

### ***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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An Introduction to Plant  
Structure and Development

Fourth Edition

PAULA J. RUDALL

*Royal Botanic Gardens, Kew*



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

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# 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<sup>23, 83</sup>. 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<sup>30</sup>. 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<sup>4</sup>, and Katherine Esau (1898–1997), recognized particularly for her work on the structure and development of phloem and her influential textbooks on plant anatomy<sup>37</sup>. Other important botany textbooks include works on anatomy<sup>28, 40, 41</sup>, embryology<sup>26, 82</sup>, morphology<sup>44</sup> and palaeobotany<sup>44, 84, 134</sup>.

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<sup>39</sup> and pollen morphology<sup>36, 125</sup>. 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<sup>139</sup>. 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 ginger. 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.