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The Dawn Angiosperms

Uncovering the Origin of Flowering Plants

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Dedicated to
the 120th Anniversary of
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Preface

Angiosperms are the most diversified plant group in the world, being represented by *ca* 300,000 species in about 400 families. Like all of Life, including ourselves, they have had their own history and undergone many evolutionary stages before they arrive at their current forms. The origin of Angiosperms (flowering plants) has been the subject of much dispute because this is a key event in the history of life and has a far-reaching influence on our understanding of relationships among seed plants as a whole as well as within the angiosperms. Despite all efforts and investigations on pre-Cretaceous fossil plants, most of palaeobotanists accepted angiosperms only from the Cretaceous and younger strata. This not only contradicts the results of molecular analyses but also makes angiosperms as if out of nowhere.

I have been working on Mesozoic fossil plants in the past two decades, during which time I have studied a number of fossil plants. Some of these fossil plants have been published as Jurassic angiosperms, and, unsurprisingly, many questions and doubts have been raised about them. These questions need to be addressed seriously and journal papers do not provide sufficient space to compare and relate these early angiosperms. In this book, these pioneer angiosperms are documented in detail, sometimes with new specimens not studied before. Also, I propose a criterion to identify angiosperms that could be adopted in palaeobotany. My aim is to improve clarity and objectivity of judgment about what constitutes an angiosperm before studying. The evolution of angiosperms is evaluated in the background of seed plants or even in whole land plants. The general patterns of plant evolution are eloaborated.

In Chap. 1, a brief introductory overview of angiosperms is given. In Chap. 2, some of the already suggested ancestors of angiosperms are noted. Chapter 3 discusses the various features scientists have used to define angiosperms, and an index character for fossil angiosperms is selected. Chapter 4 gives a brief summary of the geological and biological backgrounds of fossil plants to be elaborated upon in later chapters. Chapters 5 through 7 document in detail several angiosperms or possible angiosperms found in the Early Cretaceous and Jurassic of northeast China and south Germany, and these chapters form the core of the book. For those interested in fossil evidence, these chapters may be your favorite. Chapter 8, based on current knowledge, raises a new hypothesis on flower formation and discusses possible origin and evolutionary history of angiosperms and land plants. For those interested in general evolution patterns of plants, especially reproductive organs, this may be your favorite chapter. Chapter 9 summarizes the results as a whole and provides suggestions for future study in related fields.

There are 671 pictures and drawings in 166 figures. These pictures represent the fossil plants in a way more direct and objective than words; the latter more or less reflects my personal inclination in interpretation as well as wording. In total, 642 references are cited. The readers can refer to these references for further information.

It is expected that this book, like many others, will have certain controversial aspects. The publishing of this book can only serve as a starting rather than a concluding point for works on these fossils as well as the origin of angiosperms. Everything in this book, including criteria, definitions, interpretations, and conclusions, is open to discussion. Readers are always welcome to interpret the data in this book from their own perspectives. I hope the readers can feel free to send me their opinions. I believe the future study of early angiosperms will benefit from such feedback and interaction.

Nanjing
March 2017

Xin Wang

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Contents

Acronyms

AGS	Acta Geologica Sinica (English edition)
APG	Angiosperm Phylogeny Group
BSPG	Bayerische Staatssammlung für Paläontologie und Geologie, München, Deutschland
CNU	Capital Normal University, Beijing, China
GDPC	Günter Dütsch personal collection
IBCAS	Institute of Botany, Chinese Academy of Sciences, Beijing, China
LHFM	Lingyuan Hongtao Fossil Museum, Liaoning, China
LM	Light microscope
NIGPAS	Nanjing Institute of Geology and Palaeontology, Academia Sinica, Nanjing, China
NOCC	National Orchid Conservation Center of China
IVPP	Institute of Vertebrate Palaeontology and Palaeoanthropology, Academia Sinica, Beijing, China
SEM	Scanning electron microscope
SFLBG	Shenzhen Fairy Lake Botanical Garden
SSPC	Stefan Schmeißner personal collection
STMN	Shandong Tianyu Museum of Nature, Pingyi, Shandong, China
TEM	Transmission electron microscope

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Chapter 1
Introduction

The origin of angiosperm has been a contentious topic in botany, especially in palaeobotany. Before the 1960s there were for a long time and remains today a number of reports of angiosperms from strata older than the Cretaceous. However, mainstream palaeobotanists discount them now. Instead, palaeobotanists since 1970s have increasingly favored a rapid origin of angiosperms in the Early Cretaceous, although these conclusions have been frequently challenged by enigmatic fossil plant discoveries. The present conflicting situation, in my view, reflects a result of multiple criteria used for angiosperm definition and recognition in palaeobotany. I propose a new open criterion for fossil angiosperms as a solution for the problem. This chapter briefly summarizes the historic background of the current study.

