THIRD EDITION

Anatomy of Flowering Plants

An Introduction to Structure and Development

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Anatomy of Flowering Plants

Understanding plant anatomy is not only fundamental to the study of plant systematics and palaeobotany, but is also an essential part of evolutionary biology, physiology, ecology, and the rapidly expanding science of developmental genetics. In the third edition of her successful textbook, Paula Rudall provides a comprehensive yet succinct introduction to the anatomy of flowering plants. Thoroughly revised and updated throughout, the book covers all aspects of comparative plant structure and development, arranged in a series of chapters on the stem, root, leaf, flower, 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 also 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 Rudall is Head of Micromorphology (Plant Anatomy and Palynology) at the Royal Botanic Gardens, Kew. She has published more than 150 peer-reviewed papers, using comparative floral and pollen morphology, anatomy and embryology to explore evolution across seed plants.

Preface

In the twenty-first century, plant anatomy remains highly relevant to systematics, paleobotany, and the relatively new science of developmental genetics, which interfaces disciplines and utilizes a combination of techniques to examine gene expression in growing tissues. Modern students need to consider information from an increasingly wide range of sources, most notably integrating morphological and molecular data. The third, thoroughly revised, edition of this book presents an introduction to plant anatomy for students of botany and related disciplines.

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[27]. Other early outstanding 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. In 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 paleobotany, led by such luminaries as Dukinfield Henry Scott (1854–1934). The physiologist Gottlieb Haberlandt (1854–1945) utilized anatomical observations in his ground-breaking work on photosynthetic carbon metabolism. One of the most notable plant anatomists of the twentieth century was Katherine Esau (1898–1997), recognized particularly for her work on the structure and development of phloem and her influential textbooks on plant anatomy[30]. Other important textbooks include works on paleobotany, morphology, anatomy and embryology[13,34,68,106].

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 and pollen morphology[98]. The subsequent invention of the scanning electron microscope (SEM) provided greater image clarity and much greater depth of focus than light microscopes, and thus further increased accessibility of minute structures, including seeds, pollen grains and organ primordia[28,98]. More recent innovations, including fluorescence microscopy, differential interference contrast (DIC) microscopy and confocal imaging, have allowed enhanced visualization of tissue structure. Others, including nuclear magnetic resonance (NMR) imaging and high-resolution X-ray computed tomography (HRCT) facilitate enhanced visualization of three-dimensional objects.

Taxonomic Overview

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. Other features marked this distinction, including the absence of a vascular cambium and presence of parallel leaf venation in monocots. However, the expansion of molecular phylogenetics through the early 1990s indicated that some species that were formerly classified as primitive dicots do not belong to either category, though the monophyly of monocots was confirmed[2,3,103]. Thus, although the dicot/monocot distinction remains useful for generalized descriptions of angiosperm groups, current evidence suggests that it does not represent a wholly natural classification. It is now widely accepted that several relatively species-poor angiosperm lineages (here termed early-divergent angiosperms or magnoliids) evolved before the divergence of the two major lineages that led to the monocots and the remaining dicots (now termed eudicots, or sometimes tricolpates).

Early-divergent angiosperms (including magnoliids) 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 1% of extant species. They possess some morphological features in common with both monocots and eudicots, and include the New Caledonian shrub *Amborella*, the water lilies (Nymphaeaceae), woody families such as Magnoliaceae and Lauraceae, and herbaceous or climbing families such as Piperaceae and Aristolochiaceae. Monocots account for approximately a quarter of all flowering plants 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% of extant angiosperm species, and encompass a wide range of morphological diversity, especially in the two largest subclades, Rosidae (rosid eudicots) and Asteridae (asterid eudicots).

Contents

1

Organs, cells and tissues

1.1 Organs

Plants consist of several organs, which in their turn are composed of tissues. Broadly, vegetative organs support plant growth, and reproductive organs enable sexual reproduction. The three main types of vegetative organ are the root, stem and leaf. Roots typically occur underground, and extract moisture and nutrients from the soil, though there are many examples of plants with aerial roots. The stem and leaves together comprise the shoot (Fig. 1.1). Stems occur both above and below ground. Some stems are modified into underground perennating or storage organs such as corms or rhizomes. Leaves typically occur above ground level, though some underground stems possess reduced scale leaves, and underground bulbs possess swollen leaves or leaf bases.

