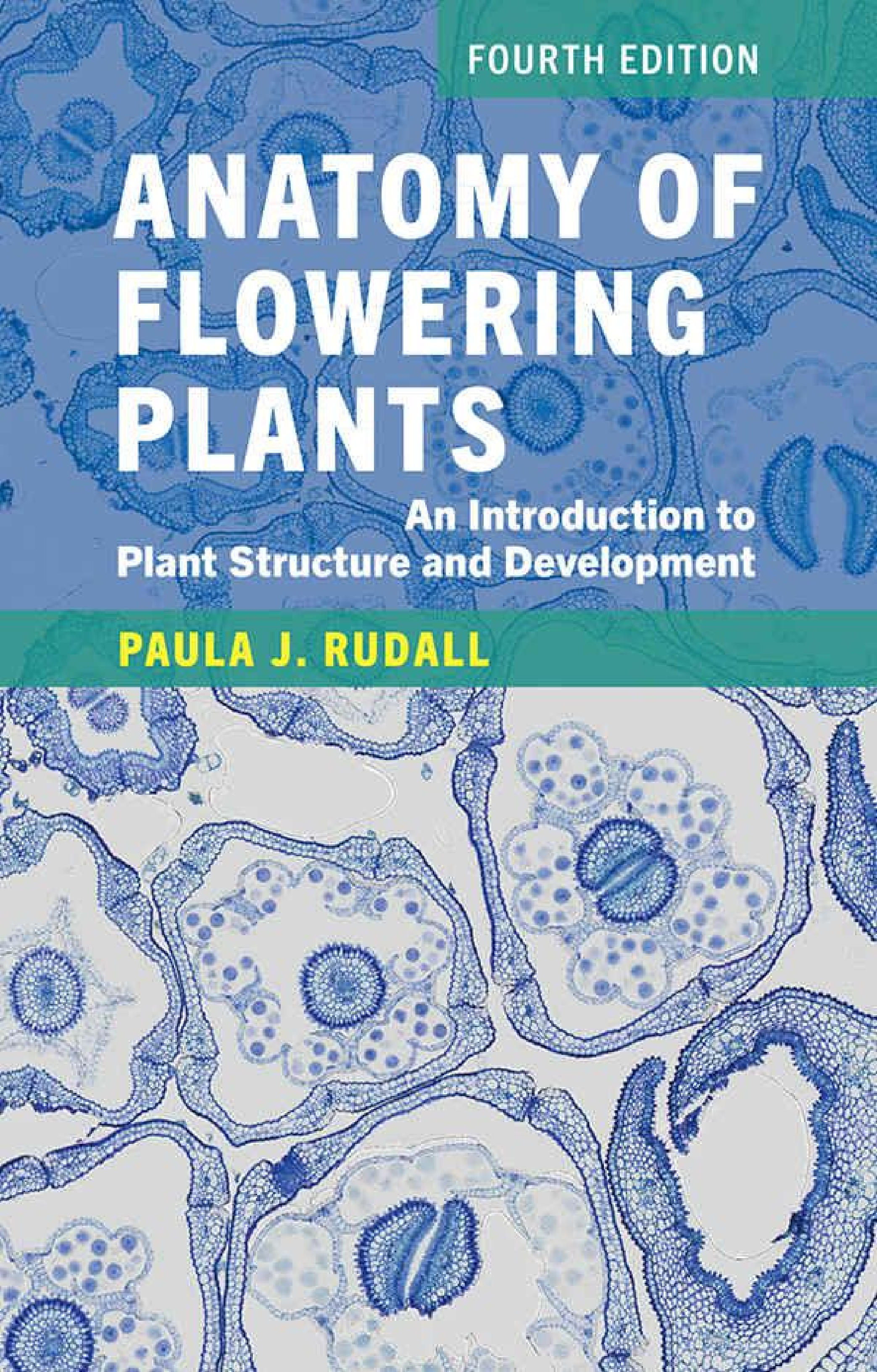

FOURTH EDITION

ANATOMY OF FLOWERING PLANTS

An Introduction to Plant Structure and Development

PAULA J. RUDALL

Anatomy of Flowering Plants

Fourth Edition

Understanding plant anatomy is not only fundamental to the study of plant systematics and palaeobotany but also an essential part of evolutionary biology, physiology, ecology and the rapidly expanding science of developmental genetics. This modernized new edition covers all aspects of comparative plant structure and development, arranged in a series of chapters on the stem, root, leaf, flower, pollen, seed and fruit. Internal structures are described using magnification aids from the simple hand lens to the electron microscope. Numerous references to recent topical literature are included, and new illustrations reflect a wide range of flowering plant species. The phylogenetic context of plant names has been updated as a result of improved understanding of the relationships among flowering plants. This clearly written text is ideal for students studying a wide range of courses in botany and plant science, and is also an excellent resource for professional and amateur horticulturists.

Paula J. Rudall is Research Professor at the Royal Botanic Gardens, Kew, UK, and an international authority on the evolution of plant form. Her research interests range from the organization of flowers and the patterning of petal surfaces to the intricate structure and development of the stomatal pores on the surfaces of leaves. Her numerous professional awards include the Dahlgren Prize, the Linnean Society Gold Medal and election as Foreign Member of both the Botanical Society of America and the American Society of Plant Taxonomists. In addition to several books, she has authored over 300 peer-reviewed papers.

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This book is dedicated to my friend and early mentor,
Dennis W. Stevenson

Contents

Preface

Plant anatomy is concerned with the structural organization of plants and the arrangements of their organs, cells and tissues. The study of comparative plant anatomy remains highly relevant to the traditional fields of systematics and palaeobotany and also to the relatively new field of developmental genetics (including evolutionary developmental genetics: evo-devo), which utilizes a combination of techniques to examine gene expression in growing tissues[23, 83]. Modern students can incorporate information from an increasingly wide range of sources, most notably integrating morphological and molecular data. The new edition of this book presents an introduction to plant anatomy for students of botany and related disciplines.

Plant anatomy is today explored using a broad range of techniques, from the compound microscope to high-resolution X-ray computed tomography (HRCT). Although the simple optical lens has been used for centuries to examine plant structure, detailed studies of plant anatomy originated with the invention of the compound microscope in the seventeenth century. Nehemiah Grew (1641–1712) and Marcello Malpighi (1628–1694), physicians working independently in England and Italy respectively, were early pioneers of the microscopical examination of plant cells and tissues. Their prescient work formed the foundation that eventually led to the development of our understanding of cell structure and cell division[30]. Other outstanding early figures included Robert Brown (1773–1858), who discovered the nucleus, and the plant embryologist Wilhelm Hofmeister

(1824–1877), who first described the alternation of generations in the life cycle of land plants. During the nineteenth and twentieth centuries, plant anatomy became an important element of studies of both physiology and systematic biology, and an integral aspect of research in the developing field of anatomical palaeobotany, led by such luminaries as Dukinfield Henry Scott (1854–1934). The physiologist Gottlieb Haberlandt (1854–1945) utilized anatomical observations in his groundbreaking work on photosynthetic carbon metabolism. Notable plant anatomists of the twentieth century included Agnes Arber (1879–1960), whose books included works on monocotyledons[4], and Katherine Esau (1898–1997), recognized particularly for her work on the structure and development of phloem and her influential textbooks on plant anatomy[37]. Other important botany textbooks include works on anatomy[28, 40, 41], embryology[26, 82], morphology[44] and palaeobotany[44, 84, 134].

The invention of the transmission electron microscope (TEM) in the mid- twentieth century allowed greater magnification than any optical microscope, and hence revitalized studies in cell ultrastructure[39] and pollen morphology[36, 125]. The subsequent development of the scanning electron microscope (SEM) provided greater image clarity and much greater depth of focus than light microscopes when examining surface structure, and thus further increased accessibility of minute structures, including seeds, pollen grains and organ primordia. More recent innovations, including fluorescence microscopy, differential interference contrast (DIC) microscopy and confocal imaging, have allowed enhanced visualization of tissue structure. Others, including HRCT and nuclear magnetic resonance (NMR) imaging, facilitate enhanced visualization of three-dimensional objects. The most effective studies employ more than one of the techniques available today.

To study plant evolution using comparative data, an understanding of taxonomy is essential. Throughout this book, species are assigned to families according to a modern understanding of their classification. In textbooks published before 1990, extant angiosperms were consistently subdivided into two major groups – dicotyledons (dicots) and monocotyledons (monocots), based partly on the number of cotyledons in the seedling. This dichotomy was long considered to represent a fundamental divergence at the base of the angiosperm evolutionary tree. However, the expansion of molecular phylogenetics through the 1990s demonstrated that some species that were formerly classified as primitive dicots do not belong to either category, though the monophyly of monocots was confirmed. Thus, although the dicot/monocot distinction remains useful for generalized descriptions of angiosperm groups, current evidence suggests that it does not represent an entirely natural classification. It is now widely accepted that several relatively species-poor angiosperm lineages (early divergent angiosperms) evolved before the divergence of the three major lineages that led to the magnoliids, monocots and the remaining dicots (now termed eudicots, or sometimes tricolpates).

Early divergent angiosperms are a small but highly diverse assemblage of taxonomically isolated lineages that probably represent the surviving extant members of their respective clades, accounting for only about one per cent of extant species[139]. They include the New Caledonian shrub *Amborella* and the water lilies (Nymphaeaceae). The magnoliids include woody families such as Magnoliaceae and Lauraceae and herbaceous or climbing families such as Piperaceae and Aristolochiaceae. Monocots account for approximately one quarter of all flowering plant species. They dominate significant parts of world ecosystems and are of immense economic importance, including the staple grass food crops (wheat, barley, rice and maize) and other important food plants such as onions, palms, yams, bananas and gingers. Eudicots represent about 75 per cent of extant angiosperm species and encompass a wide range of morphological diversity, especially in the two largest eudicot subclades, Rosidae (rosid eudicots) and Asteridae (asterid eudicots). Thus, understanding of this revised and updated phylogenetic context is essential for credible interpretation of phenotypic patterns.

1

Organs, cells and tissues

1.1 Organs

Plants are essentially modular organisms; each individual plant consists of distinct but connected organs. In their turn, the organs are composed of cells, which are mostly grouped into tissues. Vegetative organs support photosynthesis and plant growth, and reproductive organs enable sexual reproduction. In seed plants, the primary vegetative organs are the root, stem and leaf (Figure 1.1). Roots and stems have well-defined growing points at their apices, but the leaves are determinate lateral organs that stop growing when they reach a particular size and shape. When a seed germinates, the seed coat (testa) is ruptured and the embryonic structures emerge from opposite poles of the embryo: a seedling root (radicle) grows downwards from the root apex and a seedling axis (hypocotyl) bears the first leaves (cotyledons) and the shoot apex, which ultimately develops new foliage leaves.

1.2 Cells and cell walls

Plant cells consist of a living protoplast contained within a protein-rich plasma membrane, which is itself enclosed by a cell wall. During the cell-division cycle, cells undergo a series of phases that are broadly grouped as interphase, nuclear division (mitosis or meiosis) and cytokinesis (cleavage of the cytoplasm and cell-wall formation). During mitosis, nuclear division occurs first, followed by progressive deposition of membranes in the cytoplasm into a cell plate that is

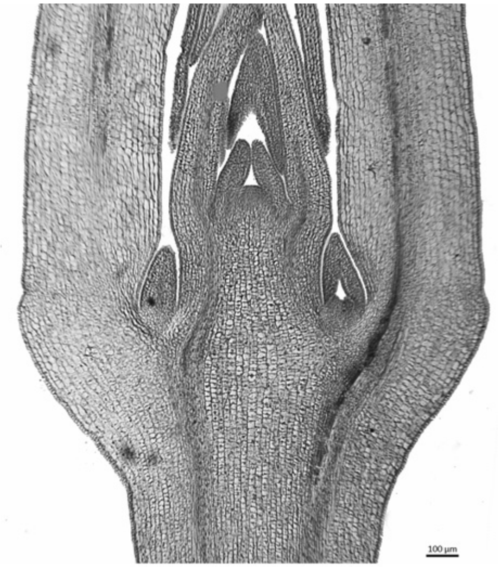

Figure 1.1 *Ligustrum vulgare* (eudicot: Oleaceae), longitudinal section of vegetative shoot apex. Scale = 100 µm

located in the equatorial zone between the two daughter nuclei[138]. The cell plate extends to join the cell wall, thus depositing a new wall.

The primary cell wall consists mostly of carbohydrates: microfibrils of cellulose and hemicelluloses embedded in a matrix of pectins (Figure 1.2). Cell walls of adjacent cells are linked together by a pectin-rich middle lamella[37, 39]. Following cell enlargement and elongation, a secondary cell wall is deposited on the inside surface of the primary wall. Secondary cell walls often appear layered and can contain deposits of complex organic polymers such as cutin, lignin and suberin. Cutin is the primary component of the plant cuticle, which covers the aerial epidermis (Section 1.8). Lignin provides strengthening and rigidity to sclerenchyma cells, especially in the secondary xylem, but also in fibres close to the vascular bundles in the stem and leaf. Suberin is a complex hydrophobic lipid that provides a protective water-resistant lipophilic barrier in periderm cells.

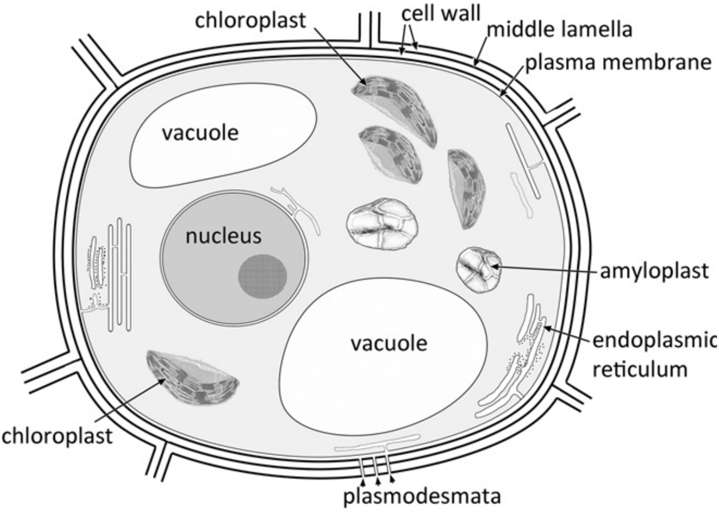

Figure 1.2 Diagram of a generalized plant cell

Primary pit fields are thin regions of the primary cell wall that correspond with similar regions in the walls of neighbouring cells. Pits have protoplasmic strands (plasmodesmata) passing through them, connecting the protoplasts of adjacent cells. The connected living protoplasts are collectively termed the symplast. Primary pit fields often persist as thin areas of the wall even after a secondary wall has been deposited. In simple pits, which occur on relatively non-specialized cells such as parenchyma, the pit cavity is of more or less uniform width. In bordered pits, which are present in tracheary elements, the secondary wall arches over the pit cavity so that the opening to the cavity is narrow and the outer rim of the primary pit field appears as a border around the pit opening when viewed through a light microscope[18].

1.3 Cytoplasm, plastids and photosynthesis

The living cell protoplast consists of cytoplasm that encloses a complex range of membrane-bound internal structures termed

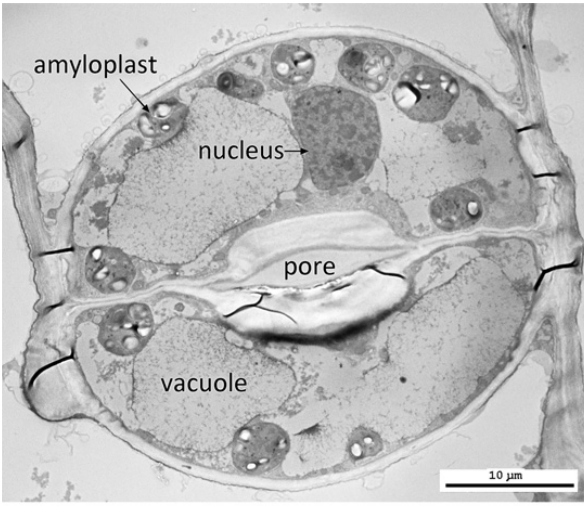

Figure 1.3 *Lapageria rosea* (monocot: Philesiaceae), stomatal pore and guard cells (TEM). Scale = 10 µm

organelles; they include mitochondria, the nucleus, plastids and vacuoles, as well as small particles termed ribosomes and sometimes inorganic contents such as oil, starch grains or crystals (Figure 1.3).

Most plant cells possess a single nucleus that is bounded by a pair of membranes; the outer membrane is continuous with the endoplasmic reticulum. At interphase, one or more nucleoli can sometimes be distinguished, together with the uncondensed chromatin within the nuclear sap. During nuclear division, the chromatin becomes condensed into chromosomes that bear the hereditary information. Vacuoles are membrane-bound structures that contain a watery sap; they can vary considerably in size and shape during the life history of a cell. They can accumulate storage products and soluble pigments such as anthocyanins.

Plastids are large cell organelles that develop from proplastids. They each contain their own genome, which is much smaller than the nuclear genome and normally heritable via the maternal parent. Each plastid is bounded by a pair of membranes, and many contain a system of membranes termed thylakoids. Plastids such as amyloplasts, chloroplasts and chromoplasts play specialized roles within the cell. Amyloplasts are the source of starch grain production. Chromoplasts contain carotenoid pigments that produce some of the colours found in some plant organs, such as flower petals. Mitochondria – the sites of respiration within the cell – are smaller than plastids; they also contain their own heritable genetic material and are enclosed within a double-membrane system. Both plastids and mitochondria originated via endosymbiotic events at an early unicellular stage in plant evolution[50].

Chloroplasts are highly specialized plastids containing green chlorophyll proteins that absorb energy from sunlight. During photosynthesis, plants convert light energy into chemical energy in energy-storage molecules such as adenosine triphosphate (ATP), which they use to make carbohydrates from carbon dioxide (CO_2) and water, releasing oxygen as a by-product. Chloroplasts occur in all green cells but are most abundant in the leaf mesophyll. In most plants, photosynthetic carbon reduction is achieved via a three-carbon compound (C_3 cycle), but some plants capture inorganic carbon more effectively using CO_2-concentrating mechanisms via a C_4 cycle or Crassulacean acid metabolism (CAM)[31]. Some C_4 plants possess a distinctive leaf anatomy, termed Kranz anatomy (Section 4.9).

1.4 Inorganic cell inclusions

Many cells possess non-protoplasmic contents such as mucilage, oils, tannins, starch granules, calcium oxalate crystals and silica bodies. Both oil and mucilage are produced in isolated specialized secretory cells (idioblasts). Tannins are phenol derivatives that are widely distributed in plant cells; they are amorphous and appear yellow, red or brown in cells of sectioned material due to oxidation.

Starch is also widespread in plant tissues but especially common in storage tissues such as endosperm or in parenchyma adjacent to a nectary. Starch granules are formed in specialized plastids

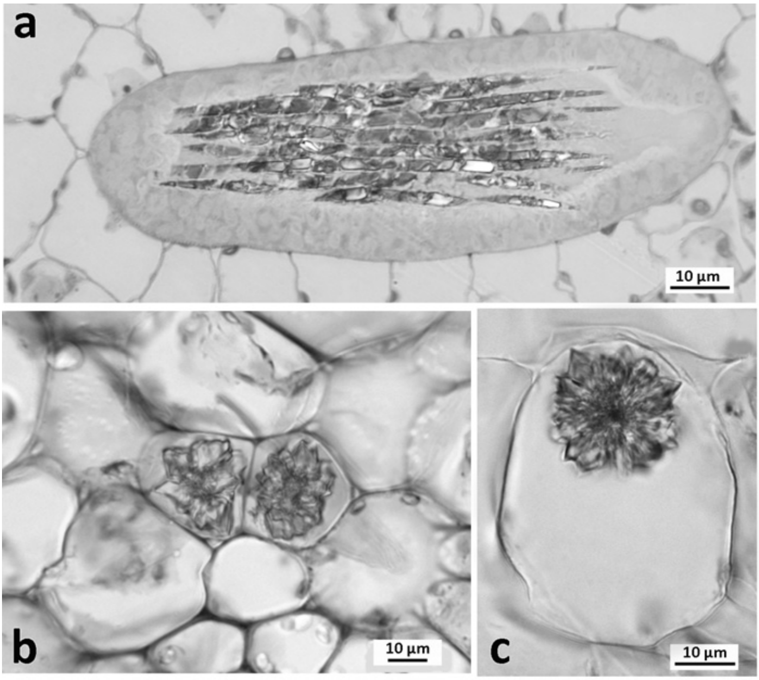

Figure 1.4 Idioblastic cells containing crystals of calcium oxalate. (a) *Dioscorea sosa* (monocot: Dioscoreaceae), raphide crystals in a mucilage sheath. (b) *Cissus rhombifolia* (eudicot: Vitaceae), druse (cluster crystal). (c) *Atriplex hymenelytra* (eudicot: Amaranthaceae), druse. Scale = 10 µm

(amyloplasts). They often appear layered due to the successive deposition of concentric rings and possess characteristic shapes. The unusual and specialized starch grains present in laticifers in some species of *Euphorbia* possess highly characteristic elongated rod- or bone-like shapes compared with the more rounded starch grains of neighbouring parenchyma cells[85].

Calcium oxalate crystals (Figure 1.4) occur within crystal idioblasts; they can be distributed in almost every part of both vegetative and reproductive organs and are often located near veins, possibly reflecting transport of calcium through the xylem. They form within the vacuoles of actively growing cells and are usually associated with membrane chambers, lamellae, mucilage and fibrillar material. Contrasting crystal shapes can be highly characteristic of different plant families; for example, styloid crystals characterize the *Iris* family (Iridaceae). Common crystal types include solitary needle-like or rhomboidal crystals (styloids), bundles of needle-like crystals borne together in the same cell (raphides), aggregate crystalline structures that have precipitated around a nucleation site (druses) and numerous fine particles of crystal sand. In some woody eudicot species, crystals occur in the secondary phloem or secondary xylem; for example, crystal cells are common in the ray parenchyma of some woods (Chapter 2). Cystoliths are calcareous bodies that are mostly located in leaf epidermal cells (Figure 4.4).

Most plants deposit silica in at least some of their tissues[101]. Some species accumulate silica in large quantities and deposit it as discrete bodies of solid silicon dioxide in the lumina of specific plant cells. Opaline silica bodies, commonly termed 'phytoliths', are

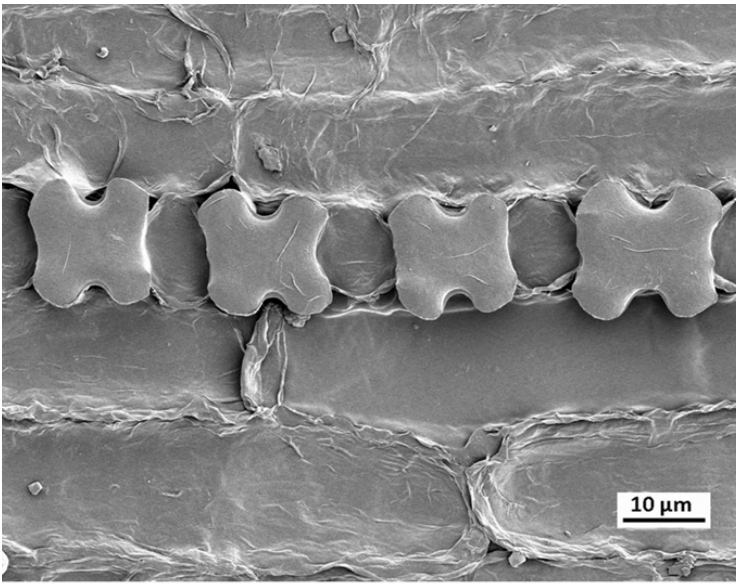

Figure 1.5 *Oryza sativa*, rice (monocot: Poaceae), H-shaped silica bodies (phytoliths) in a leaf epidermis (SEM). Scale = 10 µm

a characteristic feature of some flowering plant groups. These groups include several commelinid monocots, notably the grass family Poaceae[118], in which silica bodies are almost exclusively restricted to the epidermis, and the palm family Arecaeae, in which they are primarily restricted to the vascular bundle sheath cells. Grass phytoliths occur in various shapes that can characterize different species, so they can have immense significance as diagnostic markers in studies of grassland palaeoecology (Figure 1.5). Silica bodies are often associated with sclerenchyma. In some woody eudicot species they can occur in the secondary xylem.

1.5 Meristems

Meristems are the growing points of the plant. They represent localized regions of thin-walled, tightly packed living cells that undergo frequent mitoses and often continue to divide indefinitely. Most of the plant body is differentiated at the meristems, though cells in other regions may also occasionally divide.

Apical meristems are located at the shoot apex (Figures 1.1, 2.1), where the primary stem, leaves and flowers differentiate, and at the root apex (Figures 3.1, 3.2), where primary root tissue is produced. In flowering plants, the shoot and root apical meristems are highly organized but differ from each other in many respects. Both shoot and root apical meristems contribute to extension growth and are self-renewing. The shoot apical meristem also initiates lateral organs (leaves) at its flanks in a regular nodal arrangement, each node bearing a single leaf, a pair of leaves or a whorl of leaves. Subsequent elongation of the shoot axis occurs at the stem internodes, either by diffuse cell divisions and growth throughout the youngest internodes (uninterrupted meristem) or in a restricted region, often at the base of the internode (intercalary meristem). Both intercalary and uninterrupted meristems represent growth in regions of differentiated tissues.

Lateral meristems are important for stem thickening growth; they include vascular cambium and the primary and secondary thickening meristems (Chapter 2). Lateral meristems occur in localized regions parallel to the long axis of a shoot or root, most commonly in the pericyclic zone, at the junction between vascular tissue and cortex. The phellogen (cork cambium) is a lateral meristem that occurs in the stem or root cortex, where it forms a protective corky layer (Figure 2.10); a phellogen can also develop in the region of a wound or at the point of leaf abscission.

Meristemoids are isolated and densely protoplasmic cells that reactivate embryonic activity to allow tissue differentiation. Typically, a meristemoid either itself undergoes unequal (asymmetric) cell division or is the smaller daughter cell that results from an asymmetric division[16] (Figure 1.6). Asymmetric divisions are caused by cell polarization resulting from organized arrangements of actin filaments in the dense cytoplasm during cell plate alignment[49]. Examples of asymmetric cell divisions include

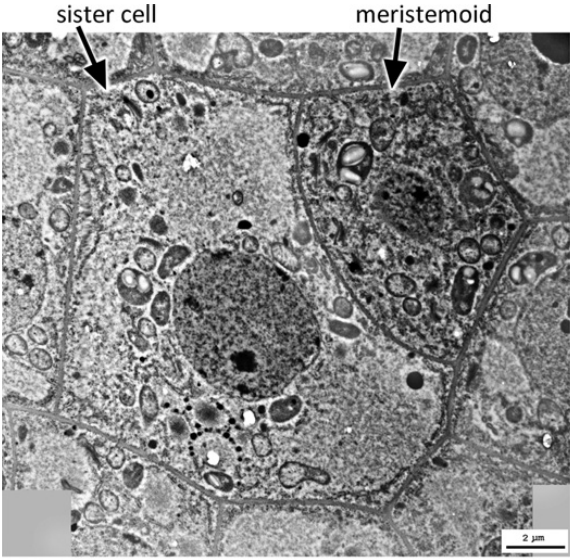

Figure 1.6 *Amborella trichopoda* (ANA-grade: Amborellaceae), developing leaf epidermis, highlighting a pair of cells that have recently undergone asymmetric mitosis to form a dense meristemoid and its larger sister cell (TEM). The meristemoid will form a guard-mother cell and will ultimately divide symmetrically to form a pair of guard cells. Scale = 2 µm

formation of a root hair initial (trichoblast), microspore division into a larger vegetative cell and smaller generative cell, a protophloem mitosis to form a larger sieve tube element and smaller companion cell, and division of a protodermal cell into two cells of unequal sizes, the smaller of which is the guard-mother cell, a meristemoid that will divide symmetrically to form the paired guard cells of a stoma.

Other types of localized meristems occur in some species, in which differentiated plant cells can become de-differentiated and meristematic. One example of such cell-fate plasticity includes localized meristems that occur on the leaf margins of some succulent Crassulaceae; these meristematic cells can give rise to entire plantlets[131]. Plants can also regenerate tissues and organs at the site of a wound by cellular proliferation on callus tissue, a process that is regulated by the plant hormones auxin and cytokinin. Callus cells formed from roots and from some aerial organs resemble the apices of lateral roots derived from the pericycle[81, 137]. Isolated callus tissue can be used in laboratory conditions to artificially grow a new plant using tissue culture methods.

1.6 Cell growth and expansion

Cells develop and expand in different ways depending partly on their location and surrounding tissue and partly on their cell-wall properties. Those in close contact with each other are initially glued together by a pectin-rich middle lamella and hence have a mutual influence on shape during early expansion. Parenchyma cells, which are largely thin walled and isodiametric, typically expand relatively evenly. Different rates of expansion of adjacent cells can result in the formation of lobes and intracellular air spaces, as in the spongy mesophyll of the leaf[5]. Adjacent tissues can also expand at different rates; for example, leaf epidermal cells continue to enlarge after the subepidermal mesophyll cells have ceased growth, influencing development of a substomatal cavity and anticlinal cell-wall undulations in abaxial epidermal cells. Epidermal cells, which

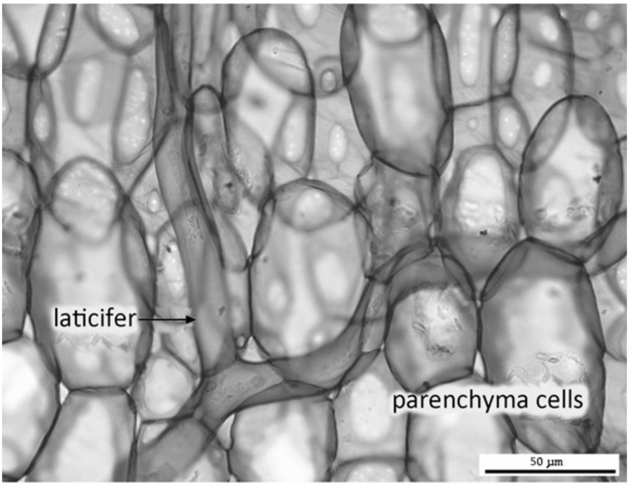

Figure 1.7 *Euphorbia eyassiana* (eudicot: Euphorbiaceae), longitudinal section of stem showing branched non-articulated laticifer. Scale = 50 µm

require additional strength in their protective role, display differential growth between their anticlinal and periclinal walls[64, 78, 126].

