### Early Flowers and Angiosperm Evolution

The recent discovery of diverse fossil flowers and floral organs in Cretaceous strata has revealed astonishing details about the structural and systematic diversity of early angiosperms. Exploring the rich fossil evidence that has been accumulated over the past three decades, this unique study follows the evolutionary history of flowering plants from their earliest phases in obscurity to their dominance in modern vegetation.

The book provides comprehensive biological and geological background information, before moving on to summarise the fossil record in detail. Including previously unpublished results based on research into Early and Late Cretaceous fossil floras from Europe and North America, the authors draw together direct palaeontological evidence of the pattern of angiosperm evolution through time.

Synthesising palaeobotanical data with information from living plants, this book explores the latest research in the field and highlights connections with phylogenetic systematics as well as the structure and the biology of extant angiosperms.

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## Preface

Developments in the study of fossil and living plants over the past few decades have greatly clarified many aspects of early angiosperm evolution. Explicit phylogenetic analyses, facilitated by the development of computer technology and based on both morphological and molecular data, have renewed interest in the relationships of angiosperms to other plants, the patterns of relationship among major groups of angiosperms, and the processes that have generated angiosperm diversity at both microevolutionary and macroevolutionary scales. At the same time, a rapid accumulation of new information on the structure and biology of many key groups of living angiosperms has catalysed comparative studies and brought to light many previously unrecognised features that provide new perspectives on angiosperm evolution.

Palaeobotanical studies have also been central in revitalising research on early angiosperm evolution and have advanced significantly our understanding of early angiosperm history. In particular, the discovery of diverse and exquisitely preserved fossil flowers and floral organs from the Cretaceous has yielded detailed information on the structural and systematic diversity of early angiosperms. These data complement the information available from living plants, and are also invaluable for testing evolutionary hypotheses based on extant taxa against palaeobotanical and stratigraphic evidence. The recognition of fossil pollen grains in situ within flowers has also provided new possibilities for interpreting the record of dispersed fossil pollen. Only a few decades ago the abundant occurrence of fossil angiosperm flowers in Cretaceous strata was unimagined, but today there is a rich floral record, much of which still remains to be analysed in detail. The key breakthrough was the recognition that numerous small fossil flowers, which are generally not visible to collectors in the field, can be extracted from Cretaceous sediments by using bulk-sieving techniques and studied with scanning electron microscopy (SEM), and now also with synchrotron X-ray microtomography (SXRTM). These techniques, modified from standard approaches to Cenozoic fossil floras in Europe, and pioneered in the Late Cretaceous of Scania, Sweden, have now yielded diverse angiosperm flowers from many new fossil floras (mesofossil floras) discovered in Lower and Upper Cretaceous strata in Europe, North America, Asia, New Zealand and Antarctica.

In this book we provide a synthesis and overview of current data and ideas on the major patterns of angiosperm evolution, focusing especially on the early evolution of the group. Our emphasis is on the new information from the fossil record that has accumulated over the past three decades and how this relates to recent findings on the phylogenetic systematics, structure and biology of extant angiosperms. Central to this synthesis of the palaeobotanical data is its integration with information from living plants and the presentation of previously unpublished results based on our research with Early and mid-Cretaceous fossil floras from eastern North America and Portugal.

Chapters 1 to 4 provide the background to information and ideas discussed in more detail later in the book. Chapter 1 introduces recent developments in angiosperm palaeobotany, molecular systematics and studies of the flowers of living plants, and briefly considers some of the ways in which these advances are changing our perspective on early angiosperm evolution. Major features of angiosperm structure and biology are also reviewed along with previous ideas on the origin and early evolution of angiosperms and their flowers, as well as the rise of angiosperms to ecological dominance. Chapter 2 provides an overview of the nature of the angiosperm fossil record. Chapter 3 briefly outlines changes in palaeogeography and climate since the Early Cretaceous, as an introduction to the changing world in which angiosperm diversification took place. Chapter 4 briefly discusses the stratigraphic framework and occurrence of the angiosperm fossils considered in this book and provides a review of the key fossil localities.

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Chapter 5 places angiosperms in context with respect to other groups of extant and extinct seed plants and focuses especially on those plants that have been thought to be closely related to angiosperms. In particular, we highlight new palaeobotanical data on the Gnetales and the potentially related extinct Bennettitales and Erdtmanithecales. Chapters 6 and 7 review the development of ideas concerning seed plant and angiosperm phylogeny.

The core of this book, Chapters 8–15, summarises in a phylogenetic framework the fossil record of angiosperms with particular emphasis on floral structures known from the Cretaceous. Brief mention is also made of key records from the Early Cenozoic.

In Chapter 16 we consider major patterns in the structural diversification of angiosperm flowers based on current phylogenetic hypotheses and evidence from the fossil record.

Chapters 17–20 consider the biological and ecological consequences of angiosperm diversification, including the nature of vegetational change during the Cretaceous and the evolution of interactions with pollinators and dispersers. Through these interactions, the diversification of flowering plants has been inextricably linked with diversification in the animal world, as well as with the origin of modern ecosystems.

All photographs and plates are by Else Marie Friis and Kaj Raunsgaard Pedersen, and all line drawings by Pollyanna von Knorring, unless otherwise specified; the maps were drawn by Wieslaw Smolinsky. We thank all staff members of the Department of Palaeobotany, Swedish Museum of Natural History, Stockholm, for much help and encouragement during the production of this book. We are also grateful for the support and patience of our families in the process of completing this work. We are also deeply grateful for stimulating discussions with many colleagues around the world over many years. We have greatly appreciated and benefited from their advice and friendship.

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