Primary organs and tissues develop initially from the shoot and root apical meristems and from cell divisions in meristems closely adjacent to them, such as the primary thickening meristem. Secondary tissues such as secondary xylem (wood) develop from lateral meristems such as the vascular cambium. Organs such as adventitious roots develop from differentiated cells that have retained meristematic capacity. At the onset of flowering, the shoot apical meristem undergoes structural modification from a vegetative to a reproductive apex and subsequently produces flowers (chapter 5). Flowers are borne on an inflorescence, either in groups or as solitary structures. A group of inflorescences borne on a single plant is termed a synflorescence[121] (Fig. 1.2).

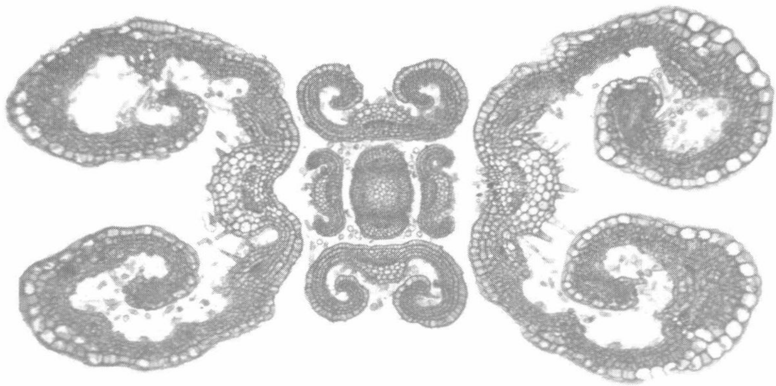

Figure 1.1 *Hyptis ditassoides* (Lamiaceae), transverse section of vegetative bud near apex, showing three successive pairs of leaf primordia surrounding central stem. Scale = 100 μm.

1.2 Cells

Plant cells typically have a cell wall containing a living protoplast (Fig. 1.3). The layer that contacts the walls of adjacent cells is termed the middle lamella. Following cessation of growth, many cells develop a secondary cell wall which is deposited on the inside surface of the primary wall. Both primary and secondary walls consist of cellulose microfibrils embedded in a matrix and oriented in different directions. Secondary cell walls consist mostly of cellulose, but primary walls commonly contain a high proportion of hemicelluloses in the gel-like matrix, affording a greater degree of plasticity to the wall of the growing cell. The secondary wall can also contain deposits of lignin (in sclerenchymatous cells) or suberin (in many periderm cells), and often appears lamellated.

Thin areas of the primary wall, which usually correspond with thin areas of the walls of neighbouring cells, are primary pit fields, and usually have protoplasmic strands (plasmodesmata) passing through them, connecting the protoplasts of neighbouring cells[36]. The connected living protoplasts are collectively termed the symplast. Primary pit fields often remain as thin areas of the wall even after a secondary wall has been deposited, and are then termed

