

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 Including previously unpublished results based on research into Early and Late Cretaceous fossil floras from Europe and North America, the authors draw together direct palaeontological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.

ELSE MARIE FRIIS is in the Department of Palaeobotany at the Swedish Museum of Natural History. Her research interests include Cretaceous flowers and other fossil reproductive structures, with particular focus on the origin and early diversification of angiosperms and related seed plants.

PETER R. CRANE is in the School of Forestry and Environmental Studies at Yale University. His research interests include large-scale patterns and processes of plant evolution and integrated palaeobotanical and neobotanical studies of plant diversity and evolution.

KAJ RAUNSGAARD PEDERSEN is in the Department of Geology at the University of Aarhus. His research interests include integrated palynological and palaeobotanical studies of Mesozoic seed plants with particular focus on Cretaceous reproductive structures and flowering plant evolution.

Cambridge University Press
978-0-521-59283-3 - Early Flowers and Angiosperm Evolution
Else Marie Friis, Peter R. Crane and Kaj Raunsgaard Pedersen
Frontmatter
[More information](#)

Early Flowers and Angiosperm Evolution

Else Marie Friis
*Swedish Museum of Natural History,
Stockholm*

Peter R. Crane
*School of Forestry & Environmental Studies,
Yale University*

Kaj Raunsgaard Pedersen
Department of Geology, University of Aarhus

Line drawings by Pollyanna von Knorring



Cambridge University Press
 978-0-521-59283-3 - Early Flowers and Angiosperm Evolution
 Else Marie Friis, Peter R. Crane and Kaj Raunsgaard Pedersen
 Frontmatter
[More information](#)

CAMBRIDGE UNIVERSITY PRESS

Cambridge, New York, Melbourne, Madrid, Cape Town, Singapore,
 São Paulo, Delhi, Tokyo, Mexico City

Cambridge University Press
 The Edinburgh Building, Cambridge CB2 8RU, UK

Published in the United States of America by Cambridge University Press, New York

www.cambridge.org

Information on this title: www.cambridge.org/9780521592833

© E. M. Friis, P. R. Crane and K. R. Pedersen 2011

This publication is in copyright. Subject to statutory exception
 and to the provisions of relevant collective licensing agreements,
 no reproduction of any part may take place without
 the written permission of Cambridge University Press.

First published 2011

Printed in the United Kingdom at the University Press, Cambridge

A catalogue record for this publication is available from the British Library

Library of Congress Cataloging-in-Publication Data

Friis, Else Marie.

Early flowers and angiosperm evolution / Else Marie Friis, Peter R. Crane,
 Kaj Raunsgaard Pedersen.

p. cm.

ISBN 978-0-521-59283-3 (Hardback)

1. Angiosperms, Fossil. 2. Angiosperms—Evolution. I. Crane, Peter R.
 II. Pedersen, Kaj Raunsgaard. III. Title.

QE980.F75 2011

561—dc22

2011001815

ISBN 978-0-521-59283-3 Hardback

Cambridge University Press has no responsibility for the persistence or
 accuracy of URLs for external or third-party internet websites referred to
 in this publication, and does not guarantee that any content on such
 websites is, or will remain, accurate or appropriate.

Contents

<i>Preface</i>	<i>page ix</i>	5 Angiosperms in context: extant and fossil seed plants	101
1 Introduction to angiosperms	1	5.1 Angiosperms among extant and fossil seed plants	101
1.1 Phylogenetic position of angiosperms	1	5.2 Bennettitales–Erdtmanithecales–Gnetales (BEG) group	104
1.2 Characteristic features of angiosperms	6	5.3 Gnetales	105
1.3 Timing of angiosperm diversification	16	5.4 Erdtmanithecales	114
1.4 Rise to ecological dominance	19	5.5 Unassigned dispersed seeds of the BEG group	119
2 The nature of the angiosperm fossil record	23	5.6 Bennettitales (Cycadeoidales)	124
2.1 Understanding the plant fossil record	23	5.7 Pentoxylales	130
2.2 The adequacy of the angiosperm fossil record	38	5.8 Other Palaeozoic and Mesozoic seed plants	131
3 The environmental context of early angiosperm evolution	39	6 Origin and age of angiosperms	141
3.1 Palaeogeography	39	6.1 Hypotheses of seed plant relationships	141
3.2 Palaeoclimate	45	6.2 Origin of angiosperm structure	150
3.3 Climate change during the Cretaceous	50	6.3 The age of angiosperms	155
3.4 Implications for angiosperm diversification	53	6.4 Pre-Cretaceous angiosperm-like fossils	158
4 Stratigraphic framework and key areas for Cretaceous angiosperms	55	7 Phylogenetic framework and the assignment of fossils to extant groups	163
4.1 The stratigraphic framework	55	7.1 Early ideas on angiosperm phylogeny	163
4.2 Key areas for Cretaceous angiosperms	56	7.2 Phylogenetic studies of angiosperms based on molecular data	163
4.3 Europe	57	7.3 Angiosperm phylogeny group classification (APGIII)	164
4.4 Eastern North America	72	7.4 Angiosperm phylogeny: future directions	167
4.5 Western Interior of the United States and Canada	79	7.5 Assignment of fossils to extant groups	168
4.6 Alaska	81	8 Fossils near the base of the angiosperm tree	169
4.7 Greenland	82	8.1 Early-diverging angiosperm lineages at the ANITA grade	169
4.8 Israel, Jordan and Lebanon	82	8.2 Amborellaceae	171
4.9 North Africa	84	8.3 Nymphaeales	171
4.10 West Africa and Brazil	85	8.4 Austrobaileyales	176
4.11 Asia	88	8.5 Chloranthaceae	180
4.12 Southern Gondwana and India	96	8.6 Ceratophyllaceae	185