Some specialized cells are capable of apical intrusive growth (tip growth) that allows them to separate the middle lamella between adjacent cell walls and intrude between them, prior to the onset of cell-wall thickening[66, 94]. Fibres, which collectively confer tensile strength to tissues such as secondary xylem, extend axially at both ends by apical intrusive growth. Similarly, non-articulated laticifers (e.g. in *Euphorbia*) branch and ramify throughout the plant by apical growth (Figure 1.7). Other specialized cells capable of apical intrusive growth include root hairs, pollen tubes and star-shaped astrosclereids.

1.7 Tissues

Simple tissues, such as parenchyma, collenchyma and sclerenchyma, consist of regions of similar individual cells, often interspersed with isolated specialized cells (idioblasts[43]) and secretory cells or canals. The bulk of the primary plant body (the ground tissue) consists of simple tissues. In contrast, complex tissues incorporate elements of several different simple cell and tissue types. Complex vascular tissues (phloem and xylem) can incorporate parenchyma, sclerenchyma and vascular cells. The epidermis is a dermal tissue that encloses the entire plant and is continuous between the various organs. Primary tissues are produced by an apical meristem, and secondary tissues are produced by lateral meristems such as the vascular cambium.

1.7.1 Parenchyma and other thin-walled cell types

The term parenchyma incorporates the relatively unspecialized cells that occur in both primary and secondary tissues of the plant body; it includes many cells with living contents that do not fit readily into other categories. Parenchyma cells are thin walled and often loosely packed together, leaving small air spaces between them where their walls are not in contact with each other. Individual parenchyma cells are polyhedral or amorphous, sometimes axially elongated or even lobed.

Chlorenchyma cells are green thin-walled cells that contain chloroplasts. In leaves (Chapter 4), chlorenchyma tissue is termed mesophyll. Mesophyll is often differentiated into two distinct zones: palisade mesophyll on the adaxial side of the lamina and spongy mesophyll on the abaxial side. Palisade mesophyll consists of rows of cells that are tightly packed together and anticlinally elongated; spongy mesophyll consists of cells of various shapes that are relatively loosely packed, with many intercellular air spaces.

Aerenchyma is a specialized parenchymatous tissue that characterizes many aquatic plants. It represents a regular, well-developed system of cells interspersed with considerably enlarged intercellular air spaces that facilitate internal diffusion of gases (Figure 1.8). Contrasting developmental patterns of aerenchyma exist in different species[38]. Lysigenous aerenchyma involves programmed cell death during development, leaving regular spaces (e.g. in the cortex of a maize root). In contrast, in schizogenous aerenchyma, which is relatively complex and more structured, the

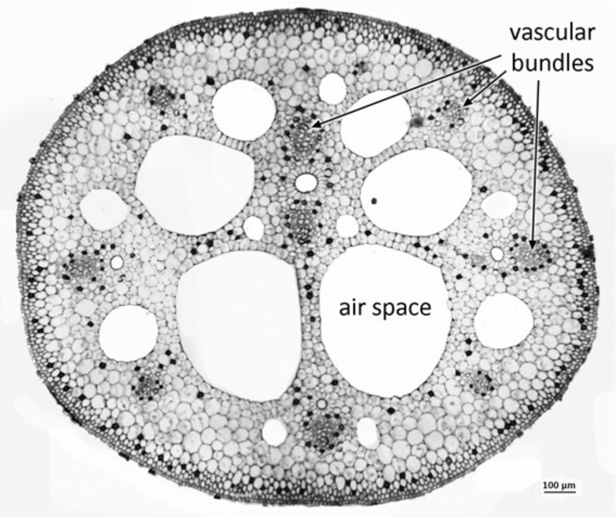

Figure 1.8 *Nymphaea miniata* (ANA-grade: Nymphaeaceae), transverse section of petiole showing aerenchyma. Scale = 100 µm

large air spaces are formed by differential growth of surrounding tissues. For example, in leaves, stems and roots of some aquatic plants (e.g. *Hydrocharis*), schizogenous aerenchyma is associated with a system of transverse septa or diaphragms that provide mechanical resistance to compression.

Transfer cells are specialized plant cells that facilitate transfer of soluble substances across tissue boundaries. They typically possess cell-wall ingrowths protruding into their protoplasts, thus increasing their surface area. They occur in companion cells in phloem (especially at the node of a stem), in root nodules, in the haustoria of parasitic plants and in the epidermis of water plants[98].

1.7.2 Thick-walled tissues: collenchyma and sclerenchyma

Collenchyma is a strengthening tissue that consists of groups of axially elongated, tightly packed cells with unevenly thickened walls. Collenchyma tissue typically occurs as primary ground tissue, often located in the angles of young stems, or in the leaf midrib or petiole. Collenchyma cells differ from fibres in that they often retain their living protoplasts and their cell walls are relatively unlignified, though they may ultimately become lignified as the tissue ages.

Sclerenchyma cells lack contents at maturity and possess evenly thickened walls that are usually lignified, with simple pits that are often slit-like. Sclerenchyma occurs in both primary and secondary tissues, either in groups or individually as idioblasts interspersed in other tissue types. Fibres are long, narrow sclerenchyma cells that are elongated along the long axis of the organ and possess tapering ends. Fibres generally occur in groups, often located at the phloem poles of vascular bundles (Figures 2.2, 2.3, 2.6). The bulk of the secondary xylem (wood) in woody eudicots consists of fibres that confer considerable tensile strength. Bast fibres are formed in the secondary phloem and cortex in some species; they are used to make textiles or rope in species such as flax (*Linum*) and hemp (*Cannabis*). Gelatinous fibres are formed in the secondary xylem or sometimes in the bark of some woody plants; they are typically formed in response to stress caused by asymmetric branch thickening (compression wood or tension wood). In gelatinous fibres, the inner secondary wall is non-lignified and rich in polysaccharides, making it more flexible[39].

Sclereids (stone cells) are variously shaped cells that develop thick secondary walls as the plant matures; they can occur throughout the plant, either as isolated cells (idioblasts) or in groups (e.g. groups of stone cells in the fruit endocarp of peach). Brachysclereids are isolated isodiametric cells dispersed among parenchyma. Astrosclereids develop projections that grow intrusively into adjacent intercellular air spaces or along middle lamellae during the growth phase of the organ, prior to cell-wall thickening. The shapes of astrosclereids are dictated by the cellular arrangement of surrounding tissues; they are often star-shaped (Figure 1.9), though sclereids located in palisade mesophyll can be bone-shaped (osteosclereids).

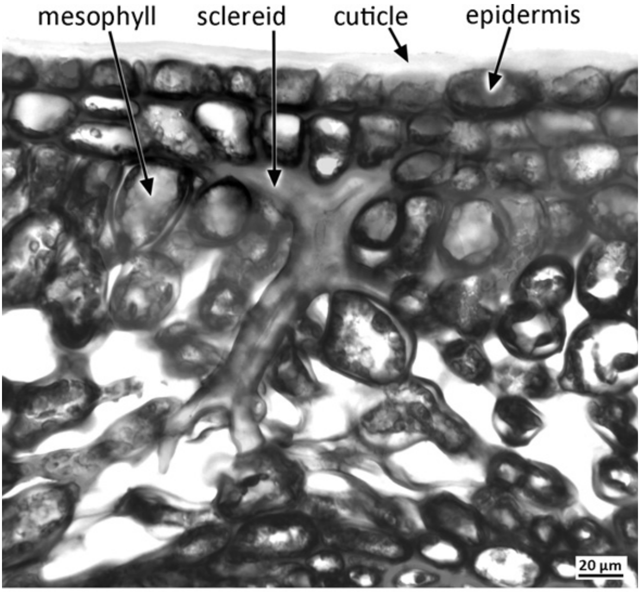

Figure 1.9 *Camellia japonica* (eudicot: Theaceae), transverse section of leaf midrib with branched sclereid. Scale = 20 µm

1.8 Epidermis

The outermost (dermal) cell layer, the epidermis, covers the entire plant surface; in the root it is sometimes termed rhizodermis. The aerial epidermis is covered with a hydrophobic cuticle layer that consists primarily of a complex polymer, cutin, which forms a protective barrier to water and CO_2 and also prevents adhesion between cells of adjacent organs in tightly packed structures such as the bud. The cuticle permeates the outermost cell wall and also forms an outer skin of varying thickness, often associated with epicuticular waxes[70] (Figure 4.7). The cuticle can be striated or variously ornamented.

The epidermis is a primary tissue that is initially derived from the protodermal cells of the apical meristem. In developing organs, both anticlinal divisions and cell elongation extend the epidermis to accommodate organ elongation and even some organ thickening. The epidermis is usually uniseriate, with rare exceptions: a few species (e.g. *Ficus elastica*) develop a multiseriate epidermis in their leaves, and the aerial roots of many orchids possess a specialized multiseriate epidermis termed velamen. The epidermis generally persists throughout the life of the plant except in regions of lateral thickening growth, where it is often replaced by a periderm. In older roots, it is sometimes worn away by friction with the soil, and the root is subsequently protected by an exodermis formed by cell-wall thickening in the outer cortical layers.

The epidermis can develop various specialized cell types. For example, in leaves, relatively undifferentiated pavement epidermal cells are interspersed with several specialized cell types, including stomata and trichomes.

1.9 Stomata

Stomata are specialized pores in the epidermis through which gaseous exchange (water release and CO_2 uptake) takes place. They occur not only on most aerial plant surfaces, especially on green photosynthetic stems and leaves, but also on some floral organs. Each stoma consists of two guard cells surrounding a central pore (Figures 1.10, 1.11). Guard cells are either kidney-shaped (in most plants) or dumbbell-shaped (in grasses, sedges and allied families); their inflation by increased osmotic potential results in opening of the pore, and their deflation causes its closure. Cuticular ridges extending over or under the pore from the outer or inner edges of the guard-cell walls help to seal the closed pore. In contrast with most epidermal cells, guard cells typically contain plastids that function as both chloroplasts and amyloplasts; these specialized plastids are smaller than those of mesophyll cells and contain photoreceptors that help to control stomatal opening[80, 122].

Epidermal cells adjacent to the guard cells are termed subsidiary cells if their shape differs from that of other pavement epidermal cells; they can be either lateral or polar with respect to

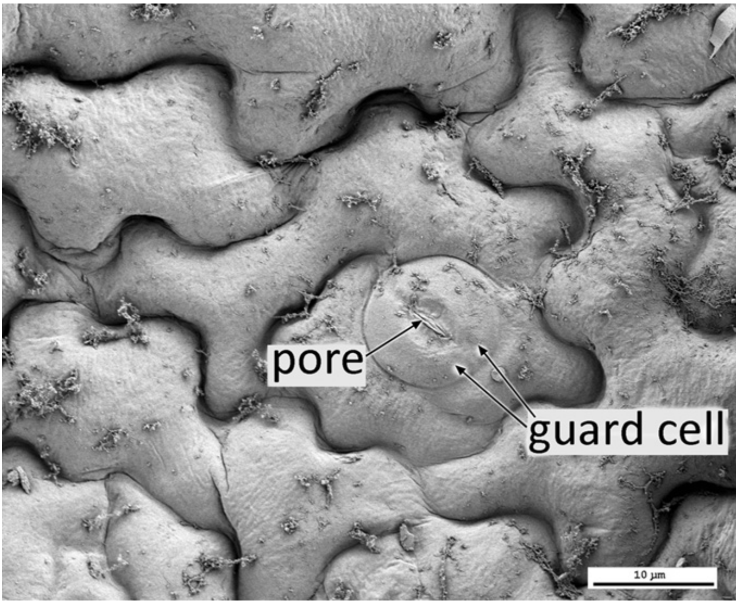

Figure 1.10 *Arabidopsis thaliana* (eudicot: Brassicaceae), abaxial leaf surface, showing a single stomatal pore (SEM). Scale = 10 µm

the guard cells. Specialized lateral subsidiary cells (e.g. in grasses and palms) can supply the guard cells with solutes that help to drive diurnal stomatal opening and closure[90].

Classifications of stomatal types are based either on the presence and arrangement of mature subsidiary cells or on their patterns of development[99, 116, 156]. Types of mature stomata include anomocytic (lacking subsidiary cells) and paracytic (possessing one or more pairs of lateral subsidiary cells oriented parallel with the guard cells). Lateral subsidiary cells of different species – though apparently similar – can have different developmental origins; mesogene lateral subsidiary cells are derived from the same cell lineage as the guard-mother cell, whereas perigene lateral subsidiary cells are derived from an adjacent cell lineage[99, 116]. During development of the leaf epidermis in many eudicots (e.g. *Arabidopsis*), an iterative

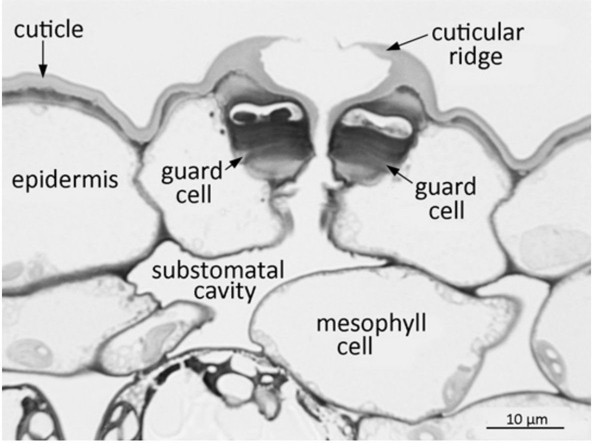

Figure 1.11 *Amborella trichopoda* (ANA-grade: Amborellaceae), transverse section of leaf epidermis through a stomatal pore. Scale = 10 µm

series of asymmetric divisions (amplifying divisions) results in a spiral arrangement of mesogene epidermal cells with a stomatal pore at the centre; the entire complex of cells is derived from the same initial cell and hence is monoclonal[92, 117].

1.10 Trichomes and papillae

Epidermal outgrowths include papillae, trichomes (hairs) and specialized domed cells that characterize many petal surfaces. Papillae are small unicellular outgrowths from a single epidermal cell; some leaf surfaces possess multiple papillae per cell. Trichomes can occur on all parts of the plant surface; they vary widely in both form and function, partly depending on their location in the plant. Trichomes (Figure 1.12) can be unicellular or multicellular, branched or unbranched; specialized forms include root hairs (Chapter 3), glandular (secretory) hairs, scales, sensory hairs, stinging hairs (Figure 1.13) and hooked hairs that facilitate seed dispersal.

Glandular trichomes usually possess a unicellular or multicellular stalk and a secretory head consisting of one or more cells. Secreted

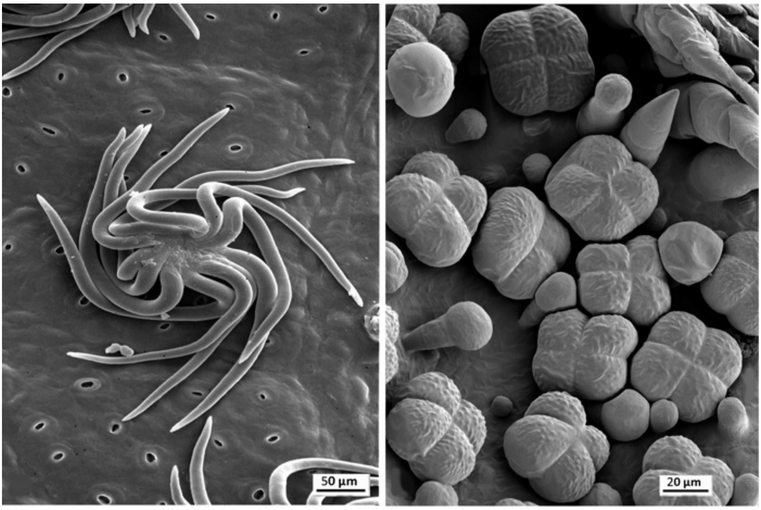

Figure 1.12 Plant hairs. (left) *Quercus ilex* (eudicot: Fagaceae), stellate non-glandular trichome on abaxial leaf surface. Scale = 50 µm. (right) *Salvia involucrata* (eudicot: Lamiaceae), trichomes on petal surface, including glandular (secretory) hairs with short stalks and either four-celled or single-celled glands. Scale = 20 µm.

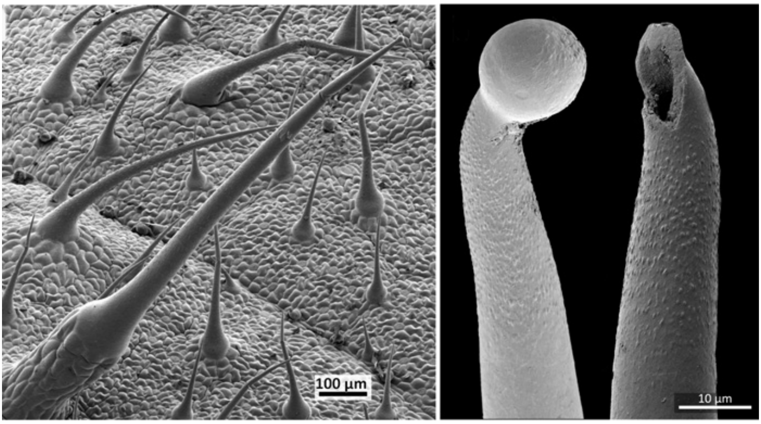

Figure 1.13 Stinging hairs in *Urtica dioica* (eudicot: Urticaceae). (left) adaxial leaf surface with many trichomes; the largest one is a stinging hair with a glandular tip. Scale = 100 µm. (right) tips of stinging hairs, with apical glands intact and broken (SEM). Scale = 10 µm.

substances such as volatile oils collect between the secretory cells and a raised cuticle, which ultimately breaks to release the exudate. There are many different types of glandular hair that secrete a variety of substances, including salt, mucilage, essential oils and even enzymes[41, 154]. Leaf glandular hairs of *Cannabis sativa* secrete a resinous substance containing cannabinoids that act as plant defense compounds. Glandular hairs of carnivorous plants such as *Drosera* secrete both sticky mucilage and proteolytic enzymes that help to capture and digest the prey. Salt-secreting glands help to modulate ion concentration in leaves of salt-tolerant plants such as the mangrove *Avicennia*[70].

Some trichomes are specialized for water absorption rather than secretion. Examples include the leaf scales that occur in many epiphytic and rock-dwelling Bromeliaceae, which represent an important source of water and mineral uptake to the plant. The specialized hairs (hydropotes) that occur on the submerged surfaces of many water plants (e.g. waterlily, *Nymphaea*) initially secrete mucilage, but following degeneration of the cap cells they absorb water and minerals and accumulate heavy metals.

1.11 Vascular tissue

Vascular tissue consists of associated networks of cells that conduct water (xylem) and nutrients (phloem). Primary vascular tissue is derived from the procambium, which is itself produced by the apical meristems. Secondary vascular tissue is derived from the vascular cambium in eudicots, and from the secondary thickening meristem in a few monocot species (Chapter 2.8). Both xylem and phloem are complex tissues composed of many different cell types.

1.11.1 Xylem

The primary function of xylem is transport of water throughout the plant, from roots via the stems to the leaves, where water is combined with carbon dioxide to make carbohydrates and oxygen during photosynthesis. Xylem is composed of several distinct cell types,

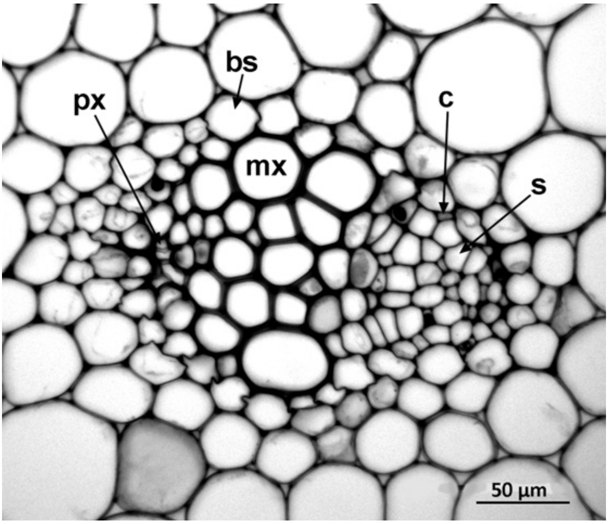

Figure 1.14 Vascular bundle. *Lilium tigrinum* (monocot: Liliaceae), transverse section of stem vascular bundle with xylem (left) and phloem (right) encircled by a ring of bundle sheath cells. bs = bundle sheath, c = companion cell, mx = metaxylem vessel, px = protoxylem vessel, s = sieve tube element. Scale = 50 µm.

often including parenchyma and fibres as well as vessels. Tracheids and vessel elements (collectively termed tracheary elements) are the water-conducting cells; they lack contents at maturity and are linked into cell chains to form vessels. Tracheary elements are elongated cells with thickened lignified walls. In a stem vascular bundle (Figure 1.14), the first-formed (protoxylem) elements often possess wall thickenings that are either helical or arranged in rings (annular). Later-formed primary tracheary elements (metaxylem) and secondary tracheary elements possess bordered pits in their lateral walls. Bordered pits[18] can be oval, polygonal or elongated (scalariform); they can be organized in transverse rows (opposite pitting) or tightly packed (alternate pitting).

The primary difference between tracheids and vessel elements is that vessel elements possess large perforations in their adjoining end walls, whereas perforations are absent from tracheids. Perforation plates are generally either simple, with a single opening, or scalariform, with a ladder-like row of openings divided by a series of parallel bars, or rarely a reticulate mesh. Vessel elements differ considerably in diameter, not only between different species but also sometimes across a single growth ring (e.g. in secondary xylem of oak).

1.11.2 Phloem

Phloem has complex roles in translocation of nutrients (sucrose and electrolytes) and hormones throughout the plant[39]. Although commonly associated with xylem, phloem can develop precociously in regions that require a plentiful supply of nutrients, such as developing sporogenous tissue. Phloem consists of conducting cells (sieve elements) and associated specialized parenchyma cells (companion cells) (Figure 1.14); these two closely interdependent cell types are produced from a common parent cell (meristemoid) that divides and develops asymmetrically to form a larger sieve element and smaller companion cell. Most angiosperms possess sieve-tube elements rather than the relatively unspecialized sieve cells.

At maturity, sieve elements lack nuclei and most organelles but retain plastids and phloem-specific proteins (P-proteins). Companion cells are densely cytoplasmic, retaining nuclei and many active mitochondria. Sieve element plastids and P-proteins occur in several morphological forms (amorphous, filamentous, tubular and crystalline) that are often highly characteristic for particular plant families and are thus of systematic and evolutionary value[11,145]. Sieve-element plastids are classified according to their inclusions: starch (S-type plastids), protein (P-type plastids), or both.

Sieve elements are linked axially to form sieve tubes via sieve plates. Slime plugs are formed when P-protein accumulates on a sieve plate[39]. The walls of sieve elements are thin and possess characteristic regions (sieve areas) that connect adjacent sieve elements; sieve areas consist of groups of pores and associated callose. In sieve tube elements, the sieve areas are localized on the adjoining end walls, forming sieve plates that are either simple or compound.

1.12 Secretory cells and laticifers

Secretory cells are specialized cells that release a broad range of substances, often targeted at a particular function. Secretory cells can occur throughout the plant body, either in the epidermis or in internal tissues. Epidermal secretory cells include glandular trichomes and nectaries, both extrafloral and floral. Internal secretory structures include idioblasts and specialized ducts or canals that are lined with cells that secrete substances such as resin or mucilage. Characteristic resin canals occur in the secondary xylem of some woody eudicots.

Laticifers are specialized latex-producing cells that permeate the tissues of a few angiosperms (Figure 1.7). Latex is an aqueous, often milky, solution that represents the source of commercial rubber, which is traditionally harvested from the rubber tree, *Hevea brasiliensis*. Laticifers of the opium poppy (*Papaver somniferum*) produce latex that is the source of narcotic analgesics such as morphine. Laticifers are traditionally classified into two cell types: non-articulated and articulated, though both types can occur within the same plant family (e.g. in Euphorbiaceae) and overlap in some of their properties[86,108,110]. Non-articulated laticifers (e.g. in *Euphorbia*, Figure 1.7) are highly branched cells that are derived from a small group of initial cells in the cotyledonary node of the embryo. These cells are coenocytes that undergo repeated nuclear divisions without corresponding wall formation. The resulting multinucleate cells grow intrusively between cells of surrounding tissues, branching frequently and eventually ramifying throughout the entire plant. In contrast, articulated laticifers (e.g. in *Hevea brasiliensis*) form complex syncytia by cell fusion and consist of linked chains of cells. Articulated laticifers can also grow intrusively between adjacent cells, though not to the same extent as the non-articulated cell type.

2

Stem

Stems are axes that are typically cylindrical, elongated and branching, though many modifications can occur in different species. Shoot apical meristems are present at the tips of all the stem branches; lateral branches are initiated from buds that are borne in the axils of leaves. Stems are most commonly aerial, though some stems occur below ground. Aerial stems are often green and photosynthetic during early growth but subsequently turn brown following radial stem thickening. Some underground stems are modified into storage organs such as corms or rhizomes that allow them to survive a harsh winter or dry season below ground.

2.1 Shoot apex

The shoot apex contributes to extension growth of the shoot and initiates the leaf primordia at the nodes. Many shoot apices continue to grow indefinitely (i.e. they are indeterminate), though some (e.g. those of shoot thorns and flowers) rapidly cease growth and become determinate. In seed plants, lateral branches develop from axillary buds located in the axils of leaves. Axillary buds possess shoot apical meristems that remain in a dormant state until they receive a growth stimulus.

The vegetative shoot apical meristem is typically dome-shaped and partitioned by clear zones of activity (Figures 1.1, 2.1). The outermost two (or more) cell layers are primarily maintained by anticlinal cell divisions. In flowering plants, these outer layers are termed L1 and L2 respectively, or collectively the tunica region.

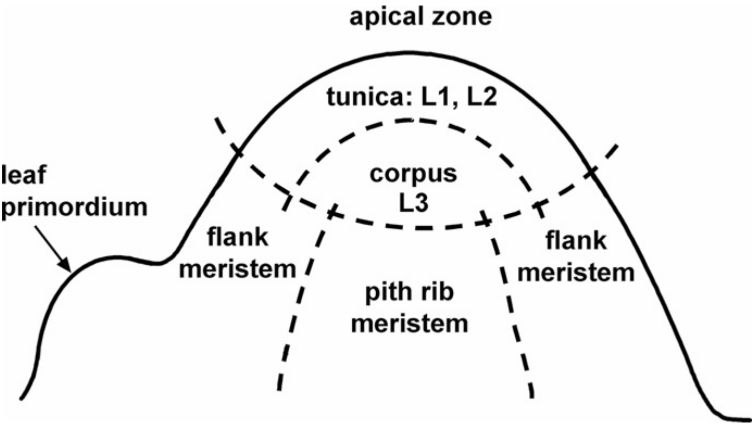

Figure 2.1 Diagram of angiosperm shoot apical organization

The inner corpus region (L3), in which cell divisions are more randomly oriented, is the region proximal to the tunica. Thus, the outer tunica region contributes to surface growth and the inner corpus region to increase in volume, though there is often slight intergradation between them[39]. The central region underlying the corpus zone is a rib meristem, which gives rise to files of cells that form the pith. It is surrounded by a peripheral flank meristem that produces the leaf primordia cortex and procambium, which itself gives rise to the primary vascular system.

Leaf primordia are initiated at or near the shoot apex in a regular arrangement. In many species, a single leaf develops at each node, though some species are characterized by a pair of leaves or a whorl of leaves at each node. Extension growth of the stem occurs at the internodes, either by diffuse cell divisions and cell elongation throughout the internode, or sometimes in a more restricted region, often localized at the base of the internode.

The reproductive shoot apex produces an inflorescence, and each flower apex produces a single flower. At the transition to flowering, there is an overall increase in mitotic activity in cells above the rib meristem, resulting in a change in shape of the shoot apex[39].

2.2 Primary stem structure

Primary vascular tissue in the stem typically consists of discrete vascular bundles supported by parenchymatous ground tissue that is present throughout the stem in the central pith and the outer cortex. In older stems the pith sometimes breaks down to form a central hollow cavity. Ground parenchyma cells frequently become lignified as the plant ages. Ridged or angled stems often possess strengthening collenchyma at the angles, located in the outer cortex immediately inside the epidermis. Many young stems are green, photosynthetic organs with a chlorenchymatous cortex. In some stems, endogenous adventitious roots are initiated at the junction between the cortex and the vascular region (the pericyclic region).

Some plant stems possess secretory cells or ducts in the ground tissue. For example, species of *Euphorbia* possess branched networks of laticifers in the cortex, which extend throughout the ground tissue of the stem and leaves. Plants with succulent stems (e.g. many Cactaceae) possess large thin-walled cells that contain a high proportion of water. Some stems that are specialized as storage or perennating organs (e.g. corms of *Crocus*) store food reserves in the form of starch granules, especially in the inner cortex. In some species, the layer of cortical cells immediately adjacent to the vascular tissue is packed with starch granules; this is termed a starch sheath, or sometimes an endodermoid layer or endodermis, although the component cells usually lack the suberinized Casparian thickenings that are found in the root endodermis.