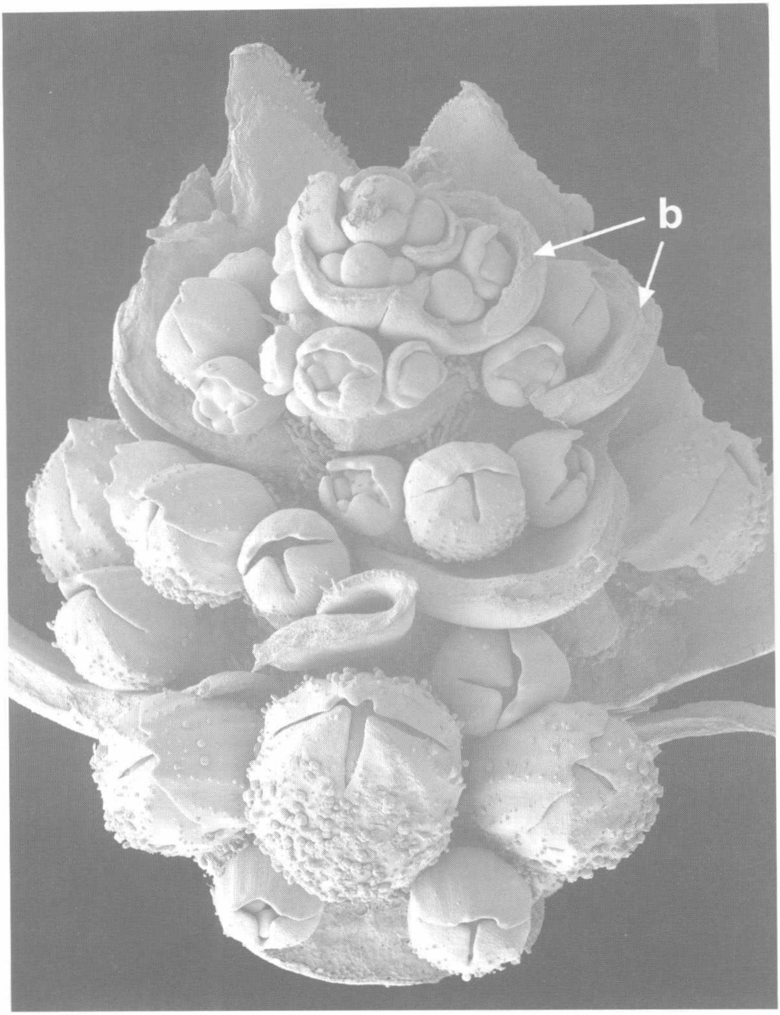

Figure 1.2 *Salvia involucrata* (Lamiaceae), dissected developing synflorescence showing flower clusters, each consisting of three flowers enclosed within a bract; younger stages towards apex. b = bract. Scale = 500 μm.

pits, or pit-pairs if there are two pits connecting adjacent cells. Pits may be simple, as in most parenchyma cells, or bordered, as in tracheary elements. In simple pits the pit cavity is of more or less uniform width, whereas in bordered pits the secondary wall

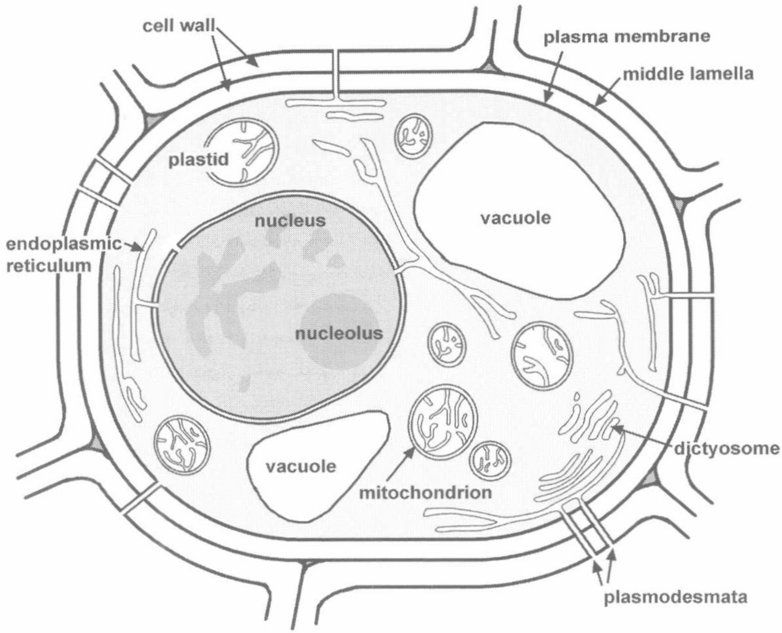

Figure 1.3 Diagram of a generalised plant cell illustrating details of protoplasmic contents.

arches over the pit cavity so that the opening to the cavity is relatively narrow. Through a light microscope the outer rim of the primary pit field appears as a border around the pit opening.