vi Contents

9 Early fossil angiosperms of uncertain relationships	189	13.7 Caryophyllales	315
9.1 Putative angiosperms	189	13.8 Saxifragales	316
9.2 Fossil flowers attached to inflorescences and stems	192	14 Fossils of core eudicots: rosids	327
9.3 Isolated flowers and fruits preserved as compressions/impressions	200	14.1 Classification of rosids	327
9.4 Permineralised flowers	201	14.2 Fossil evidence of rosids	327
9.5 Isolated angiosperm mesofossils	202	14.3 Vitales	329
9.6 Dispersed monoaperturate pollen	208	14.4 Fabids (Eurosids I)	329
9.7 Fossil leaves of uncertain relationships	215	14.5 The COM clade	329
		14.6 The nitrogen-fixing clade	332
		14.7 Malvids (Eurosids II)	354
10 Early fossils of eumagnoliids	219	15 Early fossils of eudicots: asterids	361
10.1 Classification of eumagnoliids	219	15.1 Classification of asterids	361
10.2 Magnoliales	223	15.2 Cornales	363
10.3 Laurales	231	15.3 Ericales	365
10.4 Canellales	244	15.4 Lamiids (Euasterids I)	378
10.5 Piperales	246	15.5 Boraginaceae, Icacinaceae and Vahliaceae	379
11 Fossils of monocots	249	15.6 Garryales	381
11.1 Classification of monocots	249	15.7 Gentianales	381
11.2 Fossil evidence of monocot diversification	250	15.8 Solanales and Lamiales	382
11.3 Putative early monocot fossils	250	15.9 Campanulids (Euasterids II)	382
11.4 Acorales	255	15.10 Aquifoliales, Escalloniales and Asterales	383
11.5 Alismatales	256	15.11 Bruniales, Apiales, Paracryphiales and Dipsacales	385
11.6 Dioscoreales	266	16 Patterns of structural diversification in angiosperm reproductive organs	387
11.7 Pandanales	266	16.1 Inflorescence structure	388
11.8 Liliales	267	16.2 Floral organisation	391
11.9 Asparagales	267	16.3 Other aspects of floral construction	412
11.10 Commelinids	268	17 History and evolution of pollination in angiosperms	415
12 Fossils of eudicots: early-diverging groups	275	17.1 Pollination in extant non-angiosperm seed plants	415
12.1 Classification of eudicots	275	17.2 Pollination in extant angiosperms	417
12.2 Early-diverging eudicots	276	17.3 Insects as pollinators	419
12.3 Fossil evidence of eudicot diversification	277	17.4 Vertebrates as pollinators	426
12.4 Fossils of uncertain relationships	277	17.5 History of pollination in angiosperms	428
12.5 Ranunculales	289	17.6 Large-scale trends in the history of angiosperm pollination	441
12.6 Proteales	292	18 History and evolution of dispersal in angiosperms	445
12.7 Sabiaceae	301	18.1 Dispersal in extant non-angiosperm seed plants	445
12.8 Buxales	303	18.2 Dispersal in extant angiosperms	447
12.9 Trochodendrales	308		
13 Fossils of core eudicots: basal lineages	311		
13.1 Classification of core eudicots	311		
13.2 Early fossil evidence of core eudicots	312		
13.3 Gunnerales	312		
13.4 Dilleniaceae	313		
13.5 Berberidopsidales	313		
13.6 Santalales	314		

18.3 Animal dispersers	448	20 The accumulation of angiosperm diversity	475
18.4 History of dispersal in angiosperms	450	20.1 Large-scale patterns in angiosperm diversification	475
18.5 Large-scale trends in the history of angiosperm dispersal	456	20.2 Patterns of angiosperm diversification: early lineages	477
19 Vegetational context of early angiosperm diversification	461	20.3 Patterns of angiosperm diversification: eumagnoliids	483
19.1 Transition to angiosperm-dominated vegetation	461	20.4 Patterns of angiosperm diversification: monocots	486
19.2 Components of Early Cretaceous vegetation	462	20.5 Patterns of angiosperm diversification: eudicots	488
19.3 Vegetation during the early diversification of angiosperms	467	20.6 Angiosperm evolution and global change through the Cenozoic	495
19.4 Early angiosperms: diversity in obscurity	469	20.7 Prospects	498
19.5 Mid-Cretaceous vegetation	471	<i>References</i>	501
19.6 Late Cretaceous vegetation and floristic provinces	472	<i>Index</i>	573

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.

x Preface

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.

Major support for this work was obtained from the Swedish Museum of Natural History and the Swedish Natural Science Research Council. Additional substantial support was provided by the Carlsberg Foundation, the United States National Science Foundation, The Field Museum, The Royal Botanic Gardens, Kew, The University of Chicago, Yale University and The University of Aarhus. We also acknowledge support from the TOMCAT Beamline at the Swiss Light Source, Paul Scherrer Institute, Switzerland, the Asian–Swedish Research Link Programme, and the WCU program of the National Research Foundation of Korea.