In eudicots and magnoliids, primary vascular tissue in the stem typically consists of a ring of discrete collateral bundles, in which the phloem is external to the xylem (Figure 2.2). Some stems also possess medullary (pith) bundles or cortical bundles, which are often associated with leaf vasculature. Within each primary vascular bundle, discrete strands of xylem and phloem exhibit a range of configurations: either adjacent to each other (in collateral vascular bundles), with strands of phloem on each side of the xylem

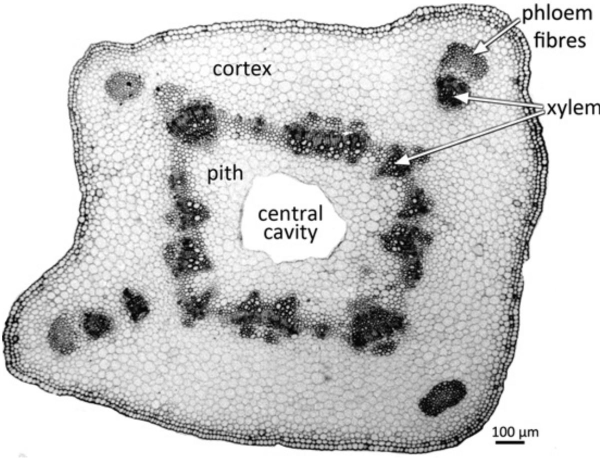

Figure 2.2 *Vicia faba* (eudicot: Fabaceae), transverse section of stem. Scale = 100 µm

(bicollateral vascular bundles), or with xylem surrounding the phloem (amphivasal vascular bundles). Amphivasal bundles are common in monocots but relatively unusual in eudicot stems. In stems with bicollateral bundles (e.g. *Cucurbita*), both internal and external phloem is present. Vascular cambium (Figure 2.3) is located between the xylem and phloem in most woody eudicots and magnoliids, but this meristem is absent from monocot vascular bundles (Figure 1.14).

In monocots, the stem vascular bundles are typically scattered through the central ground tissue (Figures 1.14, 2.4), or sometimes arranged in two or more distinct rings. Monocot vascular bundles are collateral, bicollateral or amphivasal. Cortex and pith regions are often indistinctly demarcated from each other, though the cortex may be defined by an endodermoid layer or a cylinder of sclerenchyma. The monocot vascular system can be highly complex[163]. Each bundle, when traced on an upward course from any point in the stem, often has several bridges or branches before passing into a leaf; one of its major branches continues a similar upward course

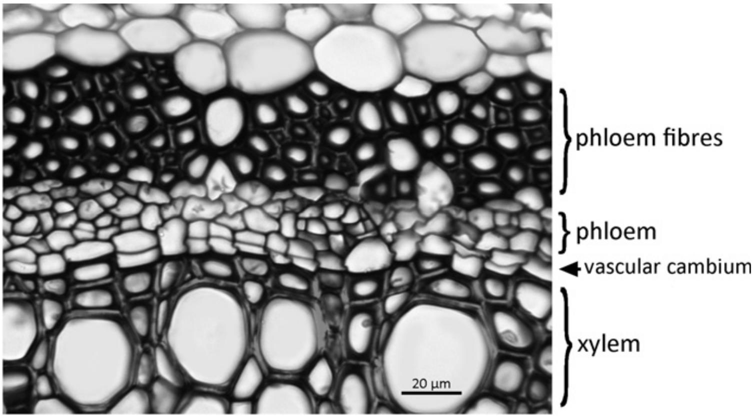

Figure 2.3 Vascular cambium. *Hyptis oblongifolia* (eudicot: Lamiaceae), transverse section of part of stem in region of vascular cambium. Scale = 20 µm

towards the apex. In some palms, thousands of vascular bundles are present in a single transverse section of the stem, though in most monocots their number is much fewer.

2.3 Nodal anatomy

The vasculature of the leaf and stem is connected at the nodes. Openings (lacunae or leaf gaps) occur in the stem vascular cylinder beneath their point of contact (Figure 2.5). In eudicots and magnoliids, nodal anatomy is often characteristic of families, particularly with respect to the number and arrangement of leaf traces and leaf gaps. Nodes are unilacunar, trilacunar or multilacunar, depending on the number of leaf gaps in the stem vascular cylinder. This feature is most apparent in stems that possess an otherwise continuous vascular cylinder, especially where a limited amount of secondary thickening has taken place, so that nodal anatomy is best understood in woody plants[62]. The number of leaf traces departing from each gap is also generally characteristic of a species, but can vary within a plant, especially in

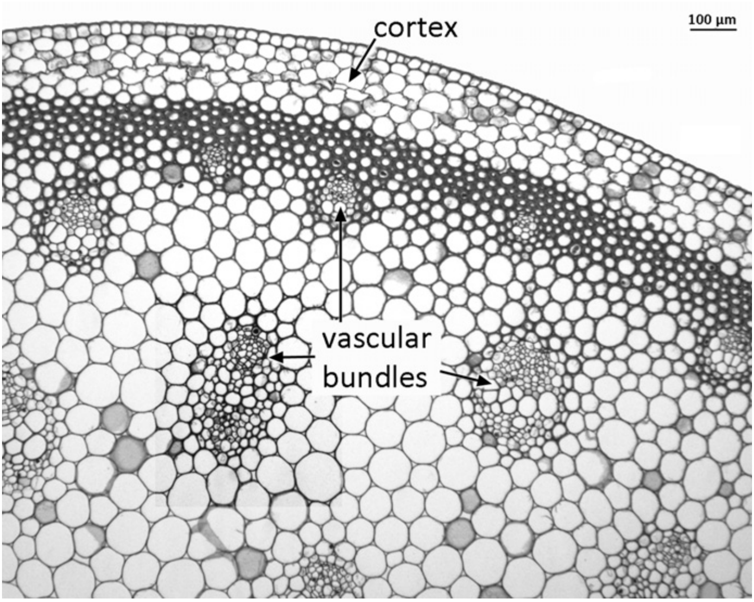

Figure 2.4 Monocot stem. *Lilium tigrinum* (monocot: Liliaceae), transverse section of stem showing outer cortex surrounding central region containing vascular bundles and demarcated by sclerenchymatous cylinder.
Scale = 100 µm

species with unilacunar and trilacunar nodes. For example, in *Clerodendrum* (Lamiaceae) two traces depart from a single gap, and in *Prunus* (Rosaceae) a single trace departs from each of three gaps in the central vascular cylinder (Figure 2.5). In oaks (*Quercus*), up to five traces depart from a trilacunar node. Leaf-trace bundles normally develop acropetally from the stem procambial system close to the shoot apex and grow towards developing leaf primordia, though in some species (e.g. *Populus deltoides*), subsidiary vascular bundles are initiated at the base of each developing primordium and grow basipetally to meet the stem procambial trace[79].

Nodal vasculature is further complicated by the axillary bud vascular traces, which are connected to the main stem vasculature immediately above the leaf gaps. In most species, two traces

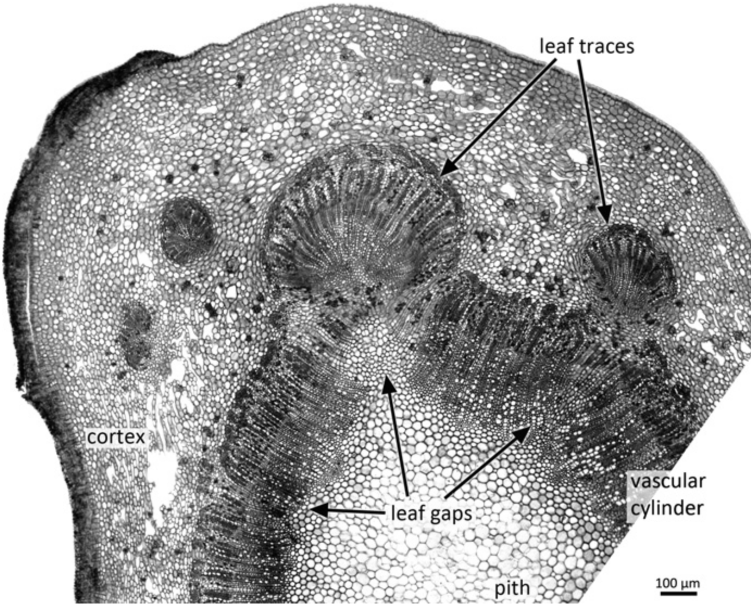

Figure 2.5 Nodal anatomy. *Prunus lusitanica* (eudicot: Rosaceae), transverse section of part of stem at node, showing connection of petiole vasculature with stem vascular cylinder. Scale = 100 μm

diverge to supply each bud or branch. In large woody eudicot trees, the junction of the trunk and its branches is characterized by a complex arrangement of secondary vascular tissue, which typically forms a collar around the base of the branch. This branch collar is enveloped by a trunk collar that links the vascular tissue of the trunk above and below the branch. There is no direct connection of xylem from the trunk above a branch into the branch xylem, as the tissues are oriented perpendicular to each other. If a branch dies, a protection zone forms around its base to prevent a spread of infection into the trunk, and the branch is often shed.

2.4 Vascular cambium and secondary vascular tissue

Increase in stem length, achieved by extension growth at the shoot apical meristem, is followed by radial growth that results in increase

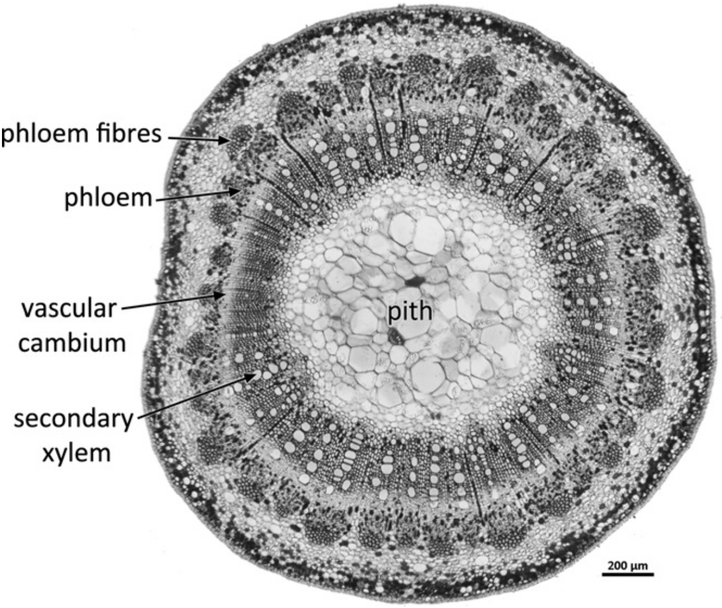

Figure 2.6 Secondary thickening in eudicots. *Cissus alata* (eudicot: Vitaceae), transverse section of stem, showing early growth in thickness. Scale = 200 µm

in stem thickness[129] (Figure 2.6). In most woody angiosperms, secondary vascular tissue (both xylem and phloem) is generated by the vascular cambium, which becomes active a short distance behind the stem apex, initially as a fascicular meristem formed within the primary vascular bundles. Subsequently, an interfascicular vascular cambium is formed in the parenchymatous region between the primary vascular bundles, resulting in a vascular cylinder.

The vascular cambium is a bifacial meristem (Figure 2.3) that generates secondary xylem (wood) at its inner edge (centripetally) and secondary phloem at its outer edge (centrifugally). It consists of both fusiform initials and ray initials, which form the axial and radial systems respectively. Ray initials are isodiametric cells that divide periclinally to form ray parenchyma cells in both xylem and phloem. Fusiform initials are axially elongated cells with tapering ends. These undergo periclinal divisions to form the axial elements of the

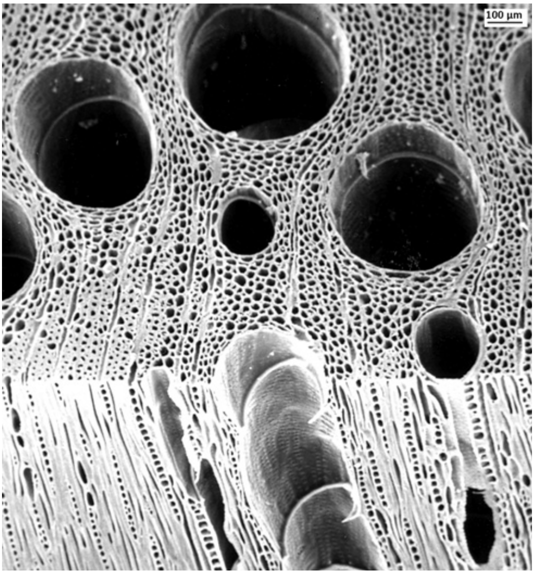

Figure 2.7 Wood. *Quercus robur* (eudicot: Fagaceae), wood block at edge of transverse and tangential longitudinal surfaces, showing large early wood vessels (SEM). Scale = 100 µm

secondary tissues, including tracheary elements, fibres and axial parenchyma in secondary xylem, and sieve elements, companion cells and fibres in secondary phloem. In addition, fusiform initials sometimes give rise to new ray initials as the stem increases in circumference and new rays are formed. Occasionally, transitional cell types can occur. For example, perforated ray cells, an unusual feature of some woods, can link two vessel elements and themselves resemble and function as vessel elements; their perforation plates correspond with those of the adjacent vessel elements, though they are formed from ray initials.

The degree of secondary growth depends on the growth habit of the plant. In some species, including all monocots, some magnoliids and some herbaceous eudicots (e.g. *Ranunculus*), a vascular cambium is entirely absent. In many woody temperate plants, cambial activity is seasonal (usually annual), resulting in the

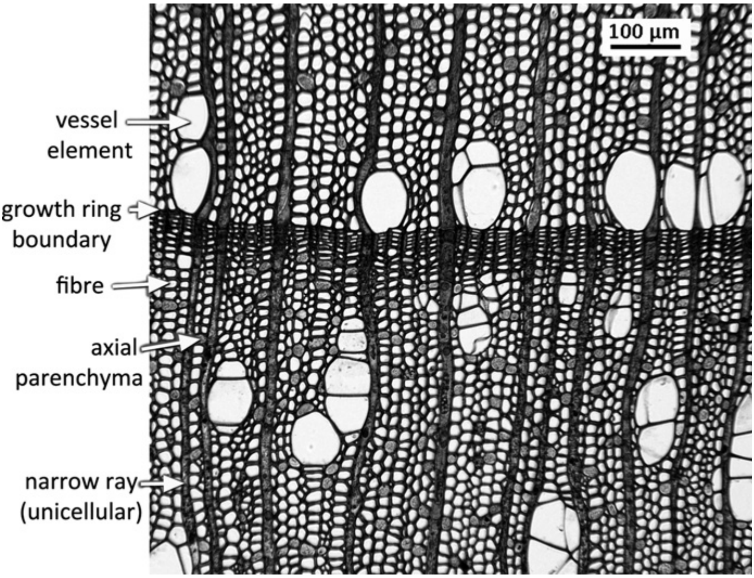

Figure 2.8 Wood. *Alnus glutinosa* (eudicot: Betulaceae), transverse section of secondary xylem, showing differences in fibre thickness on either side of growth-ring boundary. Scale = 100 µm

formation of growth rings. Xylem of early wood formed in the spring is generally less dense and consists of thinner-walled cells than that of late wood (summer wood). In ring-porous woods such as oak, the early wood vessels are considerably larger than those of late wood (Figure 2.7). In diffuse-porous woods, the main distinction between early and late wood is in relative fibre size and wall thickness (Figure 2.8).

Atypical activity of the vascular cambium characterizes some woody angiosperms with anomalous secondary growth, such as many climbing plants (lianes)[129]. For example, in some species (e.g. *Avicennia*) isolated regions of phloem (included or interxylary phloem) are formed embedded in the xylem, either in islands or in alternating concentric bands. Other species have irregularly

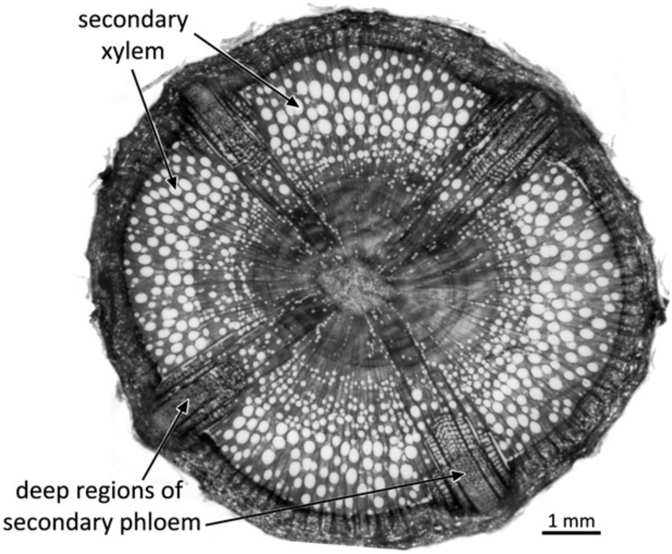

Figure 2.9 Anomalous secondary growth. *Tynanthus elegans* (eudicot: Bignoniaceae), transverse section of woody stem, showing four regions of phloem embedded in secondary xylem. Scale = 1 mm

divided or deeply fissured areas of xylem and phloem caused by differential cambial activity in different radial sectors (Figure 2.9).

2.5 Secondary xylem

Secondary xylem (wood) is produced by the vascular cambium. It is composed of a matrix of cells, some arranged axially (fibres, vessels and axial parenchyma) and others radially. The ray parenchyma forms the wood rays that radiate from the vascular cambium towards the pith. As woody plants age and their trunks increase in girth, the central area becomes non-functional with respect to water transport or food storage; the vessels frequently become blocked by tyloses that are formed when adjacent parenchyma cells grow into them through common pit fields. The central non-functional area of the trunk, the heartwood, is generally darker than the outer living sapwood; it provides a supporting skeleton for the living parts of the tree.

The precise cellular arrangement of wood is often highly characteristic of the species (Figures 2.7, 2.8). To observe their structure, woods are sectioned transversely and in two longitudinal planes: along the rays (radial or median longitudinal section: RLS or MLS) and across the rays (tangential longitudinal section: TLS). When viewed in transverse section, vessels can appear solitary (e.g. the early vessels of oak, *Quercus*) or arranged in clusters or radial chains. Axial parenchyma cells can be independent of the vessels (apotracheal parenchyma) or associated with them (paratracheal parenchyma), or they can sometimes occur in regular tangential bands. The relative abundance of axial parenchyma differs between species, ranging from sparse or absent to rare cases such as balsa wood (*Ochroma pyramidale*), in which axial parenchyma cells are often more abundant than fibres.

Rays are termed uniseriate if they are one cell wide tangentially, and multiseriate if they are more than one cell wide. Both uniseriate and multiseriate rays can co-occur in the same wood (e.g. in oak, *Quercus*: Figure 2.7). In radial longitudinal section, ray cells can be homogeneous (homocellular) or variously shaped (heterocellular). Other aspects of variation in the structure of hardwoods include the presence of either axial or radial secretory canals in some woods, storied (stratified) appearance of the rays and differences in the fine structure of the vessel walls (intervascular pitting, perforation plates and wall thickenings). For example, in lime wood (*Tilia cordata*), the vessel element walls are helically thickened, and in many legumes (Fabaceae) the pit apertures are surrounded by characteristic warty protuberances, termed vesturing.

2.6 Secondary phloem

Secondary phloem is also produced by the vascular cambium. It consists of both axial and radial systems that are formed from the fusiform initials and ray initials, respectively. In transverse section, phloem rays are radially continuous with xylem rays. Close to the vascular cambium, they can be either uniseriate or multiseriate, but they become dilated towards the cortex as a result of cell divisions that accommodate increase in stem thickness (Figure 2.6), and older ray cells often become lignified. At their outer periphery, parenchymatous ray cells are indistinguishable from cortical cells and form part of the bark. The axial system of the secondary phloem not only consists of sieve elements and companion cells, as in primary phloem, but also includes fibres, sclereids and axial parenchyma cells. In some species, the phloem fibres are formed in groups at regular intervals, resulting in characteristic tangential bands of fibres alternating with groups of sieve elements and parenchyma cells.

2.7 Periderm and bark

Periderm is a specialized protective tissue of corky (suberinized) cells that is produced in the outer layers of the cortex of a stem or root that has increased in thickness. Bark is a more generalized term that includes all tissues located outside the vascular cambium; it is commonly applied to the outermost layers of stems of woody plants, especially trees[3].

Periderm forms an impervious layer to prevent water loss and protect against injury. It is commonly formed in the cortex of secondarily thickened stems, replacing the epidermis, which splits and peels away (Figure 2.10). It can also form in response to a wound, for example forming a protective layer over a site of leaf abscission. In stems and roots, periderm consists of up to three distinct layers, termed phellogen, phellem and phelloderm[39]. The phellogen layer is a uniseriate lateral meristem composed of thin-walled cells that divide to produce phellem to the outside and (in some cases) phelloderm to the inside. Phellem represents the most prominent region of periderm; it is arranged in tightly packed rows of cells. Phellem cells lack contents at maturity and possess cell-wall deposits of suberin and sometimes lignin, especially on their inner faces. In contrast, the phelloderm cells

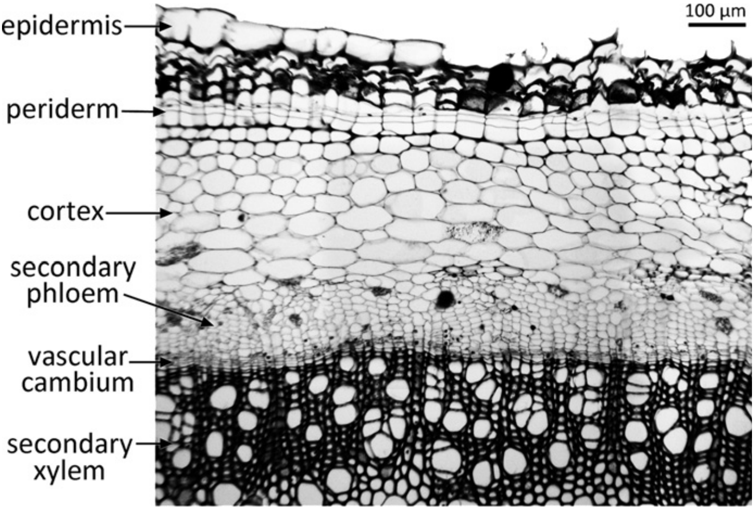

Figure 2.10 Periderm formation. *Sambucus nigra* (eudicot: Adoxaceae), transverse section of slightly thickened stem, showing periderm forming in the subepidermal outer cortex. Scale = 100 µm

located inside the phellogen layer are non-suberinized and can contribute to the secondary cortex of a stem. The initial phellogen originates either in the subepidermal (hypodermal) layer or deeper in the cortex, more rarely within the epidermis itself.

Bark tissues include secondary phloem, fibres, cortex and periderm[3]. In some woody trees, the bark can become very thick and two distinct regions are distinguishable: inner bark, consisting of secondary phloem tissues, and outer bark (rhytidome), consisting of cortex and periderm tissues. In some species, several phellogens can form sequentially or almost simultaneously; they frequently overlap each other within the bark. The pattern of periderm formation largely dictates the appearance of the bark of a woody plant. For example, the smooth papery bark of a birch (*Betula*) tree results from regular formation of abscission bands causing thin sheets to flake off. In cork oak (*Quercus suber*), the initial phellogen can maintain activity indefinitely and produces seasonal growth rings. In trees grown for the production of commercial cork, the initial phellogen is removed after about 20 years to make way for a second, more vigorous phellogen.

Many species of woody eudicots and magnoliids produce lenticels, which are restricted regions of loose cells formed within the periderm that protrude outwards from the surface of the bark. Lenticels also occur on the surface of tubers such as potato. They are initially formed in cells underlying stomata in the epidermis and have a similar role in allowing passage of gases and water vapour across the stem, at least during the summer months, though their role may change with the seasons[52]. In a few species (e.g. several Bombacoideae–Malvaceae), localized regions of the outermost phellogen formed proliferated cell layers that result in pronounced rigid outgrowths of the bark (prickles).

2.8 Primary and secondary thickening meristems in monocots

In monocots, which lack a vascular cambium, a limited degree of radial growth is achieved by a primary thickening meristem (PTM)

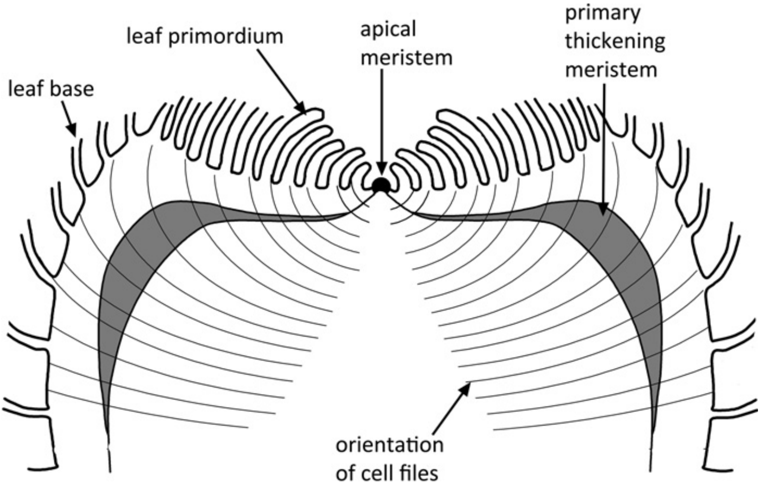

Figure 2.11 Diagram of monocot shoot apical organization showing PTM near shoot apex

near the vegetative shoot apex (Figure 2.11). The PTM is especially extensive in species with short internodes and crowded leaves, such as bulbous taxa[27, 109]. In monocots, the PTM originates in ground tissue in the pericyclic region of the stem. It is a tiered meristem, consisting of a zone of meristematic cells that produces radial derivatives. The majority of its radial derivatives are centripetal, consisting of both parenchyma and discrete vascular bundles, though it also produces some parenchyma towards the outside. In addition to primary stem thickening, the PTM forms linkages between root, stem and leaf vasculature, especially in relatively condensed bulbous plants. It typically ceases activity at a short distance behind the apex, and subsequent stem thickening is limited. However, in some species, this region retains some meristematic potential and resumes meristematic activity further down the stem; it represents the site of adventitious root production in some monocots[109].

Although monocots are predominantly herbaceous, some species achieve considerable height and girth. Tree-forming palms possess an extensive PTM that results in a large sunken shoot apex; in these species, further stem thickening occurs by subsequent division and enlargement of ground parenchyma cells, termed diffuse secondary growth. A PTM is not confined to monocots; similar pericyclic meristems also occur in some eudicots with thick stems (e.g. Cactaceae[14]). In some woody monocots of the order Asparagales (e.g. *Agave, Aloe, Cordyline, Yucca*), considerable increase in stem thickness is achieved by means of a secondary thickening meristem (STM) (Figure 2.12). The STM resembles the PTM in that it is radially located in the pericyclic region of the stem within the cortex and it produces radial derivatives, but it occurs further from the shoot apex; the two meristems are best regarded as developmental phases of the same meristem. The STM produces secondary vascular bundles that are mostly amphivasal and radially elongated. In some woody monocots (e.g. *Beaucarnea recurvata*, *Cordyline terminalis*), the PTM and STM are axially discontinuous, whereas in others (e.g. *Yucca whipplei*) they are axially continuous[29, 132, 133].

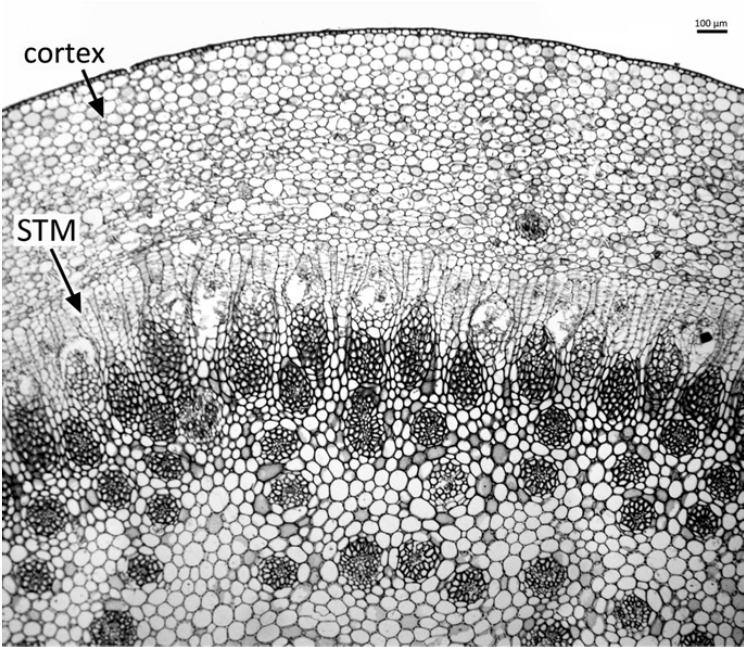

Figure 2.12 Monocot growth in thickness. *Cordyline indivisa* (monocot: Asparagaceae), transverse section of stem, showing outer cortex and inner region containing scattered vascular bundles. The STM has produced secondary vascular bundles that are radially aligned. Scale = 100 μm

The PTM and STM, although sometimes termed the monocot cambium, are not homologous with the vascular cambium. The PTM and STM originate from the pericyclic region, whereas the vascular cambium originates inside stem vascular bundles (fascicular cambium) and subsequently spreads to interfascicular regions. The PTM and STM produce discrete vascular bundles centrifugally, whereas the vascular cambium is a bifacial meristem that produces xylem centrifugally and phloem centripetally.