The cell protoplast is contained within a plasma membrane. It consists of cytoplasm that encloses bodies such as the nucleus, plastids and mitochondria, and also non-protoplasmic contents such as oil, starch or crystals. The nucleus, which is bounded by a nuclear membrane, often contains one or more recognizable bodies (nucleoli) together with the chromatin in the nuclear sap. During cell division the chromatin becomes organized into chromosomes. Most cells possess a single nucleus, but examples of multinucleate cells (coenocytes) include the non-articulated laticifers found in many plant families (chapter 1.4). Such cells elongate and penetrate established tissues by intrusive tip growth, in which the cell apices secrete enzymes that dissolve the middle lamellae of neighbouring cells; bifurcation occurs when they encounter an obstacle[36].

Mitochondria and plastids are surrounded by double membranes. Plastids are larger than mitochondria, and are classified into different types depending on their specialized role. For example, chloroplasts are plastids that contain chlorophyll within a system of lamellae that are stacked to form grana; this is the site of photosynthesis. Chloroplasts occur in all green cells, but are most abundant in the leaf mesophyll, which is the primary photosynthetic tissue (chapter 4.5). Membranes occur widely throughout the cytoplasm, sometimes bounding a series of cavities. For example, the endoplasmic reticulum is a continuous membrane-bound system of flattened sacs and tubules, sometimes coated with ribosomal particles. Dictyosomes are systems of sacs associated with secretory activity. Vacuoles are cavities in the cytoplasm; they are usually colourless and contain a watery fluid. Their size and shape varies in different cell types, and also changes during the life of a cell.

1.3 Cell Inclusions

Many cells possess non-protoplasmic contents such as oils, mucilage (slime), tannins, starch granules, calcium oxalate crystals and silica bodies. Both oil and mucilage are produced in secretory idioblasts which are often larger than adjacent parenchymatous cells. Tannins are phenol derivatives which are common in plant cells; they are amorphous, and appear yellow, red or brown in colour in cells of sectioned material. Cystoliths are cellulose bodies encrusted with calcium carbonate that occur in epidermal cells in some species (Fig. 4.4); the body is attached to the cell wall by a silicified stalk[36].

Starch is especially common in storage tissues such as endosperm or in parenchyma adjacent to a nectary. Starch granules

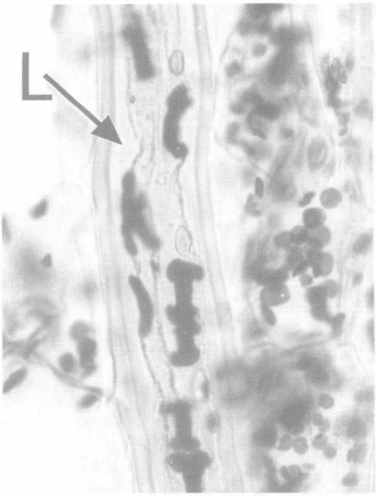

Figure 1.4 *Monadenium ellenbeckii* (Euphorbiaceae). Elongated I-shaped starch grains in laticifer (L); ovoid starch grains present in adjacent parenchyma cells. Scale = 20 µm.

are formed in plastids (amyloplasts). They often appear layered due to the successive deposition of concentric rings, and may possess characteristic shapes. For example, in species of *Euphorbia*, starch grains in laticifers are elongated and sometimes rod-shaped or bone-shaped compared with the more rounded starch grains of neighbouring parenchyma cells (Fig. 1.4)[70].

Calcium oxalate crystals (Figs 1.5, 1.13) are borne in crystal idioblasts that can occur in almost every part of the plant, including both vegetative and reproductive organs[82]. They are often present near veins, possibly due to transport of calcium through the xylem, and are sometimes associated with air space formation; some aquatic plants possess calcium oxalate crystals projecting into air spaces. Crystals form within vacuoles of actively growing cells and are usually associated with membrane chambers, lamellae, mucilage and fibrillar material. Crystal sand is relatively amorphous and represents fragmented non-nucleated crystalline particles. Druses (cluster crystals) are aggregated crystalline structures that have precipitated around a nucleation site. Raphides are bundles of needle-like crystals that are borne in the same cell; they occur commonly in monocots. In the monocot family Araceae,