Xin Wang

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The Dawn Angiosperms

Uncovering the Origin of Flowering Plants

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Uncovering the Origin of Flowering Plants

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To my parent, who have been supportive throughout my life and career.

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 gone through many evolutionary stages before they arrived at their current forms. The origin of Angiospermae (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. Until recently most of palaeobotanists recognized angiosperms only from the Cretaceous and younger strata. This contradicts the results of molecular analyses.

I have been working on Mesozoic fossil plants for 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 definition of angiosperms that could be adopted in palaeobotany. My aim is to improve clarity and objectivity of judgment about what constitutes a fossil angiosperm.

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 5–7 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. Chapter 8, based on current knowledge, raises a new hypothesis on flower formation and discusses possible origin and history of evolutionary development for carpels and flowers. Chapter 9 summarizes the results as a whole and provides suggestions for future study in related fields.

There are 362 pictures and drawings in 101 figures. These pictures represent the fossil plants in a way more direct and objective than words, which more likely reflects my personal inclination in interpretation as well as wording. Total 530 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 Xin Wang
January, 2010

Acknowledgements

My studies of the plant fossils described in this book can be dated back to the early 1990s, and some of the fossil collecting was done even before that time. During this long period I have benefitted from the constant support from my advisors, Drs. Shuying Duan, Ye Chen, David L. Dilcher, and Zhiyan Zhou. Many colleagues, including Drs. Shaolin Zheng, Jinzhong Cui, Shijun Wang, Baoyin Geng, Yong Yang, and my advisors co-authored several papers with me. Many other colleagues and friends have offered valuable support and constructive suggestions from various aspects, including Drs. Wu Zhang, Zhaoliang Xu, Jingeng Sha, Yongdong Wang, Shuangxing Guo, Qiang Ji, Jun Wang, Yi Wang, Yaosong Xue, Chuanming Zhou, Dong Ren, Yuan Wang, Shunqin Wu, Fang Zheng, Shuren Zhang, Weiming Wang, Jianguo Li, Cuiling He, Chunzhao Wang, Erjun Zhuo, Zhiqin Wang, Xiting Cheng, Kaihe Du, Yinhou Xiao, Min Feng, Jie Wen, Zhi Du, Xuejian Yang, Zhaoyi Meng, Xin Xu, Song Ge, Liangqian Li, Hongzhi Kong, Qiang Zhang, Gang Li, Haichun Zhang, Qin Leng, Yibo Luo, Hongxia Liu, Yan Liang, Gongle Shi, Yan Fang, Hongtao Cai, Gang Han, Shikuan Liang, Yan Chen, Peter Stevens, Dennis W. Stevenson, Michael Frohlich, Walter Judd, Kevin Nixon, James Doyle, Peter Crane, Michael Krings, Stefan Schmeiβner, Günter Dütsch, Martin Kirchner, Johanna H.A. van Konijnenburg-van Cittert, Steve McLoughlin, Thomas N. Taylor, Nora Dotzler, Larry Hufford, Meizhen Cao, Zhenyu Li, Jianan Zhu, Catarina Rydin, Steven Manchester, Frédéric Jacques, and Michael Heads. Drs. Douglas McKinnon, Williams Rose, and Margaret Joyner have helped with English in publications. Dr. Christopher Hill has gone through the whole book and given constructive and detailed suggestions. I wish to extend my cordial thanks to all of them.

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Acronyms

AGS Acta Geologica Sinica

APG Angiosperm Phylogeny Group

BMCEB BMC Evolutionary Biology

BSPG Bayerische Staatssammlung für Paläontologie und Geologie, München, Deutschland

CNU Capital Normal University, Beijing, China

GDPC Günter Dütsch Personal Collection

IBCAS Chinese National Herbarium, Institute of Botany, Chinese Academy of Sciences, Beijing, China

JIPB Journal of Integrative Plant Biology

JSE Journal of Systematics and Evolution

LM Light Microscope

NIGPAS Nanjing Institute of Geology and Palaeontology, Academia Sinica, Nanjing, 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

Chapter 1
Introduction

Angiosperm origin 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, palaeobotanical work since 1970s has increasingly supported 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 will 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” was coined in the form “Angiospermae” by combining two Greek words, αγγειον (receptacle) and σπερμα (seed) together 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 subtle-appearing 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 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.