The botanical term "Angiosperm" (Greek: αγγειον, receptacle, and σπερμα, seed) was coined in the form Angiospermae by Paul Hermann in 1690, as the name of one of the primary divisions of the plant kingdom. It included flowering plants possessing seeds enclosed in capsules, in contradistinction to his Gymnospermae (Harper 2001). As early as 1827, Brown demonstrated that the Angiospermae are indeed distinguished from gymnosperms, i.e. all other seed plants, by their enclosed ovules (Arber and Parkin 1908). This apparently subtle difference had a great impact on scientific thinking in the systematics of plants. Angiosperms today are by far the most diverse group in the plant kingdom. They dominate the terrestrial biota with more than 300,000 species, about 89.4% of the total species in the embryophytes (Crepet 2000). They are major sources of our fibres, food, drugs, and housing materials. They are also the predominant species of tropical rain forests and provide structural definition for most terrestrial ecosystems (Crepet 2000). An understanding of evolution and of precise relationships within the angiosperms allows a better understanding of their specific diversity, temporal and spatial distributions, and ecological implications. This in turn facilitates more efficient searching for natural resources, provides a precise framework to evaluate the plants for various applications, and helps informed decision-making regarding biodiversity conservation (Crepet 2000). The origin, evolution and sustainable

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development of ourselves, human beings, would be unimaginable without angiosperms. Because of their importance for the Earth's ecosystem and for our own survival, it is not surprising that people are curious about all aspects of angiosperms, especially their origin and evolution.

The origin of angiosperms has indeed been a riveting topic in botany for more than a century. During the time of Charles Darwin, people were already talking about the rapid diversification of flowering plants in the mid-Cretaceous, and Darwin's "abominable mystery" is related to this apparently abrupt historic phenomenon (Friedman 2009). John Ball (1818–1889) published a paper hypothesizing that atmospheric carbon dioxide concentrations had been the key factor restricting the development of angiosperms, and those angiosperms had stayed in alpine regions and had little chance to be fossilized. He believed they did not enter the fossil record until the concentration of atmospheric carbon dioxide dropped. Both Joseph D. Hooker (1817–1911) and Charles Darwin (1809–1882) were skeptical of this hypothesis (Friedman 2009), but the abrupt appearance of flowering plants in the mid-Cretaceous was a problem for Darwin because it strongly contradicted his concept of gradualism (Friedman 2009). Darwin conjectured that at one time there had been a remote continent in the southern hemisphere, where angiosperms evolved until they spread to other continents (Friedman 2009). At this time such a birthplace continent has not been identified by geologists. Gaston de Saporta (1823–1895), also perplexed by the rapid diversification of angiosperms in the mid-Cretaceous, came up with an alternate interpretation: the rapid diversification of angiosperms was due to the co-evolution of angiosperms and insects. This idea was favored and promoted by Darwin, and is still favored by many biologists (Ren 1998; Friedman 2009; Ren et al. 2009). However, according to Hughes (1994), there were no corresponding changes in insects during this period.

Since the death of Charles Darwin in 1882, there has been much progress in terms of theories and findings of earlier fossil angiosperms. Hugh H. Thomas (1885–1962) discovered a new plant, *Caytonia,* from the Middle Jurassic and related this plant to angiosperms (Thomas 1925). Despite the fact that Thomas M. Harris (1903–1983) found that the pollination in *Caytonia* was gymnospermous rather than angiospermous, this plant remains one of the most attractive candidates for angiosperm ancestry (Doyle 2006, 2008; Rothwell et al. 2009). *Corystospermum* was recognized by Thomas as another potential candidate for angiosperm ancestry (Doyle 2006, 2008; Rothwell et al. 2009). Scott (1906) and Arber and Parkin (1907) proposed a possible relationship between Bennettitales and angiosperms, which became the foundation for the so-called anthophyte theory that persists today (Crane 1985, 1986) although some details are now open to debate (Rothwell et al. 2009). In addition, Sahni related *Pentoxylon* from the Mesozoic of the Gondwana to angiosperms (Hughes 1994). Retallack and Dilcher (1981) related Glossopteridales and angiosperms, while Taylor and Hickey (1996) pointed out possible relationship between Gnetales and Angiosperms. Meyen (1988) proposed the gamoheterotopy theory, and Frohlich and Parker (2000) proposed the mostly male theory for the origin of angiosperm flowers. Asama (1982) related Gigantopterids to angiosperms based on foliar features, and Taylor et al. (2006) did so based on biogeochemistry. However, none of these fossil plants have a confirmed relationship to angiosperms, and a status intermediate between angiosperms and these groups is still hard to conceive. There appears to be insurmountable difference between these plants and angiosperms.

