associated with the vascular bundle (or bundles), and composed of short tracheid-like cells and parenchyma.

transition region A region in the plant axis where root and shoot are united and which shows primary structural characteristics transitional between those of stem and root.

transitional tissue regions Term applied to regions of tissue between the apical meristem and mature tissues such as protoderm, ground meristem, and provascular tissues, tissue regions in which cell division continues in the more distal regions and growth and differentiation take place more proximally.

transmitting tissue The tissue in the style of a flower through which the pollen tube grows.

transverse section A section cut perpendicular to the longitudinal axis of a cell or plant part. Also called a cross-section or *transection*.

traumatic resin duct A resin duct that develops in response to injury.

triarch Primary xylem of a root with three protoxylem strands (or poles).

trichoblast A cell in the root epidermis that gives rise to a root hair.

trichome An outgrowth from the epidermis. Trichomes vary in size and complexity and include hairs, scales, and other structures; may be glandular.

trichosclereid A type of branched sclereid, usually with hair-like branches extending into intercellular spaces.

trilacunar node A node characterized by three leaf traces that supply a single leaf. Typically associated with each leaf trace, and through which each leaf trace passes, is a parenchymatous region in the first-formed increment of secondary xylem, called a *lacuna*.

triple fusion In most angiosperms, the fusion of one of the two sperm nuclei with the two polar nuclei forming the triploid ($3n$) primary endosperm nucleus.

tropism Movement or growth in response to an external stimulus; the direction of the movement or growth is determined by the direction from which the stimulus comes.

tube cell The cell in a pollen grain of some gymnosperms from which the pollen tube develops.

tunica Peripheral layer or layers of an apical meristem of a shoot, the cells of which divide anticlinally and thus contribute to the growth in surface of the meristem. Forms a mantle over the *corpus*.

tunica–corpus concept A concept of the organization of the apical meristem of the shoot under which it is differentiated into two regions distinguished by their methods of growth: the peripheral tunica, one or more layers of cells showing surface growth (anticlinal divisions); the interior, corpus, a mass of cells showing growth in volume (divisions in various planes).

two-trace unilacunar node A node characterized by two traces that supply a single leaf. Typically the pair of traces traverses a single *lacuna*.

tylose (pl. **tyloses**) An outgrowth from a parenchyma cell of the xylem (axial parenchyma or a ray cell) which extends through a pit-pair into the cavity of a tracheid or vessel member partially blocking, or with other tyloses, completely blocking, the lumen of the tracheary element.

undifferentiated In ontogeny, still in a meristematic state or resembling meristematic tissues or structures; In a mature state, relatively unspecialized.

unifacial leaf A leaf having a similar structure on both sides. Conceived ontogenetically, a leaf that develops from a growth center abaxial or adaxial to the initial leaf primordium apex and which thus includes tissues only from the abaxial or adaxial side of the primordium. The validity of the ontogenetic concept is questionable. Compare with *bifacial leaf*.

unilacunar node A node characterized by one leaf trace that supplies a leaf. Typically associated with the leaf trace, and through which it passes, is a parenchymatous region in the first-formed increment of secondary vascular tissues called a *lacuna*.
uniseriate ray In secondary vascular tissues, a ray one cell wide.
unisexual Of a flower, lacking either stamens or carpels; a perianth may be present or absent.
unit membrane A three-layered membrane consisting of a light layer of lipid between two dark layers of protein.
upright ray cell In secondary vascular tissues, a ray cell, the long axis of which is parallel to the axis of the stem or root.

vacuolar membrane See *tonoplast*.
vacuolation The development of *vacuoles* in a cell.
vacuole Cavity within the cytoplasm filled with a watery fluid, the cell sap, and bound by a unit membrane, the tonoplast; a component of the lysosomal compartment of the cell.
vacuome Collective term for all of the vacuoles in a cell, tissue, or plant.
vascular Consisting of or giving rise to conducting tissues, e.g., xylem, phloem, vascular cambium.
vascular bundle A strand of vascular tissue (usually primary xylem and phloem).
vascular cambium A lateral meristem from which secondary xylem and secondary phloem are produced in the stem and root. Periclinal divisions in cambial initials produce cells, some of which differentiate into phloem cells, others of which differentiate into xylem cells.
vascular rays Radially arranged sheets of (usually) parenchyma cells that extend through the secondary xylem and the secondary phloem, and are produced by the vascular cambium.
vascular system All of the vascular tissues in an organ or a plant.
vascular tissue A general term referring to either or both vascular tissues, xylem and phloem.
vasicentric paratracheal parenchyma Axial parenchyma in the secondary xylem which forms sheaths around vessels. See also *paratracheal parenchyma*.
vein A vascular bundle that comprises part of the vascular system of a leaf.
velamen A multiple epidermis covering the aerial roots of some tropical epiphytic orchids and aroids; also occurs in some terrestrial roots.
venation The arrangement of veins in the leaf blade.
vessel A superposed series of vessel members forming a tube.
vessel element See *vessel member*.
vessel member A non-living, conducting cell of the xylem characterized by perforations in the contiguous end walls of superposed cells that form a vessel. Vessel members function in the transport of water and minerals through the primary and secondary xylem of angiosperms.
vestured pit A bordered pit with wall projections from the inner surfaces of the overhanging borders.

wall See *cell wall*.
wall loosening An enzymatic process, controlled by the enzyme, expansin, that allows wall expansion during cell growth by uncoupling the molecular strands comprising the polysaccharide network of the wall.
water vesicle An enlarged, highly vacuolate epidermal cell; a *trichome* in which water is stored.

whorl Leaves or flower parts arranged in a circle on an axis.
wood Secondary xylem.
wound cork See *wound periderm*.
wound periderm Periderm formed in response to injury. Also called *wound cork*.

xeromorphic Having the structural features typical of xerophytes.
xerophyte A plant adapted to a dry habitat.
xylem A complex tissue of parenchyma and tracheary elements that functions in the longitudinal transport of water and minerals. In secondary xylem, rays function in radial transport. The xylem is also a supporting tissue.
xylem elements Cells of the xylem tissue.
xylem initial A cambial cell on the xylem side of the cambial zone that is the source of one or more cells arising by periclinal divisions and differentiating into xylem elements either with or without additional divisions in various planes.
xylem ray The part of a vascular ray that is located in the secondary xylem.

zygomorphic Having an irregular flower form. Opposite of *actinomorphic*. See *bilateral symmetry*.
zygote The diploid ($2n$) cell that results from the fusion of male and female gametes.

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