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.

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An Introduction to Structure and Development

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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).