3

Root

Roots are typically branching cylindrical structures that develop underground to facilitate extraction of moisture and nutrients from the soil, often in association with hyphal networks of soil-dwelling fungi. In contrast, epiphytes and epiliths, which grow entirely above the ground, often develop aerial roots that absorb moisture from their environment. In vascular plants, the root apex is a growing tip where both the root cap and the primary root tissues are produced. Lateral roots are initiated some distance from the root apex, by cell divisions in the pericycle, among differentiated cells that have retained meristematic capacity.

3.1 Root apex and root cap

The root apex contributes to extension growth of the root and also differentiates the terminal protective root cap (Figure 3.1). In contrast with the shoot apex, the root apex does not produce lateral appendages and grows relatively uniformly, lacking nodes and internodes[7, 42]. The junction between the root cap and the root apical meristem is either clearly defined by a distinct cell boundary (closed organization, as in *Arabidopsis thaliana* and *Zea mays*) or ill-defined (open structure, as in *Vicia faba*), though intermediates exist (e.g. in carrot, *Daucus carota*) and the boundary between the cap and the rest of the root is sometimes unstable[55] (Figure 3.2).

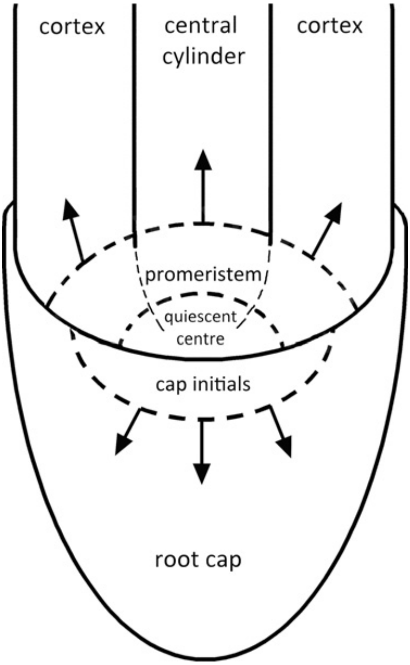

Figure 3.1 Diagram of root apical organization in *Zea mays* (monocot: Poaceae)

The root apex is structured into zones of cells of contrasting size and differential activity. The quiescent centre is a group of relatively inactive cells that divide infrequently; their role is to maintain initial cells in an undifferentiated state. Probably the region of greatest mitotic activity is the promeristem surrounding the quiescent centre, though actively dividing cells extend from the apex into older parts of the root. In some species (e.g. *Vicia faba*) there is an undifferentiated common initiating region for all root tissues[131], but in others (e.g. *Arabidopsis thaliana*), the initial cells lie in clearly defined regions. In root apices with closed organization, the root epidermis is associated either with cortical cells (in most monocots) or with cap initials (in most eudicots); in root apices with open organization the precise origin of the root epidermis is relatively difficult to determine[19].

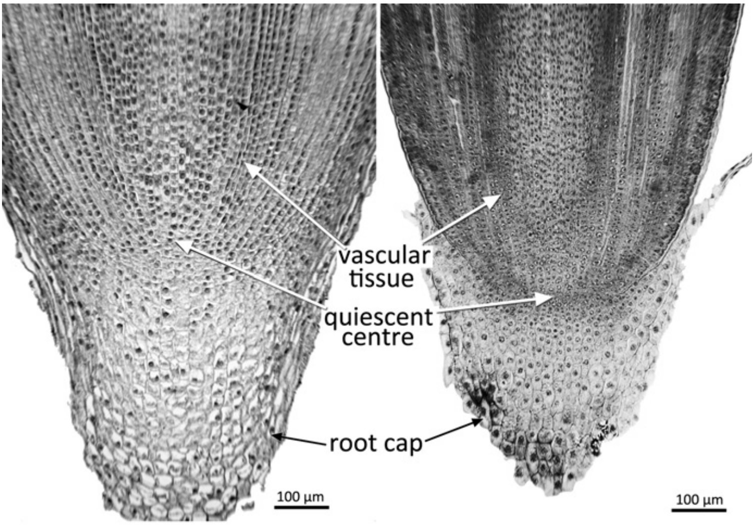

Figure 3.2 Longitudinal sections of root apices. Left: *Vicia faba* (eudicot: Fabaceae), open organization. Right: *Zea mays* (monocot: Poaceae), closed organization. Scales = 100 µm

The root cap consists of several layers of parenchymatous cells. In maize (*Zea mays*), a species with "closed" root apical structure (Figures 3.1, 3.2), the cap initials become established and independent from the apical meristem at an early stage in seedling development[7]. The cap meristematic cells, located adjacent to the quiescent centre, produce derivatives that are eventually displaced towards the outside of the root cap and are subsequently worn away, in the process contributing to the external slime that helps the root push between soil particles. Cells are generated in the root cap at approximately the same rate as they are discarded.

3.2 Primary root structure

Primary structure retains a characteristic ground plan that differs from that of the stem. Each root possesses clearly defined radial organization with concentric tissue regions. The outermost dermal tissue (epidermis, rhizodermis or velamen) develops specialized

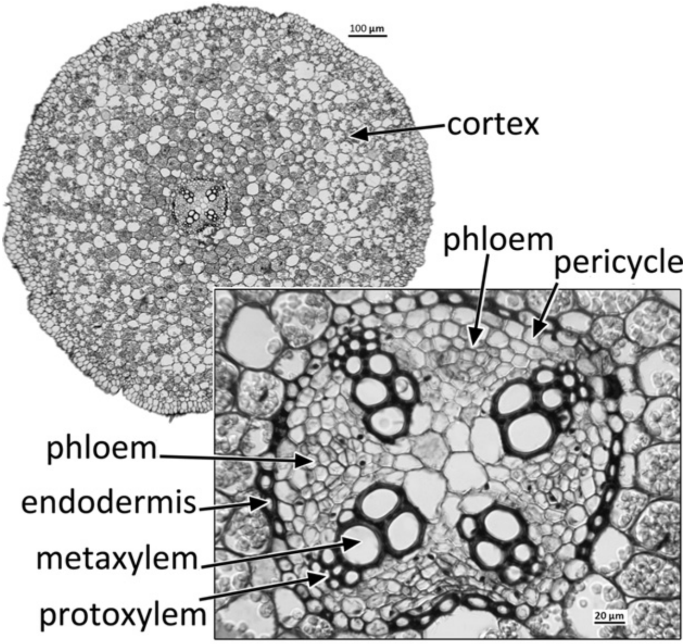

Figure 3.3 Root anatomy. *Ranunculus acris* (eudicot: Ranunculaceae), transverse section of root, with detail of central vascular region (inset). Scales = 100 µm and (inset) 20 µm

water-absorbing root hairs in well-defined regions. Inside the dermal layer lies the cortex, which includes a specialized innermost cortical layer, the endodermis. Finally, the central cylinder consists of a pericycle surrounding the central vascular tissue (Figure 3.3).

3.3 Root epidermis and root hairs

The root epidermis (rhizodermis) is typically uniseriate, though in some species, especially in aerial roots of aroids and orchids, it becomes a multiseriate tissue, termed a velamen, which has a role in water storage. Velamen cells lack a protoplast and can become saturated with water; their cell walls are often partly thickened and sometimes lignified.

In most angiosperm species, root hairs are located about a centimetre from the apex, in a region where cells have ceased division but are still enlarging. This region of the root is the most active in absorption of water and solutes; the root hairs provide a much greater surface area for this purpose. Root hairs are outgrowths of epidermal cells that form by apical intrusive growth between adjacent soil particles. The root hairs persist for a limited period before they wither, and new hairs are formed closer to the root apex. Root hairs are mostly unicellular and unbranched, but they can sometimes branch. Long root hairs characterize species that do not form ectomycorrhizal associations (e.g. sedges). In some species (e.g. rice, *Oryza*), any rhizodermal cell is capable of root hair formation, but in others (e.g. lilioid monocots and waterlilies), root hairs are produced only by specialized root epidermal cells (trichoblasts) in an alternating pattern within each cell file. In other species (e.g. *Arabidopsis thaliana*), root hairs are formed only in alternate axial cell files[25].

3.4 Root cortex and endodermis

The cortex, located between the pericycle and the epidermis, consists primarily of ground tissue formed by sequential periclinal cell divisions. The number of cell layers in the cortex ranges from one or two in some species (e.g. *Arabidopsis*) to ten or more in others. The final, innermost cortical layer becomes specialized as the endodermis. Some plants possess a dimorphic hypodermal layer adjacent to the epidermis, consisting of alternating long and short cells[73, 127]. In older roots, the epidermis often becomes worn away and its protective role is taken over by the outermost cortical cells, which can become suberinized or lignified to form an exodermis, especially in monocots. In woody eudicot species with lateral thickening growth, a periderm often forms in the outer cortex.

Apart from these specialized layers, most cortical cells are parenchymatous. Cortical cells located in the root hair region facilitate radial passage of solutes from the epidermis to the vascular tissue;

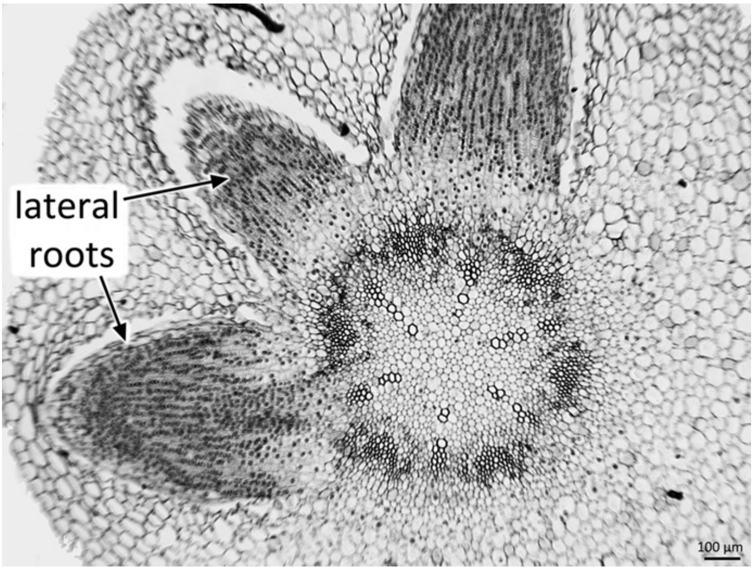

Figure 3.4 Lateral roots. *Vicia faba* (eudicot: Fabaceae), transverse section of root with three developing lateral roots. Scale = 100 µm

in other parts of the root they often have a storage role. In some plants (e.g. root crops such as carrot), the tap root is a modified swollen storage organ with a broad cortex. Contractile roots occur periodically in many plants with modified underground stems such as corms, bulbs or rhizomes (e.g. *Crocus*); these specialized roots grow downwards, then contract axially and expand radially to draw the stem deeper into the soil[67]. Contractile roots have a wrinkled surface; they possess two or three clearly distinct concentric regions of cortical parenchyma, distinguishable by cell size, including a region of collapsed outer cortical cells interspersed with occasional thicker-walled cells (Figure 3.4). In some species, centripetal collapse of outer cortical cells results from loss in turgidity following transpiration, which produces a differential between atmospheric pressure and relatively low xylem pressure.

The root endodermis is a uniseriate cylinder of innermost cortical cells surrounding the central vascular region, adjacent to the pericycle.

Endodermal cells are characterized by deposition of a band of suberin or lignin in their primary walls, termed a Casparian strip, which represents a barrier against non-selective passage of water through the endodermis. Occasional endodermal cells (passage cells) remain thin-walled, allowing selective passage of water between the cortex and vascular region. In older endodermal cells, the inner periclinal waIl becomes thickened and lamellated so that the Casparian strip is obscured. The secondary wall is often lignified and/or suberized, and acts as an effective barrier to water loss.

3.5 Pericycle and vascular cylinder

The central vascular cylinder is surrounded by a layer of thin-walled cells, the pericycle, which is mostly uniseriate, especially opposite the phloem poles (Figure 3.3). Both the pericycle and vascular tissue are derived from cells located on the proximal (shoot) side of the quiescent centre at the root apex. The pericycle is the site of lateral root initiation; it retains its meristematic potential for some distance away from the apex.

Primary vascular tissue in the root consists of several strands of phloem alternating with radially arranged rays (archs) of xylem. The xylem region often appears star-shaped in transverse section; it extends to the centre of smaller roots, which lack a central parenchymatous region. Roots possess two, three, four or more protoxylem poles, in which case they are diarch, triarch, tetrarch or polyarch respectively. There is often variation in the number of xylem poles, sometimes even within the same plant, depending on the diameter of the root. Eudicot roots possess a relatively small number of xylem poles (most commonly two, three or four) compared with many monocots. In monocots with polyarch roots (e.g. *Iris*), the centre of the root is parenchymatous, often becoming lignified in older roots.

During root development, protoxylem elements are the first to be formed and the narrowest in diameter; they are located at the tips of the archs, nearest to the pericycle. The larger metaxylem elements are located along the archs, towards the root centre. Both xylem and phloem are exarch in the root (i.e. they mature centripetally).

3.6 Lateral and adventitious roots

Lateral roots are branches of the primary root, whereas adventitious roots are initiated in other parts of the plant, most commonly in stem tissue (Figures 3.4, 3.5). Both lateral roots and adventitious roots are common in eudicots, but monocots and waterlilies rely mostly on adventitious roots, and the primary root is ephemeral.

Lateral roots are initiated some distance from the root apex, often in acropetal sequence, so that the most recently formed lateral roots are those closest to the root apex. They have a deep-seated (endogenous) origin in the parent root (Figure 3.4). They are initiated in groups of founder cells in the pericycle, following an auxin-drive stimulus[100]. In many eudicots, lateral root initiation in the pericycle occurs at a point adjacent to a protoxylem pole, though in diarch

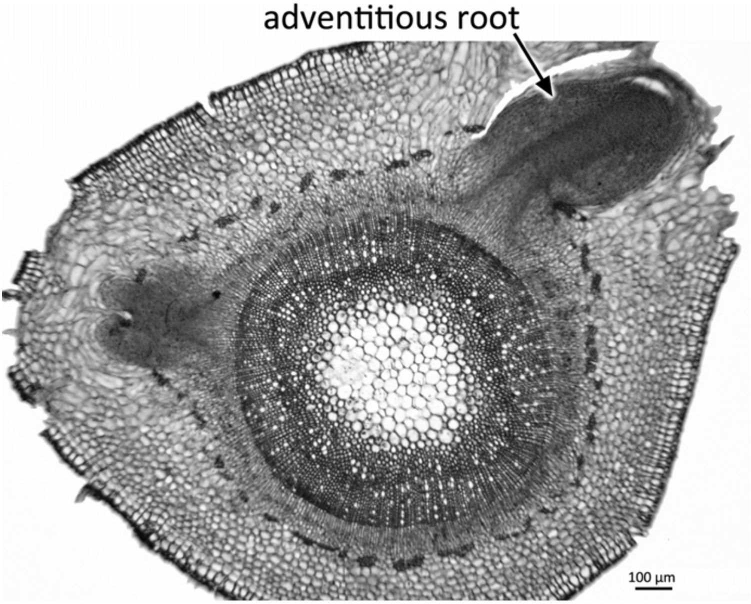

Figure 3.5 Adventitious roots. *Ligustrum vulgare* (eudicot: Oleaceae), transverse section of stem with two developing adventitious roots. Scale = 100 µm

roots (as in *Arabidopsis*) lateral roots are initiated opposite the xylem poles. In polyarch roots of monocots, the site of lateral root initiation is difficult to determine; it can be opposite either protoxylem or phloem poles[88]. The founder cells undergo a series of periclinal and anticlinal divisions to form a lateral root primordium. The first anticlinal divisions are asymmetric, resulting in daughter cells of unequal sizes. In many species, some subsequent cell divisions occur in the endodermis, so that ultimately both the pericycle and the endodermis contribute to the tissues of the lateral root. The emerging lateral root pushes its way through the cortex and epidermis of the parent root by mechanical and/or enzymatic action.

Adventitious roots have various sites of origin within a stem; they are typically endogenous (Figure 3.5), but more rarely are exogenous, arising from superficial tissues such as the epidermis (e.g. in surface-rooting *Begonia* leaves) or from callus tissue at the site of a wound. In woody species, adventitious roots are often formed at nodes on the stem, which is why horticultural cuttings are commonly taken from just below a node. In most monocots, adventitious roots arise from cell divisions in the pericyclic region of the stem.

3.7 Secondary growth in roots

In woody eudicots and magnoliids, thickening and strengthening of the root system below ground is important in supporting the enlarging stem above ground. Most eudicot roots possess at least minimal secondary thickening (Figure 3.6), with the exception of some herbaceous species such as *Ranunculus* (Figure 3.3). In contrast, secondary (lateral) growth in roots is extremely rare in monocots, even among arborescent or woody species that possess a secondary thickening meristem; the only reported exception is *Dracaena*, in which a limited region of secondary tissue is formed in the root[141].

In the roots of most woody eudicots and magnoliids, secondary vascular tissue (both xylem and phloem) is produced by a bidirectional vascular cambium, as in the stem. This tissue is

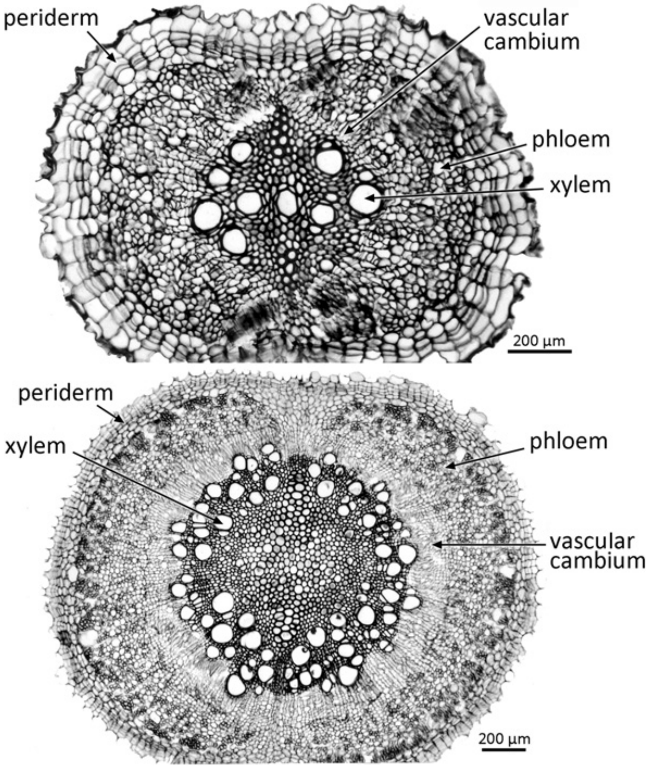

Figure 3.6 Secondary thickening in roots. *Ulmus* sp. (eudicot: Ulmaceae), transverse sections of roots with (top) early secondary growth and (bottom) more extensive secondary thickening. Scales = 200 μm

initiated in the region located between the primary xylem and phloem of younger roots, and subsequently in derivatives of cell divisions within the pericycle, close to the xylem poles. As a result of this sequence of cambial activity, the xylem cylinder soon appears circular in transverse section and the outer layers of cortex and epidermis begin to split apart. Further pericyclic cell divisions result in the formation of a secondary cortex. In many cases a periderm forms in the outermost layers, particularly where secondary growth is extensive (Figure 3.6). Root secondary xylem can differ in some respects from stem secondary xylem in the same plant. For example, in *Quercus robur* (oak), stem wood is ring porous, with earlywood vessels markedly larger than latewood vessels, but root wood is diffuse porous, with vessels that maintain a relatively even size across each growth ring.

3.8 Roots associated with microorganisms

Many vascular plants form symbiotic relationships with soil microorganisms that invade the cells of the host root and promote the uptake of mineral nutrients to the plant, especially phosphate and nitrogen, in exchange for carbon. Fungal symbioses occur in a high proportion of land plants[89]. In some temperate woody forest species, especially in the families Fagaceae and Betulaceae, ectomycorrhizal fungi form a mantle that entirely envelopes the lateral roots. Ectomycorrhizal fungal hyphae do not enter the cell lumen but grow between the host epidermal and cortical cells, forming a mantle termed a Hartig net. In contrast, arbuscular

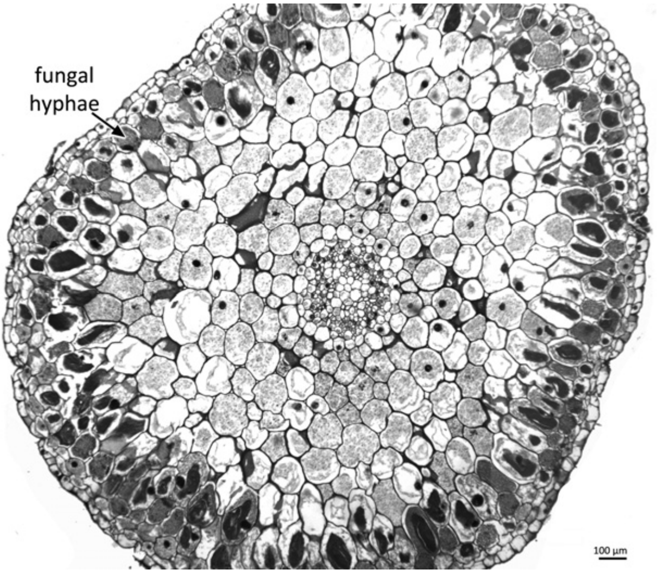

Figure 3.7 Mycorrhizal roots. *Neottia nidus-avis* (monocot: Orchidaceae), transverse section of root with fungal hyphae in outer cortex. Scale = 100 µm

mycorrhizae invade the host cortical cells and form intracellular structures (arbuscules) (Figure 3.7).

Some soil microorganisms can induce the formation of modified lateral roots. In some eudicots, including many legume species, symbiotic nitrogen-fixing bacteria (rhizobia) enter the root cortex through root hairs and stimulate meristematic activity and cell proliferation in the cortex and pericycle to form a specialized structure termed a root nodule[22, 87]. Within the nodule, the rhizobia invade host cells, where they are surrounded by a plasma membrane and resemble organelles that reduce nitrogen to ammonia. Legume root nodules can be either determinate and spherical (e.g. in soybean plants) or indeterminate and more elongated (e.g. in pea plants). Indeterminate nodules develop an apical meristem and peripheral vascular bundles connected to the central root vasculature.

3.9 Root haustoria of parasitic angiosperms

A few angiosperms are parasitic on the roots, stems and leaves of other species, including members of the families Convolvulaceae (dodders, e.g. *Cuscuta*), Loranthaceae (mistletoes, e.g. *Viscum*), Orobanchaceae (e.g. broomrapes, *Orobanche*, and toothworts, *Lathraea*) and Santalaceae (sandalwoods, *Santalum*). Parasitic plants produce specialized root haustoria that penetrate the host tissue to transfer nutrients from the host to the parasite. Some hemiparasites such as *Rhinanthus* and *Bartsia* are similarly haustorial. Haustoria are formed either directly from the root apex of the parasite or from a modified lateral or adventitious root or stem[63].

In many parasitic species, the root haustorium penetrates the host tissue to the xylem and phloem and forms a continuous vascular bridge (Figure 3.8). Haustorial epidermal cells in contact with the host become elongated and secretory, and the centre of the haustorium develops an intrusive process that grows into the host tissue by enzymatic and mechanical action. The developing parasitic haustorium often forms a mantle of parenchymatous

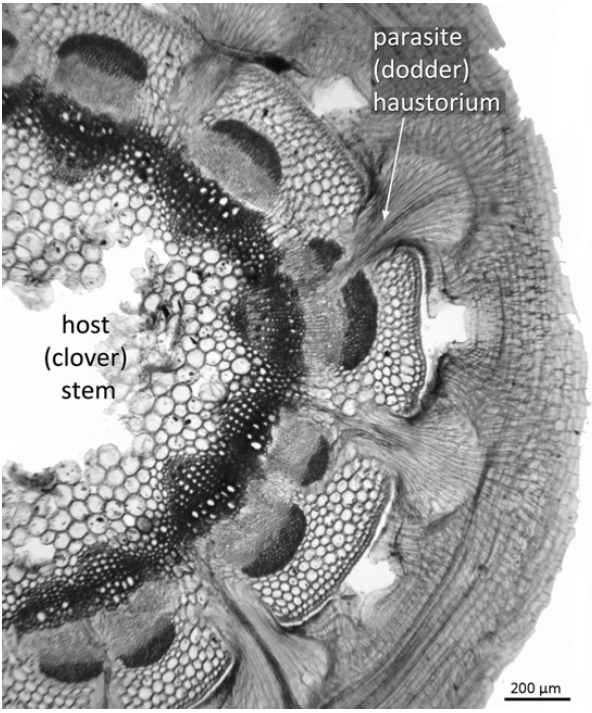

Figure 3.8 Parasite haustoria. *Cuscuta epithymum*, dodder (eudicot: Convolulaceae) parasitic on host stem of *Trifolium*, clover (eudicot: Fabaceae), with several haustoria penetrating host vascular tissue. Scale = 200 µm

tissue around the host organ. In some parasitic plants of mistletoe family (Loranthaceae), the haustorial mantle around the host tissues influences the host to develop a woodrose, which is a woody outgrowth of vascular tissue that forms a conduit for nutrients to the parasite.

4

Leaf

Leaves are determinate lateral organs that are usually dorsiventrally flattened and lack a growing tip. Foliage leaves are green; they are typically borne on stems above ground level because they require sunlight for photosynthesis. Angiosperm leaves consist of a sheathing leaf base that clasps the stem at the node and a distal zone that extends away from the stem to capture light effectively[20, 54, 72, 114, 120]. In eudicots and magnoliids, the sheathing lower zone is often reduced or sometimes absent and the distal zone forms the bulk of the leaf, consisting of a petiole and an elliptical blade (lamina) with net-like (reticulate) venation (Figure 4.1). The margins of the lamina can be smooth, lobed or toothed. Some species possess compound leaves with individual leaflets either borne on a central stem-like axis (pinnate leaves; e.g. tomato: *Solanum lycopersicum*) or radiating from a single point at the distal end of the petiole (palmate leaves; e.g. aroids such as *Arisaema*). In monocot leaves, a sheathing leaf base is typically well developed and the upper zone can be thick or radial in outline, or even reduced to a short, thickened apex. Some underground stems bear reduced scale-like leaves. Underground bulbs possess swollen leaves or leaf bases that contain storage products such as starch to allow the plant to survive below ground during harsh conditions.

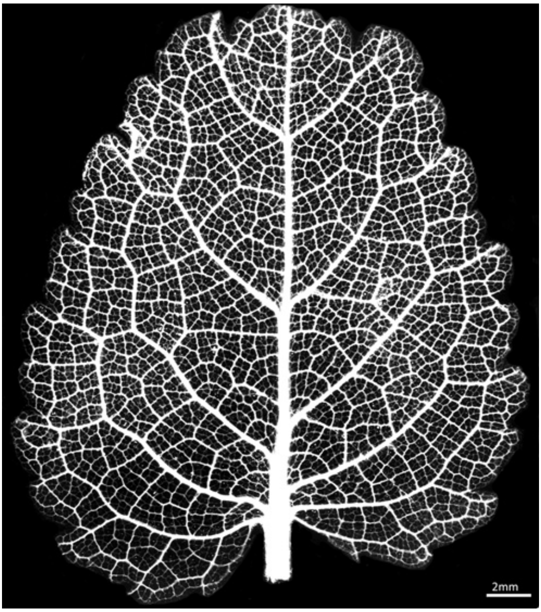

Figure 4.1 Leaf venation. *Hypenia pauliana* (eudicot: Lamiaceae), cleared leaf with reticulate venation. Scale = 2 mm.

4.1 Leaf anatomy

The mature lamina consists of an adaxial and abaxial epidermis enclosing several layers of mesophyll cells interspersed with a network of vascular bundles (Figure 4.2). The majority of species have bifacial (dorsiventral) leaves, in which the adaxial and abaxial surfaces differ and the mesophyll is differentiated into palisade and spongy regions. In unifacial (isobilateral) leaves, the epidermis is similar on both surfaces and the mesophyll is relatively undifferentiated. In monocots with unifacial leaves, the leaf base is bifacial and the lamina is unifacial and either flattened (e.g. in *Acorus* and most Iridaceae) or rounded in transverse section (e.g. terete leaves of some *Allium* species).

4.2 Leaf initiation and development

Leaves are initiated from groups of founder cells located close to the shoot apex, either in the outermost cell layers (L1 and L2) or in

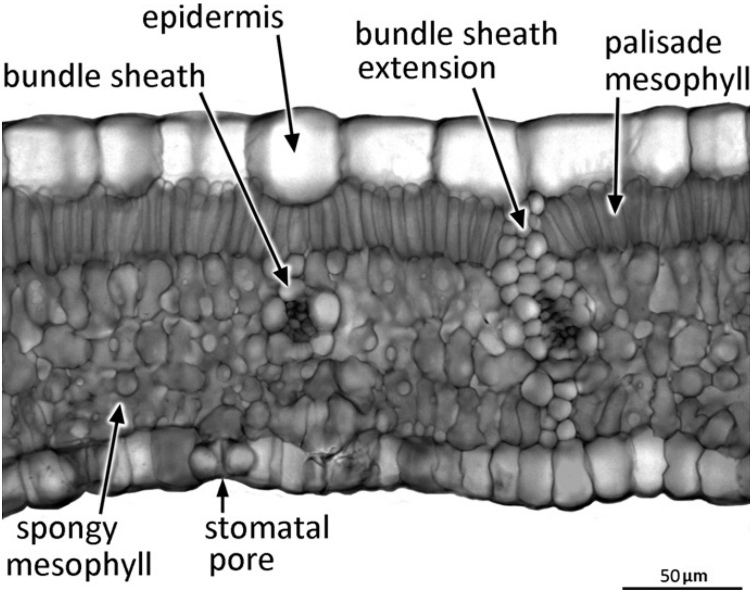

Figure 4.2 Leaf anatomy. *Ficus cordata* (eudicot: Moraceae), transverse section of leaf blade. Scale = 50 μm

the layers immediately below them (L3) (Section 2.1). Founder cells undergo periclinal divisions to form small conical projections that represent the leaf primordia. In monocots, a leaf primordium rapidly develops into a bifacial hood-like structure, its base partially or wholly encircling the stem to form a leaf sheath[71, 114, 160]. In a simple leaf, subsequent meristematic activity occurs in an adaxial transition zone between the precursor tip and sheath. In some monocots such as grasses, epidermal outgrowths (ligules) develop from an abaxial cross zone in this region.