Before 1960s many pre-Cretaceous fossils were claimed to be directly related to modern angiosperms (Wieland 1926; Eames 1961; Hill and Crane 1982); subsequently, their angiospermous affinities have been largely rejected (Scott et al. 1960). Since that time, however, several newly-found interesting fossil plants have been found in the Early Cretaceous or even earlier that appear to be more or less related to angiosperms, although their actual significance is still open to debate. These discoveries have enhanced our understanding of the diversity of ancient seed plants and repeatedly stimulated discussion. These discoveries include *Sanmiguelia, Schmeissneria, Xingxueanthus, Euanthus, Yuhania, Juraherba, Chaoyangia, Archaefructus, Sinocarpus*, *Callianthus, Baicarpus, Liaoningcarpus, Nothodichocarpum* (among many others) and various angiosperm-like pollen grains from the Triassic and Jurassic (Cornet 1986, 1989a, b, 1993; Li et al. 1989; Martin 1989a, b; Cornet and Habib 1992; Hill 1996; Duan 1998; Sun et al. 1998, 2001, 2002; Leng and Friis 2003, 2006; Hochuli and Feist-Burkhardt 2004, 2013; Wang et al. 2007a, b; Wang and Zheng 2009; Wang 2010; Wang and Wang 2010; Liu and Wang 2016, 2017; Han et al. 2013, 2016, 2017). Mesofossils described by Friis, Crane and their colleagues have by far contributed the most to our knowledge of the diversity of angiosperms in the Early Cretaceous (Friis et al. 2003, 2005, 2006, 2009, 2011) although the fragmentary nature of such fossil remains restricts us from understanding the plants as a whole (Friis et al. 2003, 2005, 2006, 2009, 2011; Rothwell et al. 2009). Macroscopically, the radiation of fossil angiosperms from the Early to Middle Cretaceous has been well documented (Doyle and Hickey 1976; Archangelsky et al. 2009). At present it is commonly believed by many botanists that the origin of angiosperms cannot be pre-Cretaceous (Cronquist 1988; Friis et al. 2005, 2006, 2011).

Some frequently overlooked information on the topic includes that tricolpate pollen grains, thought to be more derived, occurred in the Barremian, and that the angiosperms from the Yixian Formation (the Barremian-Aptian), the oldest well-accepted megafossils of angiosperms, demonstrate unexpectedly greater diversity. These facts suggest that angiosperms must have had a much earlier origin, favoring the hypotheses based on *Schmeissneria* and other older fossils (Cornet 1986, 1989a, b, 1993; Cornet and Habib 1992; Hill 1996; Duan 1998; Sun et al. 1998, 2001, 2002; Leng and Friis 2003, 2006; Hochuli and Feist-Burkhardt 2004, 2013; Wang et al. 2007a, b; Wang and Zheng 2009; Wang and Wang 2010; Wang 2010; Liu and Wang 2016, 2017; Han et al. 2013, 2016, 2017).

It is true that there is no strict consensus on these Early Cretaceous angiosperms. For example, *Archaefructus* and *Sinocarpus* have been foci of debates in the past years (Sun et al. 1998, 2002; Friis et al. 2003; Leng and Friis 2003, 2006; Dilcher et al. 2007). Other fossils have also been contentious. A layman might well ask: “Why can’t you palaeobotanists reach an agreement on these fossils?” This is a question worthy thinking about. Ideally, the authors of all publications should be honest, intelligent, and logical. They should offer detailed description and figures of their fossils, interpret them using correct botanical terms, and follow the same rules. If this were the case, there would be no controversy in palaeobotany at all. Then where did the controversies come from? Controversies arise from different criteria applied in the descriptions, discussions, and arguments. Following the above idealistic thinking, there would be a universally accorded criterion identifying fossil angiosperms. In reality, different workers have different criteria, some emphasizing one feature, others emphasizing other features. This means there cannot be a consensus on early angiosperms unless an open, applicable definition of fossil angiosperm is found. So finding an applicable definition for fossil angiosperms therefore becomes a key point in the study of early angiosperms.

In this book, I approach the origin of angiosperms from this view point, trying to construct an acceptable and applicable definition for early fossil angiosperms. Then I document several fossil plants from the Jurassic and Early Cretaceous in northeastern China and Germany, and apply this definition to justify their angiospermous identity. Based on this fossil evidence, I discuss the origin of angiosperms and related topics.

It is my expectation that many points of view in this book may not agree with existing ones, and many colleagues may feel more or less offended in one way or another. The literature cited in this book is not exhaustive, so many important, but marginal in this context, works may not be listed. This does not mean that I intend to ignore them, but simply that space does not allow me to do all the things in this book alone. The definition of an angiosperm might be the focus of the debate. However, since we are doing science, open discussion among people with different opinions is inevitable and ultimately beneficial to science. I welcome those with different opinions to stand up and offer their theories and evidence to solve the common problems we face. I would seek to incorporate any solution that is better than mine. As soon as we can reach a consensus on a definition of what constitutes an angiosperm, I think we are beginning to see the light at the end of the tunnel. Were we palaeobotanists to reach a consensus, we could end the current rather chaotic state of palaeobotany, where authority, rather than consensus, prevails.

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