The adaxial marginal cells divide rapidly to form a flattened leaf blade, though marginal growth is suppressed in the region that later becomes the petiole. Marginal growth can occur at the same time as apical growth and is subsequently replaced by cell divisions across the leaf blade; by this developmental stage, the number of cell layers is established and the entire lamina functions as a plate meristem. Subsequent cell divisions are mainly anticlinal, resulting in regular layers of cells that are disrupted only by the differentiation and maturation of the vascular bundles.

Different rates of growth and cell division can occur in different parts of the leaf, resulting in variations in leaf shape. Individual leaflets of a compound leaf can be produced either acropetally or basipetally. For example, in tomato (*Solanum lycopersicum*), the uppermost (distal) leaflets are initiated first, followed by middle and lower leaflets in a basipetal sequence[65]. Smaller intermediate leaflets are formed later, in a more chaotic sequence.

In some monocots, meristematic activity governing leaf elongation is restricted to a basal rib meristem, which results in axial files of cells of increasing maturity towards the distal end of the leaf. The unifacial leaves of some monocots (e.g. *Acorus*), which possess a bifacial sheathing leaf base and a unifacial upper blade, result from suppressed marginal growth and the presence of an adaxial (ventral) meristem in the transition zone[72].

4.3 Leaf epidermis

The leaf epidermis is generally uniseriate, though in a few eudicot and magnoliid species (e.g. *Ficus* and *Peperomia*) it can proliferate into several cell layers to form a multiple epidermis, which resemble a hypodermis. Specialized elements of the leaf epidermis include stomata, trichomes, papillae, surface sculpturing, epicuticular wax and variously differentiated pavement epidermal cells.

In surface view, pavement epidermal cells range in shape from elongated to isodiametric. Cells over veins are often elongated, especially in eudicots with reticulate venation, in which the costal regions (over veins) develop before the intervening (intercostal) regions. In the linear leaves of many monocots, the epidermal cells are elongated along the long axis of the leaf. Anticlinal cell walls can be straight or undulating; they are often more sinuous on the abaxial than the adaxial surface of the same leaf (Figure 4.3). Epidermal cells can also differ in size and wall thickness in different parts of the same

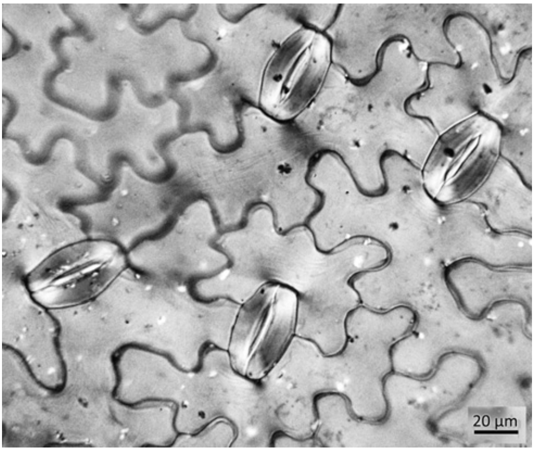

Figure 4.3 Leaf surface. *Vicia faba* (eudicot: Fabaceae), abaxial leaf surface with undulating anticlinal walls. Scale = 20 µm

leaf. In some grasses, restricted regions of the leaf epidermis contain enlarged bulliform cells that play a role in the unrolling of the leaf in response to turgor pressure and water availability.

Specialized epidermal cells can contain crystals or silica bodies (Section 1.4). For example, cystoliths are calcareous bodies that occur either solely in epidermal cells (e.g. in the family Opiliaceae) or across both the epidermis and underlying mesophyll (e.g. in *Ficus*: Figure 4.4), occasionally protruding above the leaf surface. Discrete bodies of silicon dioxide (silica phytoliths) occur in specialized epidermal cells in some monocot families (e.g. sedges and grasses). The grass epidermis is characterized by dimorphic long and short cells resulting from asymmetric divisions (Figure 4.5); each short cell often divides symmetrically to form a short-cell pair that includes a silica cell (Figure 1.5) and a cork cell[118].

Stomata (Section 1.9) occur on almost all angiosperm leaves, except the submerged leaves of some aquatic plants, which lack stomata entirely (e.g. *Ceratophyllum* and Podostemaceae). In species with amphistomatic leaves, stomata are present on both leaf surfaces, whereas in species with hypostomatic leaves they are

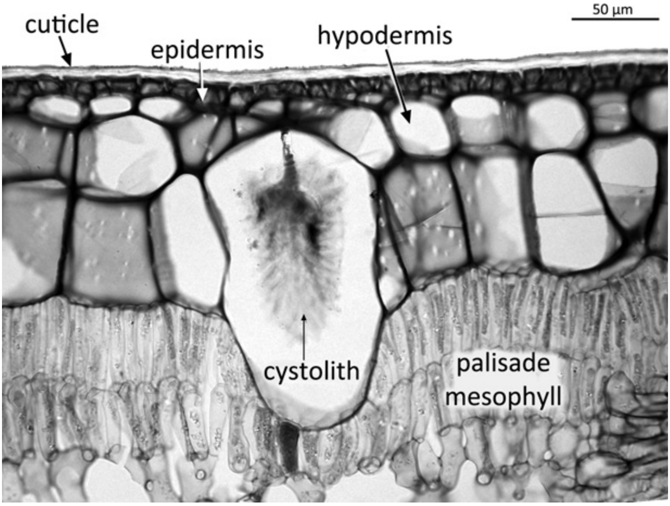

Figure 4.4 *Ficus elastica* (eudicot: Moraceae), transverse section of leaf blade showing adaxial epidermis and cystolith. Scale = 50 µm

restricted to the abaxial surface. The floating leaves of many aquatic plants are epistomatic, stomata being restricted to the adaxial surface.

4.4 Cuticle and wax

In mesomorphic leaves, the cuticle is thin and almost transparent, but many xeromorphic plants possess a thick leaf cuticle that often appears lamellated in transverse section. In some species, the outer surface of the leaf cuticle possesses characteristic patterns of ridges, folds or striations. These striations can be short or long and oriented randomly or in a regular pattern, sometimes radiating around stomata or trichomes (Figure 4.6). Surface patterning has biological significance in relation to mechanical and optical properties and wettability of the surface.

Plant leaves have a covering of epicuticular wax over the surface of the cuticle, ranging from a thin, almost imperceptible film to crystalloid particles or a dense surface crust that gives the leaf surface a whitish appearance[9] (Figure 4.7). Some species of *Euphorbia* have wax chimneys surrounding the stomatal pore,

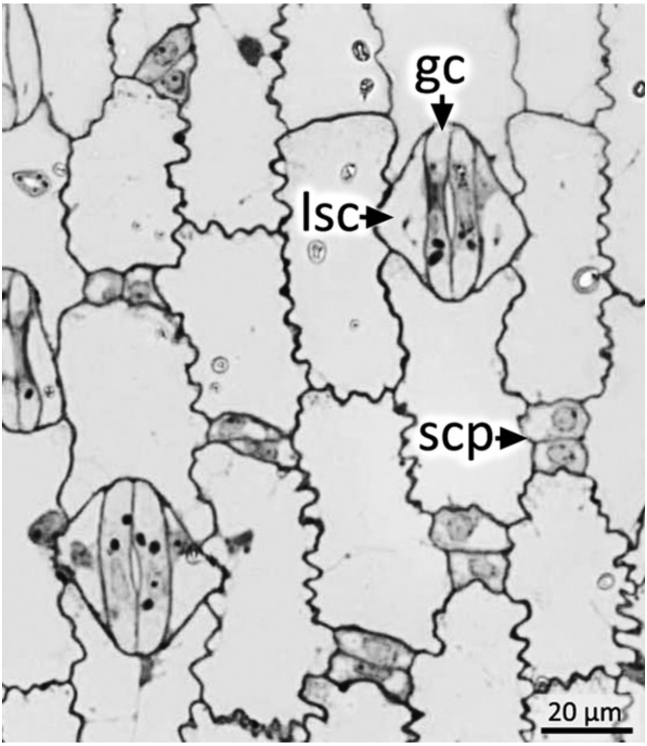

Figure 4.5 Grass epidermis. *Coix lacryma-jobi* (monocot: Poaceae), abaxial leaf surface showing short-cell pairs (scp), stomata with guard cells (gc) and adjacent lateral subsidiary cells (lsc). Scale = 20 µm

derived from an extended crust. Individual epicuticular wax particles display considerable morphological diversity that can be characteristic of the species, including irregular granules, straight or coiled rodlets, hollow tubules and flat platelets. These characteristic structures are determined by their chemistry; for example, coiled rodlets are predominantly composed of β-diketones. Epicuticular wax particles can be variously arranged in aggregates, rows or rosettes and are often oriented at a specific angle to the surface. Like the cuticle, epicuticular wax is hydrophobic and protects the plant surface from water loss, especially in species that occupy dry habitats.

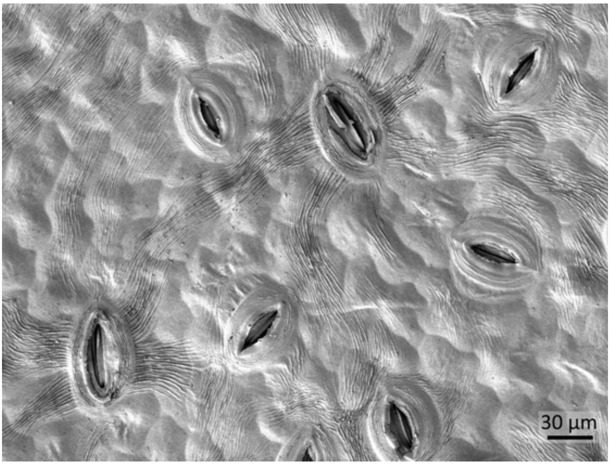

Figure 4.6 Surface patterning. *Schisandra rubriflora* (ANA-grade: Schisandraceae), abaxial leaf surface showing cuticular striations radiating around stomata (SEM). Scale = 30 µm

4.5 Trichomes and papillae

The presence, distribution and detailed structure of the leaf trichome complement (indumentum) can be highly characteristic of a species (Figures 1.12, 1.13). Trichomes are sparse or absent in glabrous leaves. Trichomes can occur over the entire leaf surface, or they can be restricted to particular regions, such as abaxial grooves (Figure 4.8) or leaf margins. In many species, several different types of trichome occur on the same leaf. For example, mints (Lamiaceae) characteristically possess two or more sizes of glandular trichome and non-glandular trichomes that are either branched or unbranched.

Specialized leaf hair types include stinging hairs, sensory hairs, water-absorptive leaf scales and salt-secreting glands that accumulate excess sodium chloride, allowing plants to colonize highly saline soils (e.g. in *Avicennia*, *Limonium* and *Tamarix*). Stinging hairs characterize five families of eudicots[91] and are epitomized by the common stinging nettle (*Urtica dioica*). They are hollow structures that are rigid (silicified or calcified) and taper to a spherical tip (Figure 1.13). The tip is readily broken off in contact with an

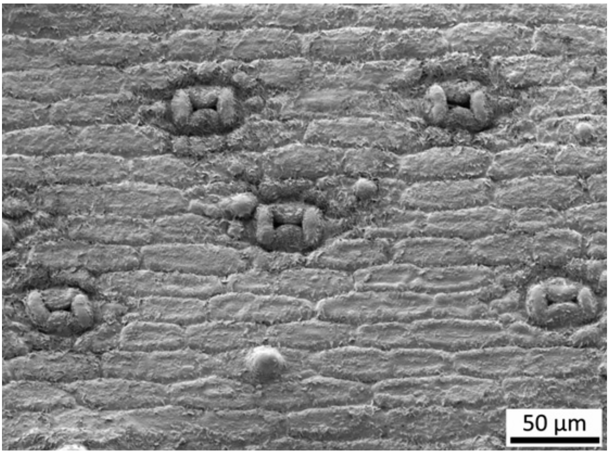

Figure 4.7 Surface waxes. *Yucca queretaroensis* (monocot: Asparagaceae), leaf surface showing epicuticular waxes around stomata (SEM). Scale = 50 µm

intruder, enabling the residual sharp point to penetrate the skin and release a toxic fluid, thus forming an effective deterrent.

Sensory trigger hairs occur on leaves of some carnivorous plants, such as the Venus flytrap (*Dionaea muscipula*), which traps insects in a highly specialized bilobed leaf structure. A mechanical stimulus such as the touch of an unwary insect on two or more of the six long trichomes generates an electrical signal; a second stimulus rapidly activates the trap to capture the insect[150]. Trichomes of other carnivorous plants (e.g. *Drosera*) secrete both sticky mucilage and proteolytic enzymes that help to capture and digest the prey.

4.6 Extrafloral nectaries, domatia and hydathodes

Localized regions of the leaf epidermis can be specialized for particular roles, including extrafloral nectaries and water pores[156]. Some plants exude water from their leaves during humid conditions when there is sufficient soil moisture; this guttation process accelerates passage of nutrients through the plant when transpiration is low (e.g. at night). Guttation is achieved

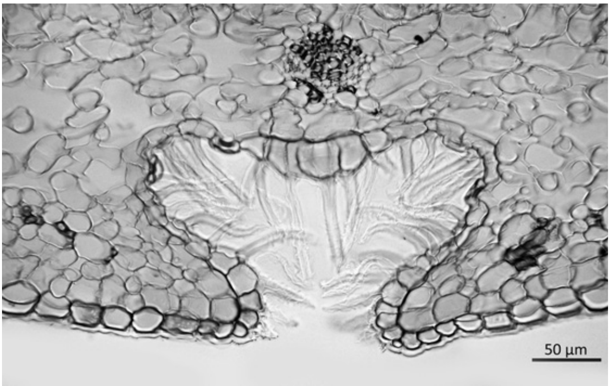

Figure 4.8 *Erica carnea* (eudicot: Ericaceae), transverse section of leaf showing abaxial groove containing trichomes and stomata. Scale = 50 µm

via specialized leaf epidermal regions termed hydathodes, which are water glands located most commonly at the leaf margins, especially at the leaf teeth. Hydathodes typically consist of a region of modified stomata located over a region of loosely arranged mesophyll cells (epithem) associated with a vein ending. They can also be involved in absorption of water from rain and dew.

Some plants provide food rewards that attract insects, especially ants, which can protect the plant against potential herbivores. Food bodies or pearl glands are scattered isolated globular trichomes that occur on leaves of some tropical eudicots and magnoliids. They are rich in carbohydrates, lipids and proteins and are harvested by ants[95]. Extrafloral nectaries are specialized epidermal regions that secrete sugary nectar, which is attractive to small invertebrates such as ants and mites (Figure 4.9). These localized structures consist either of groups of glandular trichomes (e.g. in some *Hibiscus* species) or raised regions of anticlinally elongated secretory epidermal cells, often associated with underlying vascular tissue, in which case they resemble hydathodes. Extrafloral nectaries can be located over veins, in the angles between primary and secondary veins, on inrolled leaf margins or at the proximal or distal ends of the petiole, sometimes situated in specialized pits or

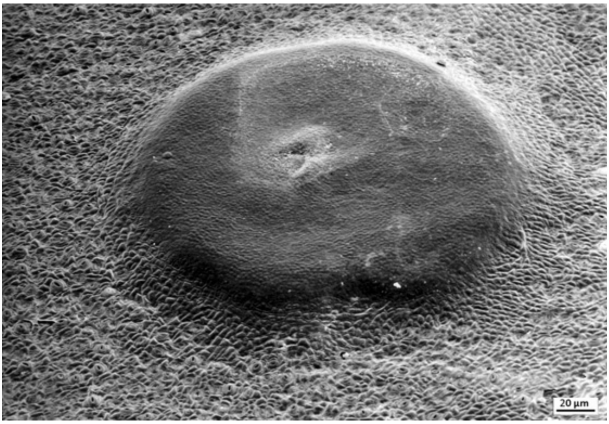

Figure 4.9 *Omphalea triandra* (eudicot: Euphorbiaceae), extrafloral nectary on abaxial leaf surface. Scale = 20 μm

hair-lined pockets (domatia) that provide accommodation for invertebrates. Increased herbivory can stimulate the plant to produce more extrafloral nectaries, and in some cases, the insects themselves can stimulate production.

4.7 Mesophyll

Chlorophyll is contained in chloroplasts in the mesophyll, which is the primary photosynthetic tissue of the leaf. In many plant species the mesophyll is demarcated into distinct regions, termed palisade and spongy tissues (Figures 4.2, 4.4), though in some species the mesophyll is relatively undifferentiated and homogeneous throughout the leaf. Palisade mesophyll is located on the adaxial side of the leaf and spongy mesophyll on the abaxial side. Palisade cells are anticlinally elongated and possess relatively few intercellular air spaces; they often occur in a single layer, but can be arranged in two or more layers. In contrast, spongy mesophyll consists of several layers of cells of various shapes interspersed with numerous air spaces.

In thick leaves, the central mesophyll cells are often large, undifferentiated and non-photosynthetic. In the thick, fleshy

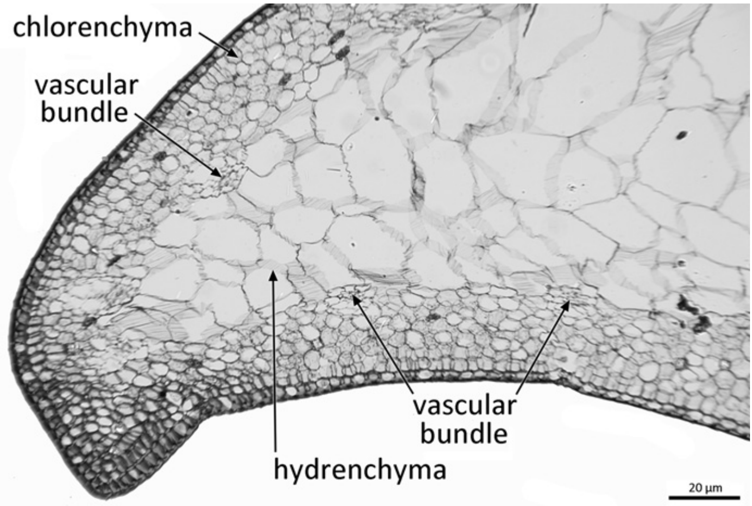

Figure 4.10 Succulent leaves. *Aloe somaliensis* (monocot: Asphodelaceae), transverse section of leaf margin showing outer chlorenchyma, inner hydrenchyma, and two rows of small vascular bundles that lack sclerenchyma. Scale = 20 µm

leaves of succulent plants such as many *Aloe* species (Figure 4.10), the inner leaf mesophyll cells have relatively elastic wall properties, enabling water storage in a specialized hydrenchyma tissue that can be utilized during periods of drought[1]. In the thick "keel" or "midrib" of *Crocus* leaves there is a region of large parenchymatous cells with thin walls, which often break down to form a cavity (Figure 4.11); this effect causes the characteristic white stripe visible in the midrib region of *Crocus* leaves.

In some plants (e.g. *Ficus*, Figure 4.4) subdermal mesophyll layers located immediately within the adaxial (or more rarely the abaxial) epidermis are modified into a hypodermis. Hypodermal tissue consists of one or more layers of non-photosynthetic cells that are usually slightly larger and thicker walled than adjacent mesophyll cells and frequently resemble epidermal pavement cells in transverse section.

Mesophyll is often interspersed with tissues that provide mechanical strengthening; for example, sclerenchyma is frequently present

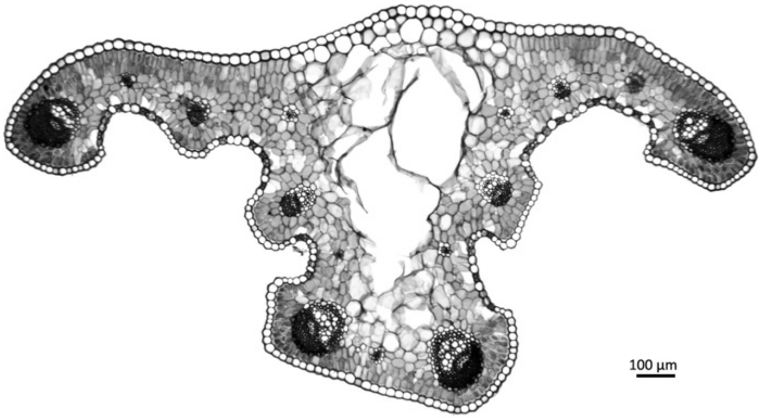

Figure 4.11 *Crocus cancellatus* (monocot: Iridaceae), transverse section of leaf. Scale = 100 µm

at leaf margins and extending as girders from the vascular bundles to the epidermis. Fibres are often present as vascular bundle caps, especially associated with the phloem poles.

Various types of idioblast are often present in mesophyll, including crystal idioblasts and non-articulated laticifers, which permeate all parts of the plant in some eudicots such as *Euphorbia* and *Ficus* (chapter 1.12). Sclereids occur in the leaf mesophyll in many species; for example, star-shaped astrosclereids occur in the lamina of *Nymphaea* and the petiole of *Camellia* (Figure 1.9) and bone-shaped osteosclereids are present in the palisade tissue of some species with centric leaves. In some eudicot species (e.g. some Melastomataceae), sclereids are associated with veinlet endings; some terminal sclereids (e.g. in *Mouriria*) resemble swollen tracheids with spirally thickened or pitted walls and are widely interpreted as storage tracheids[43].

4.8 Leaf vasculature

Many eudicots and magnoliids are characterized by densely reticulate leaf vein architecture (venation) that enables greater transpiration efficiency[15, 20, 60, 123]. Leaves with reticulate, net-like venation possess a primary vein (midrib) extending from the base to the tip (Figure 4.1). The midrib is linked to smaller secondary veins that radiate outward. They either extend to the leaf margins, where they can terminate at a leaf tooth, or loop round to join the superadjacent secondary vein. In their turn, smaller veins branch from the second-order and subsequent-order venation, thereby forming a complex network. The regions circumscribed by the smallest veins in the leaf are termed areoles. In many species, small veins branch into the areoles to form veinlet endings; the relative number of veinlet endings per areole represents a variable aspect of leaf venation.

In contrast, venation is parallel in many monocots with narrow, linear leaves. In these species, the primary veins run parallel to each other for most of their length and merge or fuse at the leaf tip. There are typically numerous small veins interconnecting the larger veins, but relatively few vein endings in the mesophyll.

Petioles also possess characteristic venation patterns. The simplest form of petiole vasculature appears in transverse section as a vascular crescent, with xylem on the adaxial side and phloem on the abaxial side (Figure 4.12). In some species, the vascular crescent is inrolled at the ends; in others it forms a ring or is divided into separate bundles. Some species possess additional bundles outside the main vascular crescent. In transverse sections of the lamina, vascular bundles are typically arranged in a single row (Figure 4.2), though two or more rows of leaf vascular bundles are present in species with very thick, succulent leaves, such as *Agave* and *Aloe* (Figure 4.10). Lamina bundles are most commonly collateral, with adaxial xylem and abaxial phloem, but orientation can vary, so that some bundles are bicollateral or even amphivasal (with xylem surrounded by phloem). The isobilateral leaves of some monocots possess two rows of vascular bundles with opposite orientation to each other; the xylem poles towards the leaf centre. Centric leaves possess a ring of vascular bundles.

Leaf vasculature develops acropetally from a primordial procambial strand[20, 79]. The central trace develops first and ultimately

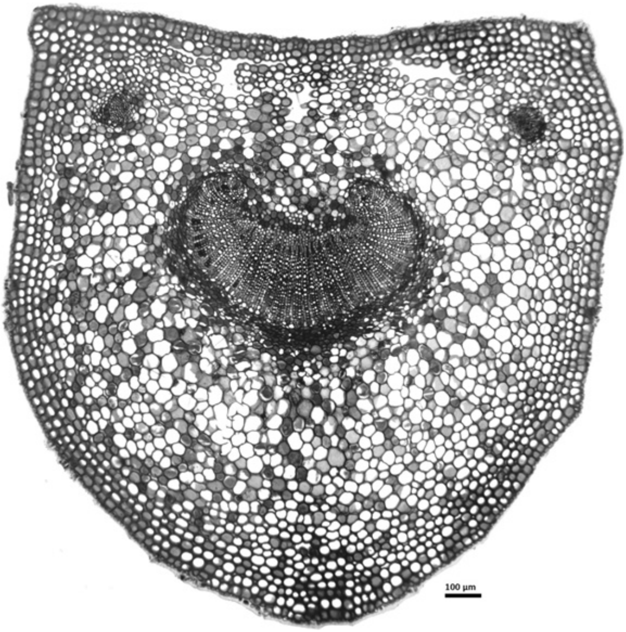

Figure 4.12 Petiole anatomy. *Prunus lusitanica* (eudicot: Rosaceae), transverse section of petiole. Scale = 100 µm

becomes the primary vein (midrib). The timing of initiation of lower-order venation differs among different species, depending on ultimate leaf shape and venation pattern. Both xylem and phloem tissues are present in the leaf blade, even in minor veins, though the smallest vascular bundles often have only one or two rows of xylem tracheids and a few files of phloem sieve-tube elements. The xylem conducting system can consist entirely of tracheids with helical or annular thickenings, though in some leaves both vessel elements and xylem parenchyma are also present.

4.9 Bundle sheath and Kranz anatomy

Most minor vascular bundles in angiosperm leaves are surrounded by a bundle sheath, which extends even to the very smallest veins. The bundle sheath usually consists of thin-walled parenchymatous cells, often arranged in a single layer. Some monocots possess distinct inner and outer bundle sheaths, of which the outer sheath is parenchymatous and the (partial) inner sheath is sclerenchymatous, forming a sclerenchyma cap that is usually located at the phloem pole. Grasses possess either a single sheath consisting of an outer layer of thin-walled cells containing chloroplasts or a double sheath consisting of an outer layer of thin-walled cells and an inner layer of thicker-walled cells. This distinction can represent an important distinguishing feature between different grass groups; for example, double sheaths often occur in festucoid grasses and single sheaths in panicoid grasses. Leaves of many plants possess regions of sclerenchyma or parenchyma that extend from the vascular bundle sheaths towards either or both epidermises. These bundle sheath extensions, termed girders if they reach the epidermis, can afford mechanical support to the leaf.

Some plants that undergo the C_4 pathway of photosynthesis, including both monocots (e.g. some grasses) and eudicots (e.g. some Chenopodiaceae), display modified leaf anatomy termed Kranz anatomy (Section 1.3)[31, 124]. Kranz anatomy is characterized by elongated mesophyll cells radiating from an outer bundle sheath consisting of a single layer of large parenchymatous cells that contain starch and enlarged chloroplasts; this specialized sheath itself surrounds an inner sheath (Figure 4.13). Carbon assimilation occurs in the radiating mesophyll cells, where the enzyme phosphoenolpyruvate carboxylase (PEP carboxylase) is localized, followed by carbon reduction in the outer bundle sheath, where the carboxylating enzyme Rubisco is localized.

4.10 Ecological adaptations in leaves

Features that are often associated with water plants (hydrophytes) include the absence of sclerenchyma and the presence of large regular air spaces in the ground tissue (aerenchyma). Submerged leaves typically lack stomata entirely. In floating leaves, stomata are restricted to the upper (adaxial) surface and water-absorptive hairs (hydropotes) are often present on the submerged surface (Section 1.10).

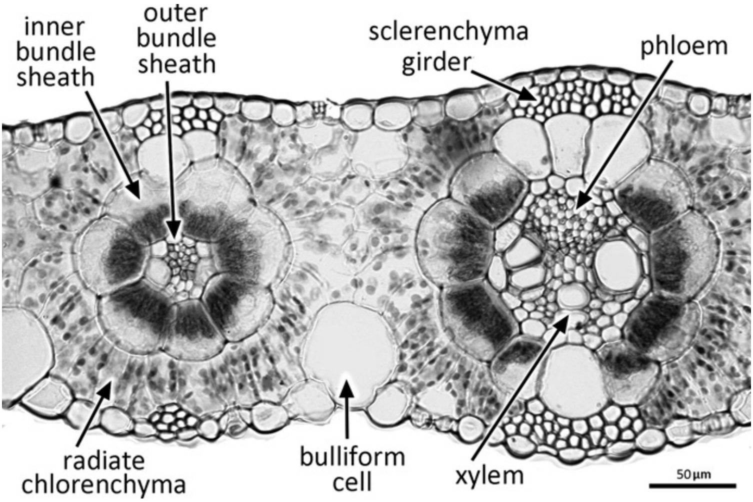

Figure 4.13 Kranz anatomy. *Eleusine coracana* (monocot: Poaceae), transverse section of leaf. Scale = 50 µm

In contrast, plants that grow in dry, seasonally dry or otherwise nutrient-deficient habitats (collectively termed xerophytes) can possess a range of specialized features that minimize collapse during drought periods; contrasting xeromorphic traits characterize different xerophytes. In some species, well-developed sclerenchyma provides mechanical support. Some xeromorphic species possess thick or succulent leaves (e.g. *Aloe*: Figure 4.10). Others have terete (centric or cylindrical) leaves, or hairy leaves, or even rolled or folded (plicate) leaves (Figure 4.14). Thick and terete leaves possess a reduced surface/volume ratio to reduce water loss. Leaf folding within a bud helps to minimize water loss in unexpanded developing leaves; on subsequent expansion, the leaf can achieve a large surface area. Succulent plants contain a high proportion of large thin-walled cells that play a role in water storage, often containing a high proportion of mucilage.

In many xeromorphic species, protected stomata restrict water loss by transpiration. For example, individual stomata can be raised

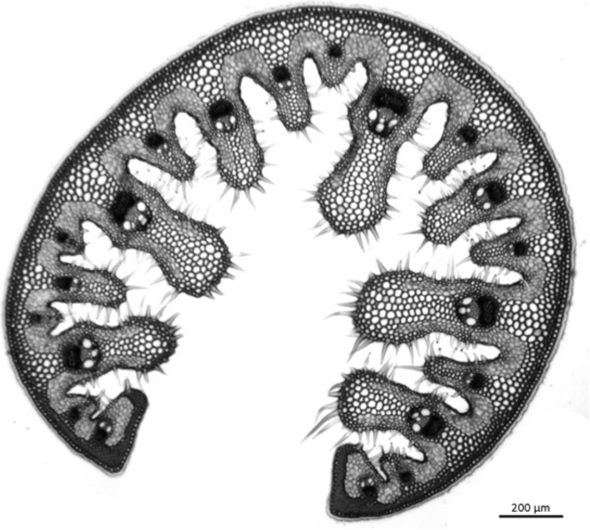

Figure 4.14 *Ammophila arenaria* (monocot: Poaceae), transverse section of rolled leaf. Scale = 200 µm

or sunken with respect to the surface, or groups of stomata can be confined to hair-lined grooves or depressions on the abaxial leaf surface, thus trapping a pocket of water vapour in an air chamber either externally or internally (Figure 4.8). A hypodermis or thick epidermis and cuticle can reduce the intensity of light that reaches the photosynthetic tissue. Well-developed palisade tissue in multiple layers is sometimes correlated with high light intensity.

Most leaf stomata are associated with a substomatal cavity in the underlying mesophyll; these cavities are also relatively high in water vapour and represent important sites for exchange of solutes and gases. During early development, the stomata are initiated over the junction between underlying cortical or mesophyll cells. Epidermal cells continue to enlarge after the mesophyll cells have ceased expansion. Differential expansion between the guard-mother cell and developing mesophyll cells influences several aspects of leaf anatomy, including the substomatal cavity[5, 49, 78].

5

Flower

Flowers are borne on reproductive axes, either as solitary structures or on inflorescences, which can be unbranched or variously branched (Figure 5.1). In a determinate inflorescence, the inflorescence apex is terminated by a flower, whereas in an indeterminate inflorescence it maintains growth until the apical meristem becomes exhausted[32, 152]. Each flower is often subtended by one or two modified leaf-like sterile bracts borne on the inflorescence axis, though bracts are entirely absent from some species. Some species also possess one or more leaf-like bracteoles on the flower axis. At the onset of flowering, the shoot apical meristem undergoes structural modification that transforms it from a vegetative apex to a reproductive apex.

5.1 Flower structure

The floral axis (receptacle) is unbranched, determinate and highly condensed. It bears several distinct organ regions in a consistent radial sequence[10, 32, 107, 152]. The densely crowded floral organs are arranged either in distinct whorls or in a spiral pattern on the axis. Each organ series consists of one or more whorls. In a typical flower bud, an outer region of sterile organs (either tepals, or sepals and petals) encloses the pollen-bearing organs (stamens), which in turn are outside the ovule-enclosing organs (carpels). The outer sterile organs represent the perianth, and the stamens and carpels form the androecium and gynoecium respectively. In

Figure 5.1 Inflorescence of *Arabidopsis thaliana* (eudicot: Brassicaceae) (SEM). Scale = 500 µm

species with a syncarpous ovary, the gynoecium terminates the short floral axis, though a residual floral axis exists in some species with free carpels (Figure 5.2).

Different organ arrangements characterize different angiosperm lineages. For example, some species possess unisexual flowers, in which one of the reproductive organ types is either absent or sterile: female flowers lack functional stamens and male flowers lack carpels. In the grass family Poaceae, the flowers are highly reduced structures (florets) that are grouped together in spikelets. Each floret is subtended by a sterile leaf-like structure, the palea, which surrounds two (occasionally three) reduced structures termed lodicules; these are widely interpreted as representing a single modified perianth whorl[2, 75, 119].

The degree of fusion of individual floral organs within each flower differs between species. Individual organs can be fused together within the same whorl (connate) or fused with other organs in adjacent whorls (adnate). A typical example of adnation occurs in

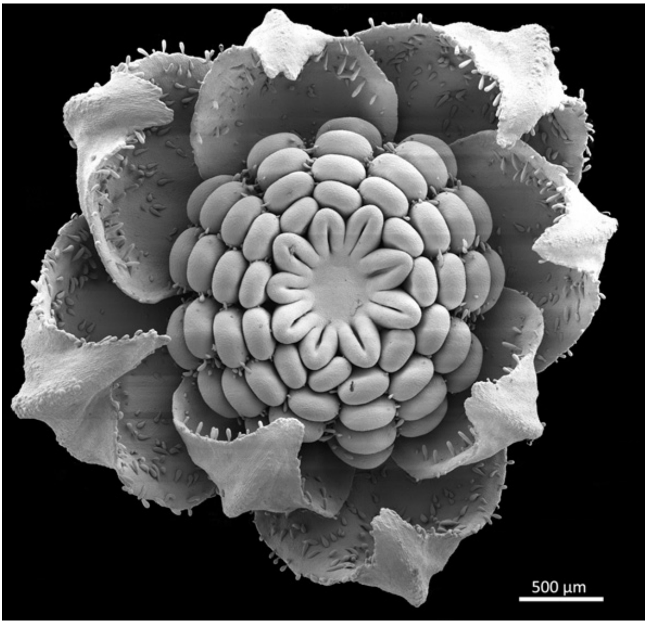

Figure 5.2 *Nigella bucharica* (eudicot: Ranunculaceae), scanning electron micrograph of developing flower bud with sepals removed, showing primordia of eight petals and multiple stamens in spiral arrangement and a single whorl of five free carpels surrounding a residual apex. Scale = 500 µm

flowers where the stamens are borne on the perianth. An example of connate organs includes species in which the petals are fused together (at least at their bases) to form a corolla tube or perianth tube, as in many asterid eudicots. Similarly, in many angiosperms, the carpels are fused into a single unified gynoecium (Figure 5.3).

5.2 Floral ontogeny

During early flower development, the lateral organ primordia are generally initiated in centripetal (acropetal) sequence, so that the latest primordia to be initiated are located close to the floral apex. For example, in the magnoliid *Drimys* (Winteraceae), the

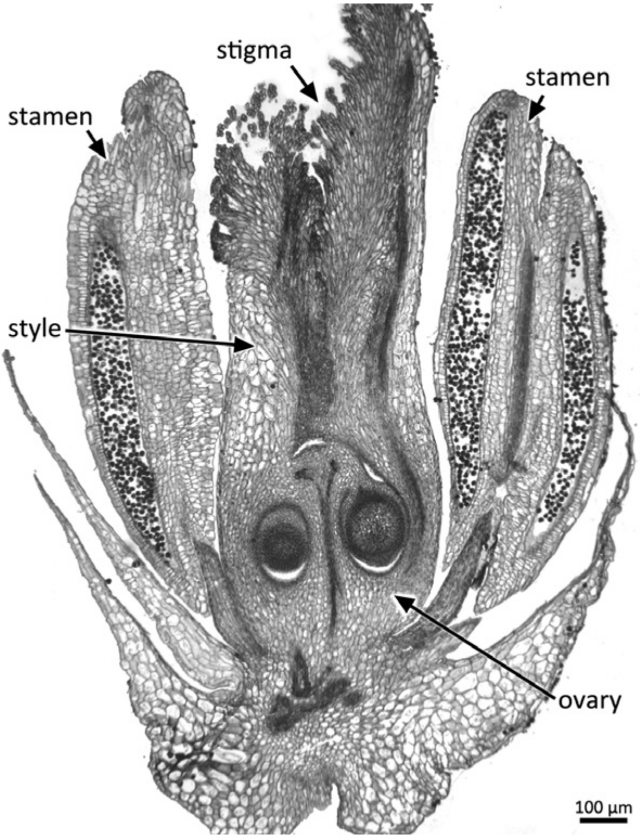

Figure 5.3 *Flagellaria indica* (monocot: Flagellariaceae), longitudinal section of flower. Scale = 500 µm

innermost stamens are the last to be initiated in the developing flower bud, even though they ultimately grow larger than the other stamens and are the first to dehisce in the open flower[142]. Some species deviate from a strict centripetal progression, so that some floral organs are initiated in a distal-to-proximal (centrifugal or basipetal) sequence, either within or between organ zones[113]. For example, in *Lythrum salicaria*, the outer sepal whorl is initiated after the inner sepal whorl, the inner stamen whorl is initiated after the gynoecium, and the petals are initiated after both the gynoecium and the androecium. In some palm flowers that contain large numbers of stamens, the inner stamens are initiated before the outer ones[144]. These examples suggest that the floral apex is pre-patterned into zones even before the organ primordia become visible. Changes in auxin levels across the apex can result in different sequences of organ initiation. In some species, groups of floral organs are initiated in clusters (fascicles) on shared primordia, which are themselves arranged in whorls; for example, stamen fascicles are common in the eudicot families Malvaceae and Hypericaceae (Figure 5.4).

Following initiation, floral organs expand both axially and laterally to assume their ultimate shape. In many flowers, organ expansion continues after bud opening; for example, many petals continue to expand in size and increase in colour after the flower bud is open. Organ fusion is important in determining flower shape and presentation to potential pollinators. In some species, floral organs are initiated separately and become fused during development, a process termed ‘postgenital fusion’. Postgenital carpel fusion characterizes many monocots, in which the contacting

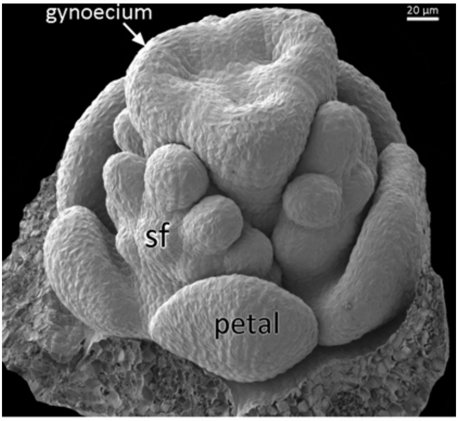

Figure 5.4 *Hypericum empetrifolium* (eudicot: Hypericaceae), SEM of developing flower bud with outer organs removed, showing primordia of petals, stamen fascicles (sf) and syncarpous gynoecium. Scale = 20 μm

epidermal cells of adjacent developing carpels become pressed together and eventually lose their epidermal identity[106]. In contrast, many floral organs are profoundly united from their inception, a mode of development that is termed congenital fusion or synorganization. An extreme example of congenital fusion occurs in the reproductive organs of most orchids, which form an integrated structure termed a gynostemium. Another example is the perianth tube of many asterid eudicots, in which the petals are congenitally fused at their bases.

5.3 Floral vasculature

In the majority of flowers, each organ is supplied by one or more vascular strands that diverge from the central vascular cylinder of the floral axis (Figure 5.5). Vascular traces often branch above their level of divergence from the stem vasculature; perianth traces are often highly branched, forming a vascular network that

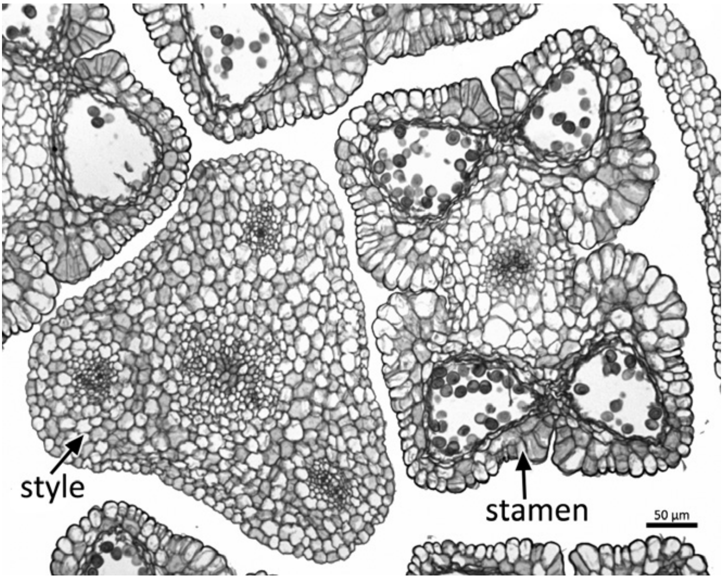

Figure 5.5 *Flagellaria indica* (monocot: Flagellariaceae), transverse section of central region of flower, showing a stamen with a single central vascular bundle and the style with three vascular bundles surrounding a central transmitting tissue. Scale = 50 µm

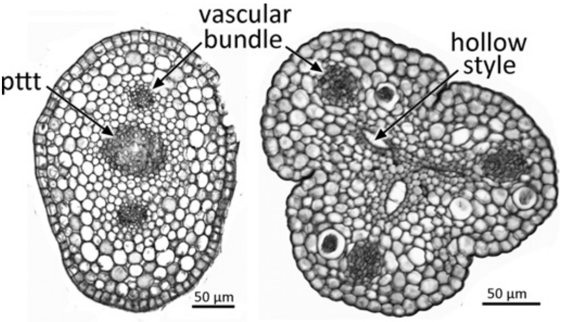

Figure 5.6 Transverse sections of styles. (left) *Salvia pratensis* (eudicot: Lamiaceae), with two vascular bundles and a central pollen-tube-transmitting tissue (pttt). (right) *Cordyline cannifolia* (monocot: Asparagaceae), with three vascular bundles and three mucilage-lined channels. Scales = 50 µm

develops as the organ expands laterally. Most stamens possess a cylindrical filament that bears a single central vascular strand, though some families are characterized by three or four stamen traces and a few species possess diverse and often branching stamen vasculature. Many carpels are supplied by three vascular bundles, of which the dorsal carpellary trace, which is typically unbranched, passes along the style and supplies the stigma, and two ventral carpellary traces, which are often highly branched, supply the placenta and ovules[6, 30, 143] (Figure 5.10). In many species, the two ventral carpellary bundles are fused together above the level of carpel closure. The number of dorsal carpellary bundles in the style of a syncarpous gynoecium is often an indicator of the constituent number of fused carpels; many tricarpellate monocots possess three stylar bundles whereas many bicarpellate eudicots possess only two (Figure 5.6).

5.4 Perianth

Perianth organs are dorsiventrally flattened. They consist of an abaxial and adaxial epidermis enclosing three or four (or more) layers of undifferentiated isodiametric or elongated mesophyll cells, interspersed with a row of vascular bundles. In most eudicots, the perianth is differentiated into two distinct series or whorls: an outer sepal whorl (calyx) and an inner petal whorl (corolla). In contrast, there is little clear morphological distinction between the inner and outer perianth organs of many early divergent angiosperms, monocots and some basal eudicots; such undifferentiated perianth organs are termed tepals rather than petals and sepals. Sepals, which envelop the unopened flower bud, are typically green and photosynthetic, with stomata and trichomes commonly present on their surfaces. Petals are typically large and colourful in insect-pollinated plants but reduced or absent in many wind-pollinated plants. Tepals often display a gradual transition from outer, green (i.e. sepaloid) organs to inner, coloured (i.e. petaloid) organs[33, 151].

Flower colour is primarily controlled by pigment chemistry. Anthocyanins, betalains and ultraviolet-absorbing flavonoids are largely confined to the epidermal cells of the petal, whereas other pigments, such as carotenoids, mostly occur in the mesophyll[74]. Petal surfaces frequently lack stomata and the petal epidermal cells are often domed or papillate (Figure 5.7). The effect of the domed cell surface is to guide incident light into the petal, where it is reflected outwards from the inside walls of the epidermal cells or from the multifaceted walls of mesophyll cells, thus passing through the pigments inside the cell. Many petal surfaces possess a strongly striated cuticle, which further scatters incident light. In contrast, some petal surfaces are smooth and mirror-like, strongly reflecting incident light and resulting in a glossy effect (e.g. in buttercup and mirror orchids[74, 146, 147]).

5.5 Androecium

Stamens typically consist of a stalk-like filament that supports the pollen-producing anther[24]. Most stamen filaments are

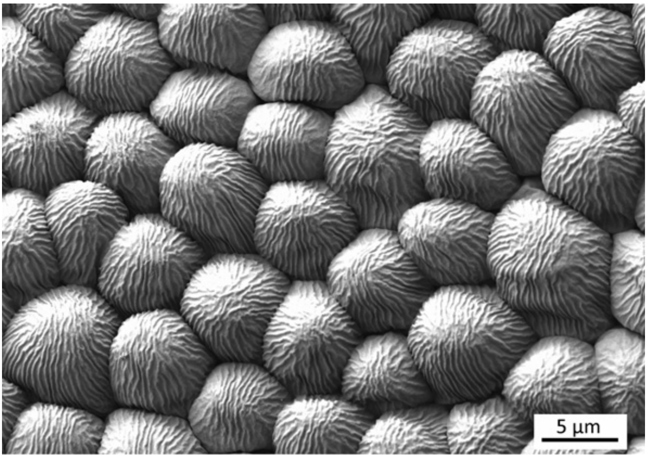

Figure 5.7 *Arabidopsis thaliana* (eudicot: Brassicaceae), scanning electron micrograph showing domed cells on petal surface. Scale = 5 µm

slender and cylindrical, but in some species they are flattened and leaf-like (e.g. in *Nymphaea odorata*) or even branched (e.g. in *Ricinus communis*). In some polyandrous angiosperms (bearing multiple stamens), the stamens are borne in clusters, termed fascicles, each fascicle developing from a single primordium on the early floral apex (Figure 5.4). The filament surface can bear trichomes and stomata and sometimes displays cuticular patterning. In transverse section, the filament contains parenchymatous ground tissue surrounding a single vascular bundle that extends into the connective tissue between the anther locules.

The anther bears four sporangia separated into two pairs (thecae), linked together by a connective. Each theca possesses two sporangia or anther locules divided by a septum[24]. The anther wall consists of several cell layers: the outer epidermis encloses the endothecium, which in turn encloses one or more middle layers; the tapetum is the innermost layer, which surrounds the anther locule (Figures 5.8 and 5.9). The endothecium and tapetum are the most specialized layers; their enlarged cells

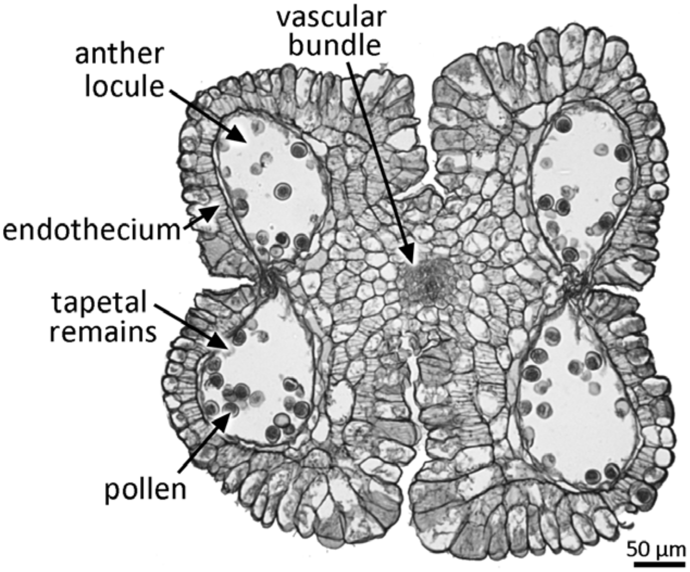

Figure 5.8 *Flagellaria indica* (monocot: Flagellariaceae), transverse section of anther containing mature pollen; by this stage the tapetum has largely degenerated. Scale = 50 µm

often crush the intervening middle layers in older anthers. Endothecial cells develop fibrous wall thickenings that contribute to the anther dehiscence mechanism.

In some species, a layer of tapetal cells persists around the anther locule; this type of tapetum is termed the secretory type. In contrast, in species with a plasmodial tapetum, the tapetal cells undergo programmed degeneration and their protoplasts fuse to form a multinucleate tapetal plasmodium (a periplasmodium) inside the anther locule. Transitional types of tapetum occur in some species, especially among early divergent angiosperms[45]. Tapetal cells are often multinucleate and contain dense cytoplasm. They can produce a range of substances, including sporopollenin, which forms a major component of the pollen wall (exine), and also proteins and lipids that are retained in chambers in the exine and allow sporophytic recognition when the pollen arrives on a stigma.

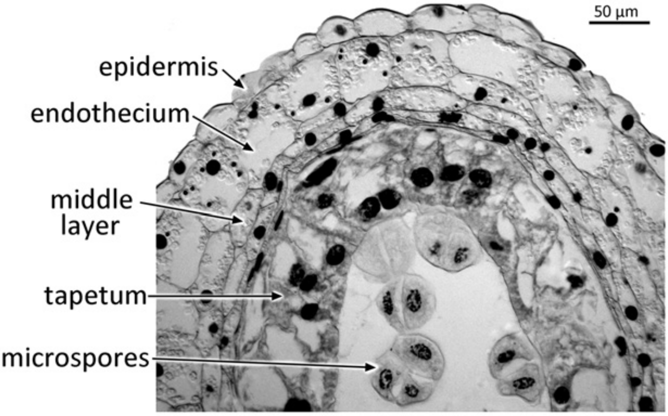

Figure 5.9 *Lilium martagon* (monocot: Liliaceae), transverse section of anther wall containing developing microspores and tapetum. Scale = 50 µm

5.6 Gynoecium

Carpels are the ovule-bearing floral organs. The number of carpels per flower ranges from a single carpel to multiple carpels in different species. Monocots typically possess three carpels (Figure 5.10), whereas the most common carpel numbers in eudicots are two and five[34]. In the majority of flowering plants, the carpels are fused together to form a syncarpous gynoecium, which represents the central region of the flower. In contrast, the carpels remain unfused (free) in apocarpous species, especially among early divergent angiosperms (e.g. *Amborella*, *Illicium*), but also in many eudicots, magnoliids and monocots[34].

A syncarpous gynoecium consists of an ovary, style and one or more stigmas (depending on the degree of fusion of the carpels). The stigma provides a receptive surface for pollen grains. Stigmatic epidermal cells are usually secretory; they are often domed or possess variously elongated papillae and a specialized cuticle[58, 59] (Figure 5.11). Stigmas of some species possess little or no surface secretions (termed dry stigmas), whereas wet stigmas exude copious surface secretions that play a role in pollen recognition

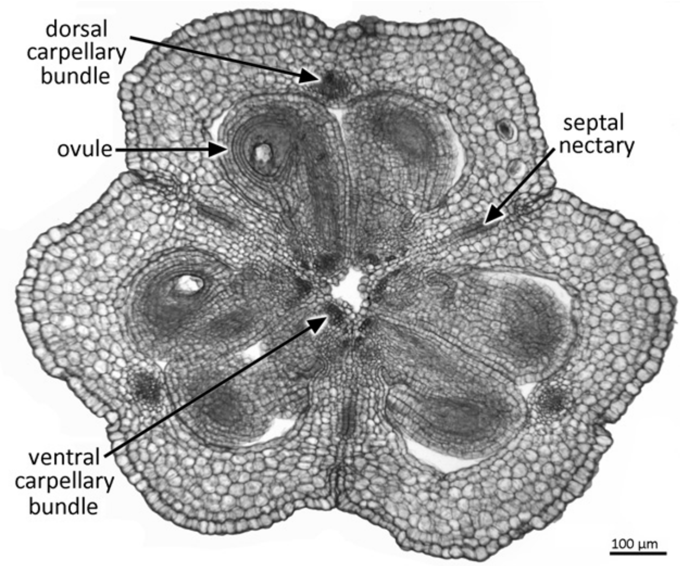

Figure 5.10 *Asparagus officinale* (monocot: Asparagaceae), transverse section of central region of ovary, which consists of three postgenitally fused carpels. Scale = 100 µm

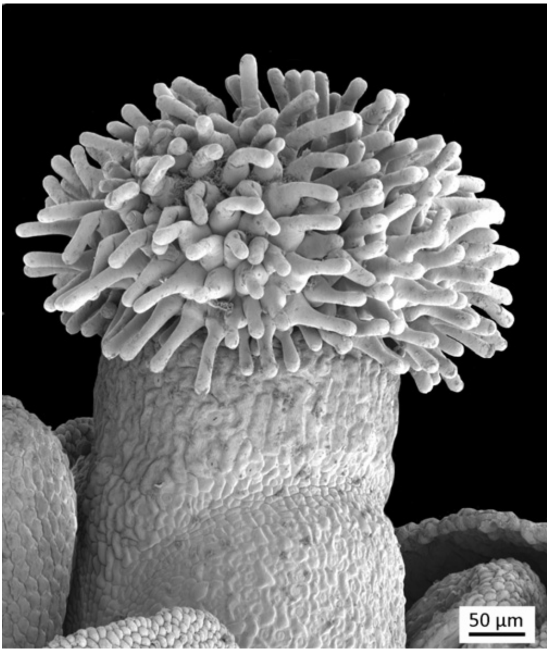

Figure 5.11 *Arabidopsis thaliana* (eudicot: Brassicaceae), scanning electron micrograph of stigma. Scale = 50 µm

and germination. The stigmatic cuticle is often layered, with a lamellated outer layer and reticulate inner layers. Some *Crocus* species possesses a chambered cuticle, and in some *Euphorbia* species the cuticle is fenestrated.

Style anatomy can differ between species. Many syncarpous eudicots possess solid styles, in which there is a central specialized secretory tissue, termed transmitting tissue or compitum, which serves as a nutrient-rich tract for pollen-tube growth from the stigma to the ovary[140] (Figure 5.6). Transmitting tissue is derived from the superficial tissue of the fused carpel margins. In contrast, most syncarpous monocots possess open styles with a central stylar canal that is typically filled with mucilage.

The ovary is the ovule-bearing part of a syncarpous gynoecium. In many syncarpous species, the transmitting tract (compitum) allows the pollen tubes to reach any of the ovules located in the ovary locules. Many species possess a proliferation of secretory tissue around the base of the funicle of each ovule; this papillate tissue (obturator) provides nutrients for the developing pollen tubes and helps to guide them into the micropyles[140]. Ovules are borne on placentas, which are meristematic regions located at the carpel margins within the ovary locules[128]. Ovule primordia are initiated as small swellings on the placenta in the developing ovary. Placental arrangement can differ between species. In species with two or more ovary locules and axile placentation, the ovules are borne on placentas located on the central axis, but in species with unilocular ovaries, the placentas can be located on the ovary wall (parietal placentation), at the base of the ovary (basal placentation) or on a central column of tissue that is linked to the ovary wall only at the top and bottom (free-central placentation).

5.7 Floral secretory structures

Many flowers bear specialized secretory structures, such as nectaries, elaiophores and osmophores, which secrete nectar, oil and scent respectively. Their secretion products help to attract potential pollinators. These specialized secretory structures are often formed after the primary floral organs have already been initiated.

Nectaries are localized areas of tissue that regularly secrete a sugary nectar. They consist of secretory epidermal cells with dense cytoplasm, sometimes modified into trichomes. Adjacent subepidermal cells can also be secretory; in some species, nectar passes to the surface through modified stomatal pores. The nectary is associated with vascular tissue that consists predominantly of phloem, which transports sugars to the secretory region. Nectaries can occur on any floral organ, or they can form part of an entire modified organ, or even a novel structure, such as a nectar spur[35]. Most species of the mint family (Lamiaceae) possess an enlarged nectariferous disc surrounding the base of the ovary, which is derived from proliferated ovary tissue. In most Brassicaceae (e.g. *Arabidopsis thaliana*) the nectary is located at the base of the stamen filament. Septal nectaries are characteristic of many monocots; these secretory regions occur at the unfused carpel margins in monocots with postgenitally fused ovaries[106] (Figure 5.10). Nectar produced from septal nectaries is exuded from secretary epidermal cells and emerges from slit-like openings on the surface of the gynoecium[112].

Flowers of some insect-pollinated species lack nectaries but possess other secretory structures that attract potential pollinators. For example, some flowers bear oil-secreting glands, termed elaiophores (Figure 5.12), which resemble nectaries in their morphology. Osmophores are modified floral structures that produce volatile scents; the scents released by some orchid flowers can resemble insect pheromones[149]. They typically possess a relatively thick, domed or papillate epidermis with densely cytoplasmic contents. In *Platanthera bifolia* (the Lesser Butterfly orchid) the epidermis of the labellum secretes a nocturnal scent, and in several *Ophrys* species osmophores on the labellum consist of

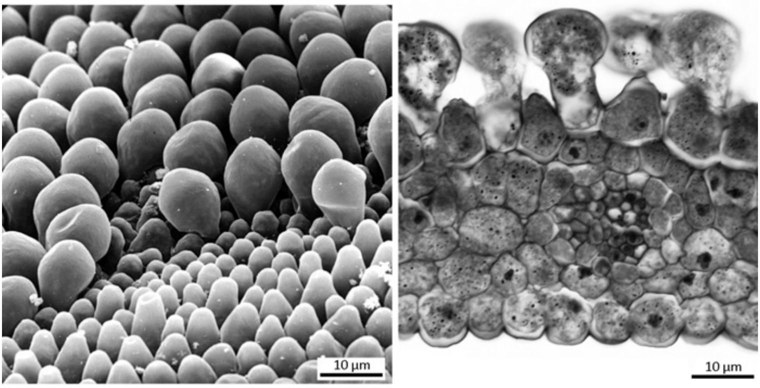

Figure 5.12 *Tigridia meleagris* (monocot: Iridaceae), elaiophores on tepal surface. (left) SEM, (right) transverse section. Scales = 10 µm

regions of dome-shaped, papillate, dark-staining epidermal cells. Flowers of *Narcissus* emit pollinator-specific volatiles that are derived from the colourful corona.

5.8 Pollen development

During development inside the anther, primary sporogenous cells are derived from the same initials as the primary parietal cells of the anther wall. The sporogenous cells give rise – either directly or by successive mitotic divisions – to microsporocytes, which are the parent cells of the microspores. Each microsporocyte undergoes two meiotic divisions, either successively or almost simultaneously, to form a tetrad of four haploid microspores, a process termed microsporogenesis. Pollen tetrads can occur either in tetrahedral or tetragonal arrangement, depending on whether microsporogenesis is simultaneous or successive. A wall of callose (a β-1,3-linked glucan) develops during microsporogenesis, forming a transient but highly significant and effective barrier between the diploid somatic tissue and the haploid developing spores. In the successive microsporogenesis type, callose walls are formed after both meiosis I and meiosis II, forming four microspores embedded in callose. In the simultaneous type, cytokinesis and callose deposition does not occur until both meiotic nuclear divisions are complete. Microsporogenesis is simultaneous in most eudicots, whereas both successive and simultaneous types occur in monocots and early divergent angiosperms[12, 48].

In most species, the tetrad separates into individual microspores, though in some species, microspores are released as permanent tetrads or even remain clumped into larger clusters (e.g. orchid pollinia can each contain many thousands of pollen grains[68]). Before anthesis, each microspore undergoes an unequal division to form a larger vegetative cell and a smaller generative cell. The generative cell migrates into the cytoplasm of the vegetative cell and subsequently divides to produce two sperm, a mitosis that occurs either inside the pollen grain or in the pollen tube. The mature pollen grain is therefore usually bicellular, or rarely tricellular.

Development of the pollen-grain wall is also highly regulated[12, 103]. Initially, a primexine layer is formed around the microspore within the callose wall. The primexine is a cellulosic matrix traversed by a radial system of rod-like probacula[56, 77]. It accumulates pollen-wall material that causes it to become undulating within the callose shell, forming the basis for the pollen exine sculpturing of the dispersed pollen grain. The innermost layer of the exine and the intine are the final wall layers to be formed. The transient callose wall is digested by enzymes; in many species, further sporopollenin secreted by the tapetum or the tapetal plasmodium is deposited on the pollen surface. In many plants, pollen-wall apertures, which represent regions that lack sporopollenin and have reduced primexine deposition, are located in sites that are predetermined by the contact points of the microspores during the tetrad phase[12, 47, 77].

5.9 Pollen grains at anthesis

At anthesis, pollen grains are radially or bilaterally symmetrical bodies that represent units of dispersal from the anther to the stigma (Figure 5.13). They differ considerably in size and shape in different species, though they are predominantly spherical or ellipsoidal. Each individual grain consists of a layered wall enclosing a bicellular (or tricellular) microspore, which represents the male gametophyte[12, 77]. The pollen-grain wall consists of two distinct domains: an exceptionally hard and durable outer exine, which is composed mainly of sporopollenin (a carotenoid polymer), and a relatively soft inner intine, which consists of polysaccharides. The exine is itself often differentiated into an outer sculptured ectexine (sexine) and an inner non-sculptured endexine (nexine). In some monocots, such as *Heliconia*, the exine is reduced to isolated spinules of sporopollenin and the intine is correspondingly thick and channelled[77, 135].

Typically, openings (apertures) are present in the exine layer that reveal the underlying intine. Apertures range in shape from elongated, slit-like furrows to circular pores. Some apertures are partly covered by an operculum, which is an island of exine that resembles

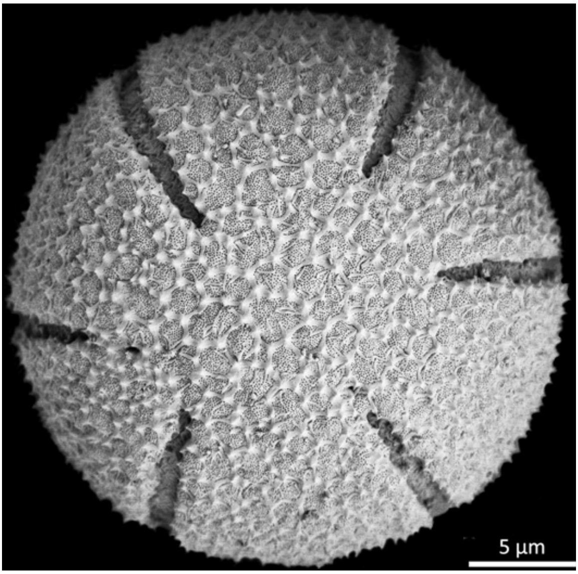

Figure 5.13 *Eschscholzia californica* (eudicot: Papaveraceae), scanning electron micrograph of pollen grain with six apertures (colpi). Scale = 5 µm

a lid[46]. In spiraperturate pollen grains (e.g. in some *Crocus* species), the aperture spirals around the grain. Apertures that lie along the distal face of the pollen grain (normally the face that was directed outwards in the tetrad) are termed sulci, whereas apertures located along the equatorial face of the pollen grain, as defined during the tetrad phase of development, are termed colpi (Figure 5.13). Sulcate pollen grains characterize monocots and basal angiosperms. Pollen with three equatorial apertures (tricolpate pollen) is highly characteristic of eudicots. In most eudicots, microspore tetrads are tetrahedral with three apertures (colpi) arranged equidistantly around the equator of the microspore, though the number of colpi is increased to four or more in many species[47].

There are many different patterns of pollen exine sculpturing. Wind-borne pollen grains are generally small and light, with relatively little surface sculpturing. Water-dispersed pollen often possesses adaptations such as a slime coating (e.g. in Hydrocharitaceae[77]). In other species, the exine can be reticulate or areolate, or it can possess surface holes (puncta), granules, warts or spines[102]. The surface patterning ensures elasticity of the wall and resistance to collapse. In species with animal-dispersed pollen, substances derived from the tapetum – including lipids, proteins and carbohydrates – are retained in the intercolumellar spaces of a deeply chambered exine. These substances can confer odour or cause grains to aggregate into sticky masses, which aids animal dispersal. Following anther dehiscence, pollen grains dehydrate after contact with the air, and the exine contracts. Subsequently, rehydration and exine expansion occur on the stigmatic surface. In some species (e.g. in Brassicaceae), exine-borne substances derived from the tapetum are released onto the stigma after rehydration, allowing species recognition on a compatible host stigma[96].

5.9 Pollen-tube growth and fertilization

Pollen tubes emerge from the apertures of pollen grains that have landed on a receptive stigma and carry the male gametes to the ovules, a process termed siphonogamy. Typically, each pollen grain produces a single unbranched pollen tube, but some species produce multiple or branched pollen tubes[69].

A pollen tube is an extension of the vegetative cell of the male gametophyte. The generative cell is contained within the cytoplasm of the vegetative cell; it divides into two sperm cells, either inside the pollen grain or in the pollen tube itself. The two sperm cells are often fusiform in shape, allowing them to move with the cytoplasmic streaming of the vegetative cell, close to the tip of the pollen tube. Some angiosperms produce callose plugs that block the pollen tube as it extends, sealing off the growing tip from the older part of the tube[158]. The pollen-tube wall represents an extension of the intine; it consists of an outer pectic layer and an inner callosic layer[57, 97, 130].

Germinating pollen tubes (Figure 5.14) grow rapidly by intrusive apical growth between the stigmatic papillae. In species with a dry stigma, the pollen tube tip uses enzymes to pass through the stigmatic cuticle. The pollen tubes extend through the style. In syncarpous eudicots with closed styles, pollen tubes grow along the middle lamellae of the loosely packed cells of the stylar transmitting tissue. In monocots with open styles, pollen tubes grow along the mucilagenous surface of the hollow stylar canal. In both cases, they obtain nourishment (polysaccharides and proteins) from these richly cytoplasmic stylar tissues. When pollen tubes reach the ovary, they are nourished by specialized secretory tissues such as the obturator or the outer integument of the ovule.

A pollen tube typically enters an ovule through its micropyle, though in a few species it enters via the chalaza[69]. After discharging the male gametes into the embryo sac, the pollen tube begins to degenerate. One of the discharged male gametes enters the haploid egg cell and fuses with its nucleus to form a diploid zygote. Nuclear fusion between the second male gamete and the diploid central cell of the embryo sac results in a triploid primary endosperm nucleus. This process, termed double fertilization, represents a key feature

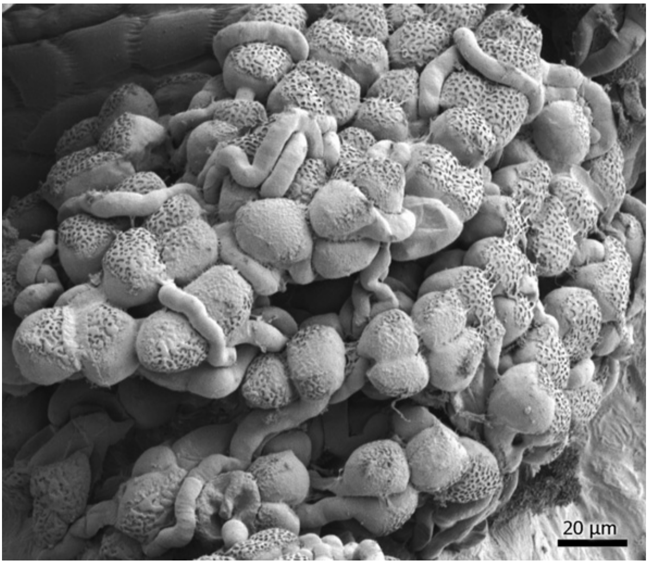

Figure 5.14 *Gymnadenia frivaldii* (monocot: Orchidaceae), scanning electron micrograph of pollen mass (pollinium) on stigmatic surface, with many germinating pollen grains. Scale = 20 µm

of angiosperms. Following double fertilization, the zygote and primary endosperm nucleus undergo mitoses to form the embryo and endosperm respectively (Chapter 6).

5.10 Ovule and embryo sac

Each carpel typically contains one or more ovules, though in some syncarpous ovaries only one carpel is fertile. Each ovule is attached to the placenta by a stalk (funicle or raphe), which contains a vascular strand that usually terminates in the chalazal region, where the funicle, integuments and nucellus meet (Figure 5.15). The chalaza is often differentiated into specialized structures. In some species, the nucellus proliferates in this central chalazal zone to form a hypostase, which consists of suberized or lignified tissue (e.g. in many monocots, such as *Acorus* and *Crocus*).

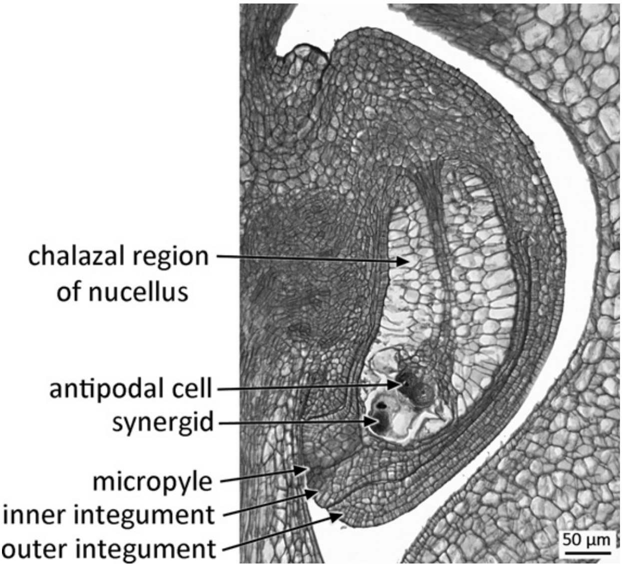

Figure 5.15 *Lomandra longifolia* (monocot: Asparagaceae), longitudinal section of ovule. Scale = 50 µm

During early ovule development, a nucellus is formed from the apex and body of the ovule primordium. Subsequently, one or two integuments are initiated around the primordium base and ultimately grow to encircle its apex, forming the micropyle. The inner integument is usually initiated before the outer integument. The micropyle is a narrow opening in the ovule formed by one or both integuments, located at the opposite end of the embryo sac to the chalaza. The possession of two integuments is the most common condition in angiosperms, but a single integument characterizes some eudicots; a few species even lack integuments entirely. In some species, the dermal nucellar cells surrounding the embryo sac degenerate and the innermost epidermal layer of the inner integument becomes differentiated to form an endothelium (integumentary tapetum) that envelopes the embryo sac and transfers nutrients from the integument. The endothelial cells are enlarged and densely cytoplasmic, sometimes becoming polyploid.

Within the nucellus, a single hypodermal cell becomes a primary sporogenous cell (archesporial cell, or archespore). Occasional species (e.g. *Brassica campestris*[105]) possess a multicellular archespore, of which one cell produces the megagametophyte. The archesporial cell either gives rise directly to the megaspore mother cell (megasporocyte) or undergoes mitosis to form a primary parietal cell and a megasporocyte. The megasporocyte then undergoes two meiotic divisions to form a tetrad of four megaspores, which are usually either in a linear or T-shaped arrangement, a process termed megasporogenesis (Figure 5.16). In the majority of angiosperm flowers, only one of the four megaspores is functional, most commonly the chalazal one. The functional megaspore gives rise to the mature embryo sac by further mitotic divisions, and the other three megaspores degenerate[84, 157, 159]. This type of development is termed monosporic or *Polygonum*-type. In relatively few angiosperms, two or four megaspores play a role in embryo sac formation; these types are termed bisporic or tetrasporic respectively.

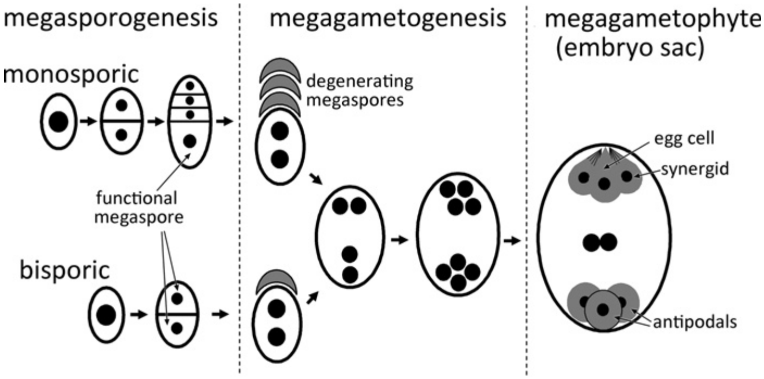

Figure 5.16 Diagram showing stages of development of the megagametophyte and megasporophyte, resulting in an eight-nucleate embryo sac

In most angiosperms, the mature embryo sac (the megagametophyte) possesses eight nuclei arranged in seven cells, though types with four and sixteen or more nuclei have also been recorded. At the binucleate stage, the two nuclei migrate to the micropylar and chalazal poles respectively and subsequently divide further to form four nuclei. One of the two micropylar nuclei divides to form the synergids, and the other divides to form the egg cell and one of the polar nuclei. The two chalazal nuclei each divide so that one forms two antipodal cells and the other forms an antipodal and a polar nucleus. The two polar nuclei migrate to the centre and fuse to form a diploid fusion nucleus. Subsequent cellularization results in a mature megagametophyte with seven cells and nuclei: three antipodal cells at the chalazal pole, a central cell with a fusion nucleus and two synergids plus an egg cell at the micropylar pole. The synergids and the egg cell are tightly compressed together and are collectively termed the egg apparatus. The synergids help to direct the pollen tube through the micropyle into the embryo sac; they are calcium-rich and normally possess a series of wall thickenings, the filiform apparatus, which extends into the micropyle. In many species, the antipodal cells degenerate at an early stage, but in others they persist, and sometimes undergo endoreplication or cell division, as in many grasses.

6

Seed and fruit

The seed represents the dispersal unit of a plant. Seeds are dispersed from the flower either as separate units or enclosed inside a fruit. Each seed develops from a fertilized ovule. Fruits can develop from various structures, including a single ovary (simple fruits, found in the majority of angiosperms), a flower with multiple free carpels (aggregate fruits, e.g. in *Ranunculus*), a single carpel (e.g. the monocarpellate pod of the legume family Fabaceae) or even from an entire inflorescence (e.g. in pineapple, *Ananas comosus*).

Seeds and fruits often possess specialized structures that are related to dispersal[13, 76, 136]. For example, some wind-dispersed seeds possess outgrowths that function as wings. Some animal-dispersed seeds are fleshy and often edible, whereas others possess structures that are attractive to animals, such as arils and elaiosomes. Some plants, especially parasitic or mycoheterotrophic plants such as *Monotropa* or orchids, produce large numbers of highly reduced dust seeds from each ovary; these minute seeds can be blown over long distances.

6.1 Seed coat

The seed coat is formed from ovule tissues, including the chalaza, raphe (funicle) and integuments. Its primary role changes over time. During early development, the seed coat can provide nutrients for the developing embryo and endosperm; during seed dispersal it protects these soft tissues from dehydration or predation. Many angiosperms have bitegmic seeds with two distinct layers, testa and tegmen, which are derived from the inner and outer integuments respectively[13, 21, 153] (Figure 6.1). In contrast, unitegmic seeds possess a single integument and lack a tegmen.

Seed-coat vasculature consists of a single vascular bundle that passes through the stalk (raphe) to the chalaza. The vascular bundle often remains unbranched and terminates in the chalaza, but in some species it can extend further and even ramify, especially in larger seeds, though the extent and degree of branching can vary. The seed coat of many orchids lacks vasculature (Figure 6.2).

At dispersal, the seed coat typically includes a hard, protective mechanical region. In exotestal seed coats, this mechanical layer forms from the outer epidermis of the outer integument. In endotegmic seed coats, it forms from the inner epidermis of the inner integument. In some species, the mechanical layer consists

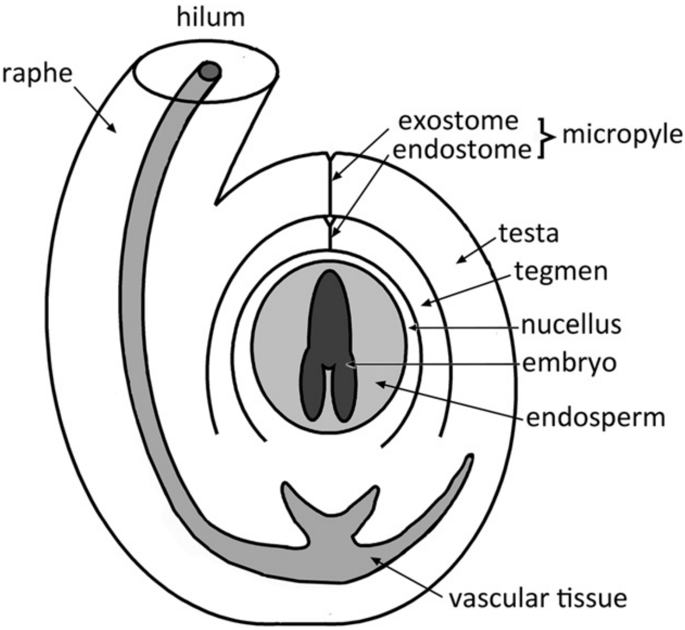

Figure 6.1 Diagram of a generalized campylotropous bitegmic dicotyledonous seed with perisperm

Figure 6.2 *Cypripedium calceolus* (monocot: Orchidaceae), minute "dust" seed, with thin testa surrounding a globular embryo. Scale = 100 μm

of one or more rows of elongated, palisade-like cells, such as the macrosclereids in the exotesta of many legumes (Fabaceae). In fleshy seeds, the fleshy part of the seed coat, termed the sarcotesta, is most commonly formed from part of the outer integument. Arils are fleshy outgrowths of the funicle.

Seed surfaces exhibit a variety of cellular patterns[8] and sometimes display characteristic surface sculpturing that is papillate or striate (Figures 6.3 and 6.4). Some seeds possess epidermal trichomes; the long, twisted seed-coat hairs of *Gossypium* (cotton) represent an important source of textile fibres. Many indehiscent seeds and fruits produce mucilage when they become wet, providing a sticky adhesive glue for animal-mediated dispersal, a phenomenon termed myxospermy (in seeds) or myxocarpy (in fruits)[121, 161]. Mucilage is produced in specialized cells in the seed coats of flax (*Linum usitatissimum*), plantain (*Plantago*) and dodder (*Cuscuta*)[153]. In the fruit (nutlet) walls of *Coleus* and some other Lamiaceae, the epidermal cells absorb water and rupture, producing large amounts of slime interspersed with coiled thread-like protuberances.

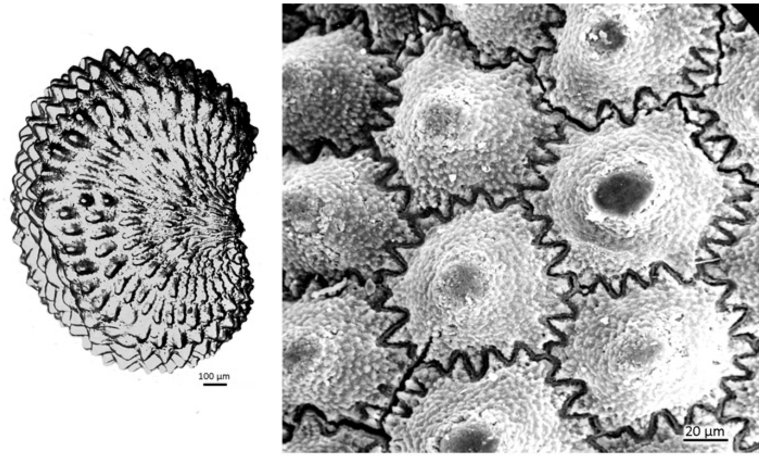

Figure 6.3 *Silene nutans* (eudicot: Caryophyllaceae), entire seed (left) and detail of seed surface (right) showing papillate epidermal cells with sinuous anticlinal walls. Scales: left = 100 μm, right = 20 μm

6.2 Fruit wall (pericarp)

In simple fruits, the pericarp is derived from the ovary wall. The pericarp displays a range of variation depending on whether the fruit is dry or fleshy and dehiscent or indehiscent. It is typically divided into three layers: the outer exocarp, central mesocarp and inner endocarp, though in some fruits the three layers are not readily distinguishable. At least one layer of the fruit wall usually consists of thick-walled lignified cells (Figure 6.5), though in some fleshy fruits (berries), such as those of *Vitis vinifera* (grape), the entire endocarp consists of thin-walled succulent cells. In other fleshy fruits (drupes), such as those of *Prunus persica* (peach), the endocarp cells are thick walled, and only the mesocarp is fleshy, the exocarp being a narrow epidermal layer. In many fruits (e.g. *Olea europaea*, olive) the fleshy mesocarp is textured with thick-walled sclereids.

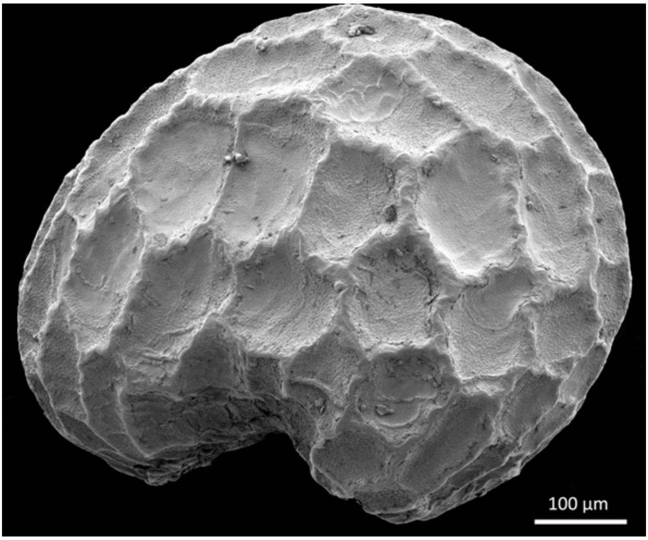

Figure 6.4 *Papaver rhoeas* (eudicot: Papaveraceae), SEM of entire seed. Scales = 100 µm

6.3 Grass caryopsis

The grass dispersal unit, often called a seed, is actually an indehiscent one-seeded fruit (a caryopsis) in which the testa and pericarp are fused together (Figure 6.6). The grass caryopsis is an indehiscent fruit (an achene) in which the seed coat has undergone further reduction[104, 119]. After fertilization, the pericarp consists of a few cell layers and the integuments largely disintegrate, leaving only a hyaline membrane derived from the outer layer of the inner integument. Grass seeds possess highly differentiated embryos with a unique highly characteristic prominent outgrowth of the embryo, termed the scutellum, which represents a modified cotyledon. Grass embryos are well differentiated within the seed, prior to germination. They characteristically possess a sheath (coleoptile) surrounding the epicotyl and plumule, and a well-developed radicle also surrounded by a sheath (the coleorhiza). Some grass species possess an outgrowth opposite the scutellum, termed the epiblast, which has been variously interpreted as a second cotyledon, an

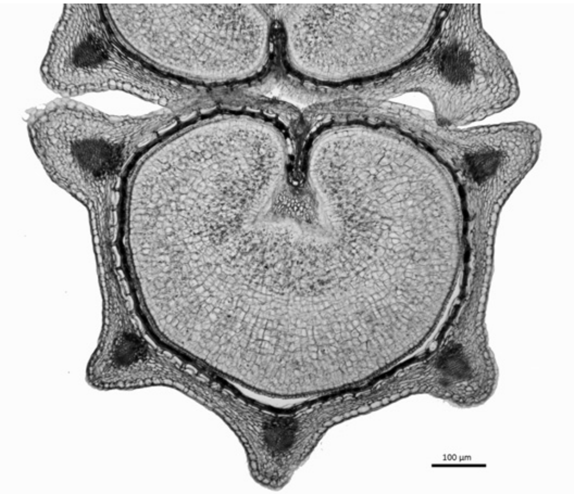

Figure 6.5 *Conium maculatum*, hemlock (eudicot: Apiaceae), transverse section of one of a pair of endospermous seeds. Scale = 100 µm

outgrowth of the first cotyledon or the coleorhiza. In some grasses, the outermost layer of the endosperm (the aleurone layer) is a specialized tissue of enlarged cells containing protein bodies and large nuclei.

6.4 Endosperm

Endosperm forms a food-storage tissue contained within the seed, facilitating dispersal and promoting longevity and growth. Mature endosperm generally consists of tightly packed cells that contain food reserve materials such as starch grains or protein bodies. In contrast, the liquid milk of the coconut palm (*Cocos nucifera*) is a syncytium that contains many free endosperm nuclei in addition to oil droplets and protein granules. In the majority of angiosperms, endosperm is a triploid tissue formed by fusion of a single male nucleus with two female polar nuclei. Endosperm is present in most angiosperm seeds but in greatly varying amounts; for example, endosperm formation is negligible in orchid seeds but extensive in grass seeds, in which it forms the basis for several crucially important food sources (e.g. barley, maize, oats, rye).

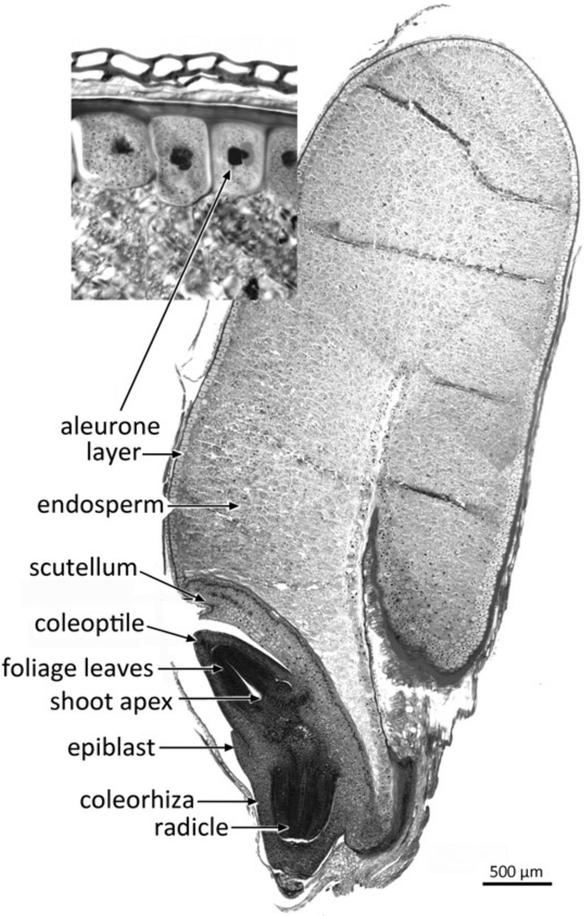

Figure 6.6 *Triticum vulgare,* wheat (monocot: Poaceae), longitudinal section of caryopsis, with detail of aleurone layer (inset). Scale = 500 µm

Early endosperm development is traditionally classified into three types, termed nuclear, cellular and helobial, based on the timing and degree of cell-wall formation[148]. Nuclear endosperm, which characterizes many eudicots (e.g. *Arabidopsis thaliana*) possesses both a syncytial (free-nucleate) phase and a cellular phase. In this type, early cell divisions are not followed by cell-wall formation, and the nuclei are initially free in the cytoplasm of the embryo sac, usually surrounding a central vacuole. Cell walls eventually form, but sometimes the nuclei at the chalazal end remain free. In the cellular type of endosperm formation, which occurs in some eudicots (e.g. Acanthaceae), even the earliest nuclear divisions are followed by cell-wall formation. In the helobial endosperm type, which is restricted to monocots, the primary endosperm nucleus undergoes division to form two unequal chambers, normally a small chalazal chamber and a large micropylar chamber. The nucleus of the micropylar chamber migrates to the top of the embryo sac, and its initial divisions are not accompanied by cell-wall formation, though cell walls are formed with later mitoses. The chalazal chamber has far fewer nuclear divisions, and its nuclei remain free in the cytoplasm; it often has a haustorial role.

Endosperm haustoria can develop in all three types of endosperm. Haustoria assist nutrient absorption and sometimes invade adjacent tissues. For example, most species of the mint family (Lamiaceae) possess both chalazal and micropylar haustoria (Figure 6.7), which can be either free-nucleate or cellular, sometimes even amoeboid[115]. In these species, the first division of the primary endosperm nucleus is longitudinal, followed by formation of a transverse wall. The chalazal nucleus forms a small chalazal haustorium close to the antipodals, and the micropylar nucleus divides further to form a micropylar haustorium and a central cellular endosperm. The micropylar haustorium transfers nutrients from the integument to the embryo and cellular endosperm. The chalazal haustorium transfers nutrients from the vascular bundle to the endosperm.

6.5 Perisperm

In some plants, especially monocots, parts of the nucellus enlarge or proliferate after fertilization and have a role as a regulating or storage tissue for the developing embryo. Seed storage tissues derived from the nucellus are termed perisperm[111]. In some monocots, endosperm is entirely absent from the mature seed, and perisperm represents the primary storage tissue (e.g. in some Poales[119]). Seeds of *Yucca* possess

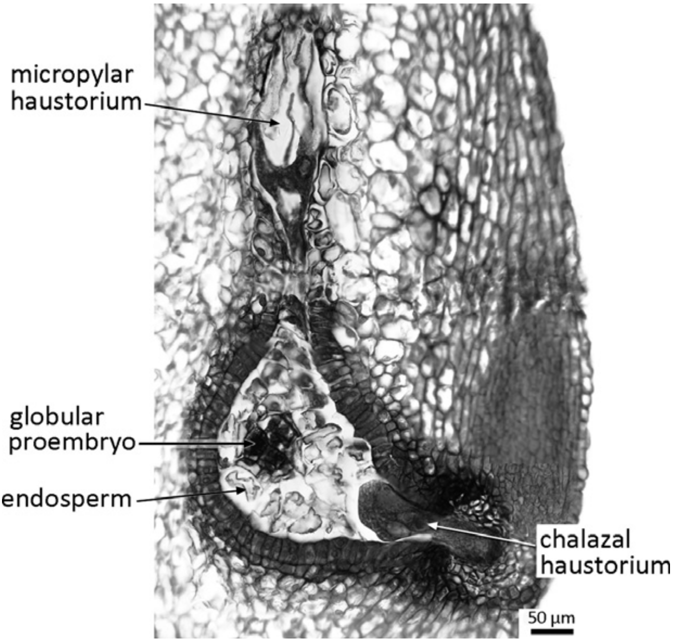

Figure 6.7 *Prunella grandiflora* (eudicot: Lamiaceae), longitudinal section of young developing seed, showing globular proembryo and two endosperm haustoria. Scale = 50 µm

perisperm that contains membrane-bound protein and oil bodies within the cells, together with reserve carbohydrates in the thick cell walls[61]. Some members of the ginger order (Zingiberales) possess perisperm, but this is often entirely compressed in the mature seed, only the cell walls remaining (e.g. in *Musa*[51]). In other Zingiberales (e.g. *Canna*[53]), mitotic activity during ovule development causes the chalazal region of the nucellus to become massive; this region is sometimes termed a pachychalaza. In *Acorus* the perisperm is dermal in origin, formed from nucellar epidermal cells that elongate and become filled with clear, transparent, proteinaceous cell contents.

6.6 Embryo

In a typical angiosperm reproductive system, the embryo develops from the diploid fertilized egg cell (zygote). Following fertilization, the zygote often undergoes a change in volume, either shrinkage or enlargement, before cell division commences. The initial cell division is usually transverse and sometimes asymmetric, to form a small apical and larger basal cell[155]. The pattern of subsequent cell division differs between species and has been classified into several types[93]. Most embryos eventually differentiate into an undifferentiated globular mass of cells (the proembryo) attached to the embryo sac wall by a stalk (the suspensor) (Figure 6.8). In *Arabidopsis*, the apical cell gives rise to the proembryo, which ultimately forms the bulk of the embryo, and the basal cell produces the suspensor and the hypophysis, which is the precursor of the root cortex initials and the central region of the root cap[17]. The proembryo can be massive (e.g. in *Degeneria*), or small, as in *Capsella*, in which it consists of only eight cells[131].

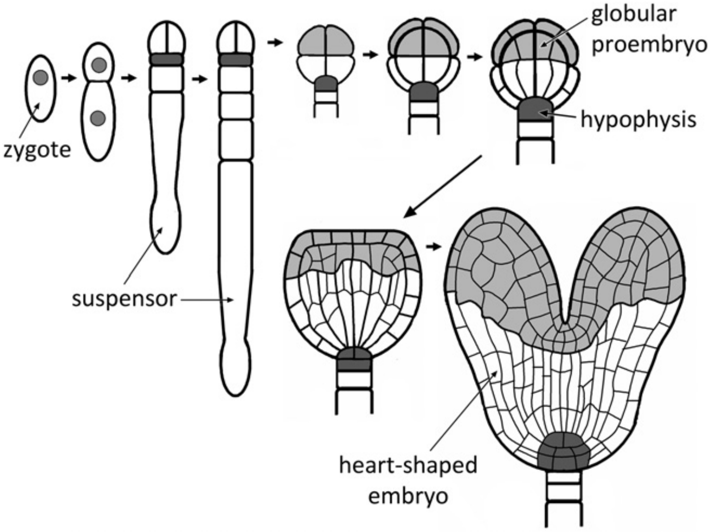

Figure 6.8 Diagram showing stages of embryo development in a eudicot (e.g. *Arabidopsis*), from a zygote to a two-celled stage resulting from an unequal cell division, followed by growth of the suspensor, globular proembryo stages, to a heart-shaped embryo

The angiosperm suspensor exhibits considerable diversity in angiosperms; it can be uniseriate or multiseriate, and filamentous, spherical or irregular[93, 162]. Cells of large suspensors, such as those of *Phaseolus*, are often endopolyploid. Suspensors of some species are secretory, and those of others (e.g. *Sedum* and *Tropaeolum*) produce haustoria that invade surrounding endosperm tissue.

The suspensor ultimately degenerates, and the globular proembryo undergoes a process of irregular meristematic activity that results in a shift from radial to bilateral symmetry. The proembryo eventually becomes organized into a structure with root and shoot apices at opposite ends of an embryonic axis (the hypocotyl). Many dicotyledonous embryos become bilobed or heart-shaped as the two cotyledons differentiate (Figure 6.9). Monocot embryos develop a single, often elongated cotyledon. The degree of differentiation of mature embryos varies considerably; for example, in orchids the embryo remains a simple undifferentiated mass of cells (Figure 6.2). Some highly differentiated embryos possess, in addition to the hypocotyl and cotyledons, a short primordial root (radicle), often with a root cap, and a shoot bud or short shoot (the epicotyl) developed beyond the cotyledons.

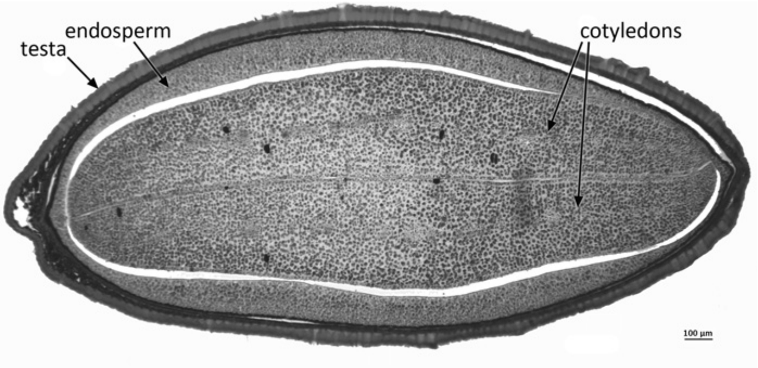

Figure 6.9 *Linum usitatissimum* (Linaceae), transverse section of seed. Scale = 100 µm

6.7 Seedling

At germination, the testa is ruptured and the seedling radicle emerges through the micropyle and pushes through the substrate. Seedlings possess a root (radicle) and a hypocotyl, which bears the cotyledons (seed leaves) and shoot apex. The hypocotyl varies in size and form, from a swollen food-storage organ to a very short structure, in which case the radicle extends almost to the cotyledonary node. Following the emergence of the radicle, either the hypocotyl elongates and the cotyledons and shoot apex emerge (epigeal germination), or the cotyledons remain enclosed in the testa and the internode above them (the epicotyl) elongates, pushing the shoot apex upwards (hypogeal germination). Epigeal germination is the most common type in angiosperms; the cotyledons are borne above ground and are usually photosynthetic. In contrast, some larger-seeded eudicots such as the legume pea or bean (e.g. *Vicia faba*) are hypogeal and possess fleshy, swollen cotyledons.

In monocots, the seedling radicle withers at an early stage, and subsequent roots are shoot-borne (adventitious); they are each initially surrounded by a sheath (coleorhiza), which develops from the outer cortical tissue by cell elongation. The cotyledons are usually morphologically different from the first foliage leaves, often possessing simpler vasculature with a single vascular bundle (Figure 6.7). In monocot seedlings, the cotyledon typically consists of three parts: a basal sheath, a ligule or ligular sheath, and a limb, though the relative differentiation of each region varies; for example, in *Tigridia* seedlings both the hypocotyl and the basal sheath are extremely reduced.

Glossary

abaxial: away from the axis. cf. adaxial

abscission layer: well-defined region of tissue separation, e.g. for abscission

acropetal: towards the apex. cf. basipetal

adaxial: towards the axis. cf. abaxial

adventitious roots: stem- or leaf-borne roots

aerenchyma: specialized parenchymatous tissue associated with aquatic plants, characterized by a regular, well-developed system of intercellular air spaces

aleurone layer: specialized outermost cell layer of endosperm in some grasses

amphistomatic [leaf]: with stomata present on both surfaces

amphivasal [vascular bundle]: with xylem surrounding phloem

amyloplast: plastid containing starch

anisocytic [stomata]: surrounded by three unequal subsidiary cells

anomalous secondary growth (e.g. xylem with included phloem): growth in thickness that is secondary (i.e., not produced by an apical meristem) but does not fit the typical pattern of xylem and phloem production

anomocytic [stomata]: lacking subsidiary cells

anticlinal: perpendicular to the surface. cf. periclinal

antipodal cell: part of megagametophyte. One of a group of (most commonly three) cells at the chalazal end of the mature embryo sac

aperture [of pollen grain]: thin or modified region of pollen exine, through which the pollen tube grows at germination

apocarpous gynoecium: one in which carpels are not fused

apoplast: cell areas not bounded by plasmalemma (i.e. cell wall, middle lamella, intercellular spaces)

apotracheal: parenchyma (in secondary xylem): axial parenchyma not associated with vessels

archesporial cell: primary sporogenous cell

areole: region of mesophyll between smallest veins in leaf

aril [in seeds]: fleshy outgrowth of the **funicle**

articulated laticifer: one composed of several cells, their adjoining walls often partly broken down

astrosclereid: star-shaped or highly branched sclereid

bark: region of woody stem located outside the **secondary** xylem; i.e. including vascular cambium, phloem, cortex and periderm

basipetal: towards the base; i.e. away from the apex. cf. acropetal

bast fibre: extraxylary fibre in stem; i.e. cortical or phloem fibre

bicollateral vascular bundle: one with phloem on both sides of the xylem

bifacial (**dorsiventral**) leaf: one with both adaxial and abaxial surfaces, usually differing morphologically from each other

bitegmic seed: one with two seed-coat layers, derived from two integuments

brachysclereid (**stone cell**): more or less isodiametric sclereid

bulliform cells (usually in grass leaves): groups of epidermal cells that are markedly larger than neighbouring epidermal cells

bundle sheath: layer of cells surrounding leaf vascular bundles

callose (β–1,3–Glucan) product of plasma membrane that is primarily a component of the cell wall; acts as a permeability barrier or sealant in developing tissues such as microspore tetrads or pollen tubes, or in response to wounding or pathogens

callus tissue: undifferentiated mass of thin-walled cells; usually wound tissue

cambium: meristematic band of cells; e.g. cork cambium or vascular cambium

campylotropous [ovule]: bent through 90° during development and fused to the funicle

Casparian strip, or thickening: band of suberin in primary walls of cells of root endodermis (sometimes also found elsewhere, e.g. in root exodermis, or stalks of glandular hairs)

cellulose: a carbohydrate; a crystalline compound that is a major component of plant cell walls

centric (terete) leaf: one that is cylindrical or circular in transverse section

centrifugal: outwards (from the inside)

centripetal: inwards (from the outside)

chalaza: region of the ovule or seed where nucellus and integuments merge, opposite the micropyle

chlorenchyma: photosynthetic tissue; specialized parenchyma containing chloroplasts

chlorophyll: green photosynthetic pigment contained within chloroplasts

chloroplast: plastid containing chlorophyll, the site of photosynthesis

coenocyte: multinucleate cell; i.e. one in which cell division has occurred without cell-wall formation, e.g. non-articulated laticifer

coleoptile (in seedlings): parenchymatous sheath enclosing plumule

coleorhiza (in monocot seedlings, especially grasses): parenchymatous sheath covering primary root

collateral: vascular bundle: one with xylem and phloem adjacent to each other

collenchyma: strengthening tissue, consisting of groups of axially elongated, tightly packed cells with unevenly thickened walls

colpus (pl. **colpi**): aperture in pollen grain wall, aligned equatorially during the tetrad stage, and usually elongated (slit-like)

companion cell: parenchymatous cell associated with sieve-tube element in phloem.

compitum: opening in transmitting tissue of ovary, near micropyle

cork: suberized tissue (periderm)

cortex: region in stems and roots between epidermis and central vascular region

cotyledon: first leaf of the embryo

cuticle: non-cellular layer of a fatty substance (cutin), covering surface of epidermis

cystolith: calcareous body found in epidermal cell, or in leaf mesophyll

cytokinesis: cytoplasmic cleavage following nuclear division

diacytic [stomata]: with one or more pairs of subsidiary cells with their common walls at right angles to the guard cells

diarch [root]: with two protoxylem poles

dictyosome or Golgi body: cell organelle associated with secretory activity

distal: located away from the centre of a body or its point of attachment; sometimes terminal on axis (cf. proximal)

domatia: specialized pockets or tufts of hairs on some leaf surfaces, providing shelter for small insects; sometimes associated with extrafloral nectaries

dorsiventral or **bifacial** [leaf]: with the two surfaces morphologically different from each other

druse: cluster crystal, or compound crystal

ectomycorrhizal [fungal mycelium on roots]: associated with the surface (cf. endomycorrhizal)

ectexine (**ektexine** or **sexine**): outer, sculptured part of exine in pollen grain wall

egg apparatus (in mature embryo sac): egg cell and two synergids

egg cell: part of megagametophyte; haploid cell at micropylar end of mature embryo sac that will fuse with male haploid nucleus to form a zygote

elaiophore: oil-secreting trichome or tissue in flower

embryogenesis: embryo development

endexine (nexine) inner layer of exine in pollen grain wall

endocarp: inner layer of fruit wall (pericarp)

endodermis: innermost cell layer of cortex (mainly in roots)

endogenous: of deep-seated (internal) origin (cf. exogenous)

endomycorrhizal [fungal mycelium on roots]: invading tissues and cells (cf. ectomycorrhizal)

endoplasmic reticulum (**ER**): series of membranes permeating the cytoplasm

endosperm: seed storage tissue, formed by fusion of one male nucleus with two female polar nuclei (i.e. usually triploid)

endotegmic seed coat: one with thickened, mechanical layer derived from the inner epidermis of the inner integument

endothecium: anther wall layer immediately within the epidermis; often possessing characteristic thickenings

epiblast: in grass embryos, outgrowth opposite scutellum

epicotyl: seedling axis above cotyledons

epidermis: outermost layer of cells, covering entire primary plant surface

epigeal germination: seedling germination type in which cotyledons are green and borne above ground

epigynous flower: one with inferior ovary (i.e. the ovary is attached to the receptacle above the level of insertion of the stamens and perianth parts)

epistomatic leaves: with stomata found on adaxial surface only

epithem: tissue (often loosely packed parenchyma) in hydathode between epidermis and vascular tissue

equatorial (pollen grain aperture): located at or crossing a line midway between the two poles of a microspore or pollen grain

exarch root: one that matures centripetally

exine: outer coat of pollen grain, often differentiated into outer ectexine and inner endexine

exocarp: outermost layer of pericarp

exodermis: outer few cell layers of root cortex that have become thicker walled and lignified

exogenous: of superficial (external) origin (cf. endogenous)

exotestal: seed coat: one with mechanical layer formed from the outer epidermis of the outer integument

fibre: axially elongated, thick-walled cell, usually occurring as part of a group, lacking contents at maturity, and with simple pits

fibre-tracheid: cell type that is transitional between a fibre and a tracheid, possessing bordered pits

filament: (in flower) stalk of stamen

filiform apparatus: wall thickenings in synergid cells of mature embryo sac

funicle (**funiculus**): stalk attaching ovule to placenta in ovary

fusiform: elongated with pointed ends

generative cell: part of male gametophyte; divides (usually within pollen tube) to form two sperm cells

girder (or **bundle sheath extension**): in leaves, usually a group of cells (parenchymatous or sclerenchymatous) linking a vascular bundle sheath with either or both epidermises

graft: union (by cell differentiation) of tissues of two different individuals so that one (the scion) can survive through dependency on the other (the stock)

ground tissue: tissue (usually parenchyma) surrounding vascular tissue

growth ring: (in secondary xylem) a distinct growth increment caused by differential rates of growth during a growing season

guard cell: one of a pair of cells of a stoma, together surrounding a pore

guttation: secretion of water droplets, often occurring at hydathodes

gynoecium (in flower): collective term for carpels; including **ovary**, **style**(s) and **stigma**(s)

hair: epidermal appendage, or trichome

haustorium (pl. **haustoria**): cellular process that penetrates adjacent tissues and has a role in nutrient transport. For example, haustoria of parasitic plants are modified roots; endosperm haustoria are specialized absorptive cells

hemicellulose: one of the carbohydrate constituents of plant cell walls

heterocellular ray: one composed of cells of different shapes and sizes

hilum: scar on seed indicating point of attachment of funicle to ovary wall

histogenesis: tissue differentiation

homocellular ray: one composed of cells which are the same shape and size

hydathode: region of secretion of water droplets (usually on leaf margin)

hydrophyte: water plant, sometimes displaying hydromorphic features (e.g. aerenchyma)

hypocotyl: seedling axis bearing cotyledons and shoot apex

hypodermis: (often applied to leaves) distinct cell layer(s) immediately within epidermis

hypogeal germination: type in which cotyledons remain enclosed in seed coat after radicle has emerged

hypogynous flower: one with superior ovary; i.e. ovary attached to the receptacle above the level of insertion of the stamens and perianth parts

hypophysis: uppermost cell of the suspensor

hypostase: proliferation of nucellus at chalazal end of embryo sac, often bearing antipodals

hypostomatic leaves: with stomata found on abaxial surface only

idioblast: isolated specialized cell that differs from cells of adjacent tissue in size, shape and function

included phloem: areas of phloem embedded in secondary xylem

inaperturate (microspore or pollen grain): one lacking a clearly defined aperture on the surface, so that the pollen tube can potentially emerge at any point

integument: structures enclosing the embryo sac and nucellus

intercalary growth: cell divisions in region apart from apical meristem or other well-defined meristems

internode: region separating two nodes on stem

intine: inner layer of pollen grain wall

isobilateral leaf: one with both surfaces similar, or with palisade tissue on both sides (abaxially and adaxially)

Kranz anatomy: (in some plants with C_4 photosynthesis) distinctive leaf anatomy with mesophyll cells radiating from the vascular bundle sheaths

lateral roots: branches of the tap root; they have an endogenous origin

latex: fluid contained within laticifers, consisting of a suspension of fine particles

laticifer: latex-secreting cell

lenticel: region of loose cells in the periderm (bark)

lignin: substance often deposited in cell walls of strengthening tissues (e.g. fibres), giving rigidity

ligule: outgrowth of the abaxial epidermis of a leaf in the region between the sheath and petiole (or between sheath and lamina if the petiole is absent)

macrosclereid: elongated sclereid often found in seed coat

megagametophyte: mature embryo sac, most commonly consisting of eight nuclei

megaspore: female haploid cell resulting from meiosis; usually one of two or four, of which only one is functional

megasporogenesis: process of megaspore formation from a megaspore mother cell

megasporocyte: a diploid cell that will give rise to (usually) four haploid megaspores following meiosis

meiosis: two successive divisions of a diploid nucleus to form a haploid gamete

meristem: region of cell division and tissue differentiation (e.g. **apical** meristem, intercalary meristem, lateral meristem, vascular cambium, primary and **secondary thickening** meristems)

meristemoid: isolated meristematic cell, usually the smaller cell resulting from an asymmetric division (e.g. guard-mother cell)

mesocarp: middle layer of pericarp

mesogene cell: stomatal subsidiary cell derived from meristemoid

mesomorphic: displaying no xeromorphic or hydromorphic characteristics

mesophyll: ground tissue of leaf; mainly consisting of parenchyma or chlorenchyma; often differentiated into **palisade** and **spongy** mesophyll

metaxylem: primary xylem formed after protoxylem

microfibril: thread-like component of cell wall, usually of cellulose

micropyle: opening at one end of the ovule, usually formed by the integuments

microsporangium: pollen sac, contained within anther

microspore (male spore): individual haploid cell that will give rise to male gametophyte (pollen grain)

microsporocyte: a diploid cell that will give rise to four haploid microspores following meiosis

microsporogenesis: developmental process leading to the production of four haploid microspores from a diploid microsporocyte by meiosis and cytokinesis

middle lamella: layer between the walls of neighbouring cells

mitochondrion (pl. **mitochondria**): respiratory cytoplasmic organelle

mitosis: cell division to form two cells of equivalent chromosome composition to parent cell

mucilage (**slime**): compound that swells in water

multiseriate: consisting of more than one layer or row of cells

nectary: (floral or extrafloral) localized cell or cells that secrete a sugary liquid (nectar)

nexine: inner, non-sculptured part of exine

node: part of stem where leaves are attached

non-articulated laticifer: one composed of a single multinucleate coenocytic cell

nucellus: ovule cell layer(s) immediately surrounding megagametophyte

obturator: proliferation of (usually) ovary tissue near micropyle, with secretory function, to guide growing pollen tubes into micropyle

ontogeny: development; differentiation and growth

osmophore: scent-producing gland

osteosclereid: bone-shaped sclereid

papilla (pl. **papillae**): epidermal appendage; small unicellular trichome

paracytic [stomata]: with one or more subsidiary cells at either side of the guard cells

paratracheal parenchyma: (in secondary xylem) associated with the vessels

parenchyma: tissue composed of thin-walled cells with living contents

passage cell: an endodermal cell that remains thinner walled than neighbouring endodermal cells

pearl glands (**pearl bodies**): secretory, often globular, leaf emergences or trichomes that provide food (carbohydrates, lipids and proteins) for ants

perforated ray cell: (in secondary xylem) ray cell linking two vessel elements, and itself resembling and functioning as a vessel element

perforation plate: opening in end wall of vessel element

perianth: outer sterile part of flower

pericarp: fruit wall

periclinal: parallel with the surface. cf. anticlinal

pericycle: in roots, a distinct layer of thin-walled cells located within the endodermis

periderm: cork tissue

perigene cell: in stomatal complex, neighbour cell that is not derived from the same cell lineage as the guard cells

periplasmodium: coalescent mass in anther locule, formed from protoplasts of tapetal cells

perisperm: food-storage tissue in the seed, derived from part of the nucellus

phellem: external derivatives of phellogen

phelloderm: internal derivatives of phellogen

phellogen: cork cambium, or cork meristem

phloem: tissue that transports food in the form of assimilates; either primary (produced by the apical meristem) or secondary (produced by the vascular cambium)

phyllotaxis: the pattern of arrangement of organs on an axis, e.g. leaves on a stem, flowers on an inflorescence

pith: central parenchymatous region of stem

pits: thin areas of the primary and secondary cell wall, often corresponding with pits in adjacent cells (pit-pairs)

placenta: region of attachment of ovules on ovary wall

placentation: arrangement of placentae and locules in ovary (e.g. axile, basal, free central, parietal)

plasma membrane (plasmalemma): cell membrane (within cell wall) that encloses protoplast

plasmodesmata: protoplasmic strands passing through primary pit fields between adjacent cells and connecting their protoplasts

plastid: cell organelle contained within cytoplasm, often with specialized function (e.g. chloroplast, amyloplast)

polar nucleus: one of a pair of nuclei of the mature megagametophyte, often in a central position

pollen grain: male gametophyte; bicellular (or rarely tricellular) at maturity

pollen tube: tube emerging from germinating pollen grain on stigma, which will transport male nuclei to megagametophyte

polyarch root: one with several (more than four) protoxylem poles

primordium: newly differentiating organ

procambium: primary tissue near (shoot or root) apex that gives rise to primary vascular tissue

proembryo: young globular embryo prior to differentiation of cotyledons and hypocotyl

promeristem: (in root apices) region of greatest mitotic activity

protoplast: living part of cell, surrounded by a plasma membrane

protoxylem: first-formed primary xylem

proximal: situated closer to the centre of a body or its point of attachment (antonym: distal)

quiescent centre: region of cells at root apex, with little or no cell division activity

radicle: first-formed root of seedling

raphe: stalk attaching seed to ovary (directly derived from the funicle)

raphide: fine, needle-like crystal, one of a group of several raphides formed within a single cell

ray: (in secondary xylem) tissue of radially oriented cells, usually parenchymatous

root cap: protective covering of cells over root apex

root hair: water-absorbing hair on root epidermis

sarcotesta: fleshy part of seed coat
scale (peltate hair): a modified trichome, consisting of a fused disc of cells attached to the epidermis by a stalk
sclereid: thick-walled sclerenchymatous cell, usually lacking contents at maturity
sclerenchyma: strengthening tissue, consisting of cells with thickened lignified walls, usually lacking contents at maturity
scutellum: specialized structure in grass embryos, often interpreted as a modified cotyledon
sieve tube element: conducting cell in phloem; possessing sieve areas and sieve plates in walls. Groups of sieve tube elements are linked axially to form sieve tubes
sporopollenin: a highly resistant complex polymer that forms the outer wall of a pollen grain
stipules: appendages at base of leaf sheath, often paired and sometimes leafy
stoma (pl. **stomata**): pore in aerial epidermis
stone cell: isodiametric sclereid
styloid: elongated prismatic crystal
suberin: fatty compound sometimes deposited in cell walls, e.g. in cork cells
subsidiary cells: epidermal cells adjacent to stomata or other subsidiary cells, which differ from surrounding epidermal cells
sulcus (pl. **sulci**): aperture in pollen grain wall on its distal face (i.e. the face that is normally directed outwards in the tetrad)
suspensor: row of cells attaching globular proembryo to wall of embryo sac
symplast: connected living protoplasts of adjacent cells
syncarpous gynoecium: one in which carpels are more or less fused, though stigmas and styles may remain separate
syncytium: cytoplasmic region enclosed by a single plasma membrane and bearing several nuclei

synergid: part of megagametophyte; one of a pair of cells at micropylar end of mature megagametophyte

tannins: a broad group of phenol derivatives

tap root: main central root, formed directly from seedling radicle

tapetum: layer of nutritive tissue between the microsporocytes or developing pollen grains and the wall of the anther locule

tegmen: the inner layer of the seed coat, formed from the inner integument

testa: seed coat; or in bitegmic seeds, the outer layer of the seed coat, formed from the outer integument

tetrad: group of four microspores or megaspores, the daughter cells of a single microsporocyte or megasporocyte

tetrarch (root): one with four protoxylem poles

tracheid: xylem water-conducting cell, usually possessing bordered pits but lacking perforation plates

transfer cell: specialized plant cell that facilitates transport of soluble substances across tissue boundaries

transmitting tissue (stigmatoid tissue): secretory tissue through which pollen tubes grow, linking stigma with centre of ovary

triarch (root): one with three protoxylem poles

trichoblast: root epidermal cell with dense cytoplasm, which will give rise to a root hair

trichome: epidermal outgrowth (hair)

tricolpate (microspore or pollen grain): one with three colpi

tunica-corpus: regions of central shoot apical organization

tylose: (in secondary xylem) outgrowth of the wall of an axial parenchyma cell into a vessel element through a pit; eventually often completely blocking vessel

unifacial leaf: one with both surfaces similar, sometimes derived from a single (usually abaxial) surface

uninterrupted meristem: region of diffuse cell divisions that is continuous with the apical meristem; producing extension growth of the axis

uniseriate: consisting of a single layer or row of cells

vacuole: cavity

vascular cambium: bifacial meristem that produces secondary vascular tissue (phloem and xylem)

vascular tissue: conducting tissue (phloem and xylem)

vegetative cell: one of two cells of the male gametophyte

velamen: outer dermal layer on the aerial roots of some tropical epiphytes

venation: arrangement of vascular bundles in leaf (e.g. parallel or reticulate venation)

vessel element: water-conducting cell of xylem, possessing bordered pits on lateral walls and perforation plates on end walls; groups of axially linked vessel elements form a vessel

vestured pitting (in secondary xylem): bordered pits surrounded by numerous warty protuberances

wax: fatty substance often deposited on the surface of the cuticle

whorl: ring of organs; sometimes applied to a region of a similar organ type, e.g. the stamen whorl

wood: secondary xylem

xeromorphic: showing characteristics that are often associated with dry environments

xerophyte: plant that grows in a dry (xeric) environment

xylem: water-transporting tissue, consisting of several different cell types

zygote: cell formed by fusion of megasporocyte and microsporocyte; will eventually divide to form the proembryo

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