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The origin of angiosperms has indeed been a riveting topic in botany for more than a century. During the time of Charles Darwin (1809–1882), 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 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). Arber and Parkin (1908) proposed a possible relationship between Bennettitales and angiosperms (according to Rothwell et al. 2009), which became the foundation for the so-called anthophyte theory that persists today (Crane 1985, 1986; Friis et al. 2009) 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). Meyen (1988) proposed the gamoheterotopy theory, and Frohlich and Parker (2000) published the Mostly Male Theory for angiosperm ancestry. Asama (1982) related Gigantopterids to angiosperms based on foliar features, and Taylor et al. (2006a) did so based on biogeochemistry. However, none of these fossil plants have a confirmed relationship to angiosperms. There appears to be insurmountable difference between these plants and angiosperms.

Before 1960s many pre-Cretaceous fossil records were claimed to be directly related to modern angiosperms (Wieland 1926; Eames 1961; Hill and Crane 1982); subsequently, these 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 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, Chaoyangia, Archaefructus, Sinocarpus*, and *Callianthus* (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; Ji et al. 2004; Hochuli and Feist-Burkhardt 2004, Wang et al. 2007b, c; Wang and Zheng 2009; Wang and Wang 2010; Wang in press). 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. 2000, 2001, 2009, 2010) although the fragmentary nature of such fossil remains normally restricts us from understanding the plants as a whole (Friis et al. 2009; Rothwell et al. 2009). Macroscopically, the radiation of fossil angiosperms from the Early to Middle Cretaceous has been well documented (Dilcher 1979; Crane and Dilcher 1984; Dilcher and Crane 1984; Dilcher and Kovach 1986; Retallack and Dilcher 1981a; Doyle and Hickey 1976; Archangelsky et al. 2009). At present it is commonly believed by palaeobotanists that the origin of angiosperms cannot be pre-Cretaceous (Cronquist 1988; Friis et al. 2005, 2006, 2010).

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 (also the Barremian), the oldest well-accepted megafossils of angiosperms, demonstrate an unexpectedly greater diversity. Both 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; Ji et al. 2004; Hochuli and Feist-Burkhardt 2004; Wang et al. 2007b, c; Wang and Zheng 2009; Wang and Wang 2010; Wang in press).

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. 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. The terrible thing is that the authors frequently assume others have known and agreed on their hidden criteria, and they use these criteria without any clarification. Therefore it becomes rather natural that there are controversies on this issue. 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 definition for early fossil angiosperms. Then I document several fossil plants from the Jurassic and Early Cretaceous in northeastern China and southern 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 so. 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 problem we face. I would seek to incorporate any solution that is better than mine in my future work. 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.

Chapter 2
Suggested Angiosperm Ancestors

There have been many proposals of candidates for the ancestors or closest relatives of angiosperms. Some of the currently more frequently cited examples are introduced here. Although none of them has been confirmed to be closely related to angiosperms, a comparison between them and angiosperms helps to identify where the problem and gaps in knowledge are. It is these candidates and their possible relationships to angiosperms that compose the foundation on which the current systematics of seed plants is based. Understanding them is also helpful to make a balanced judgment of the point of view in this book.

At one time or another almost all gymnosperms, and even ferns, have been proposed either as angiosperm ancestors or as their close relatives by various scholars based on various reasons in the past century (Maheshwari 2007). Even today some systematic botanists still favor some of these views. There is currently no consensus as to which of the several fossil taxa most appropriately bridges the gap between angiosperms and gymnosperms, and most of the dawn angiosperms documented later in this book appear to fall well within the scope of angiosperms. The suggested angiosperm ancestors or close relatives of angiosperms therefore still very much deserve our attention with regard to understanding angiosperm origin. They can help us to trace the development of the science, and constitute the background from which this book originates. Here I briefly introduce Gnetales, *Gigantopteris*, *Sanmiguelia*, *Leptostrobus, Caytonia*, Bennettitales, *Umkomasia*, *Problematospermum*, *Dirhopalostachys*, *Ktalenia*, and Pentoxylales, as examples among many (Fig. 2.1), and discuss their similarities to as well as differences from angiosperms. To a few taxa new information will be added.

2.1 Gnetales

Among living plants the Gnetales (*Ephedra*, *Gnetum*, and *Welwitschia*) are a group considered currently by many to be most closely related to the angiosperms. *Gnetum* lives today in tropical forests, while *Ephedra* and *Welwitschia* are dry-climate or desert plants. These three genera in Gnetales are fairly isolated from each other although they share many synapomorphies, including multiple axillary buds,

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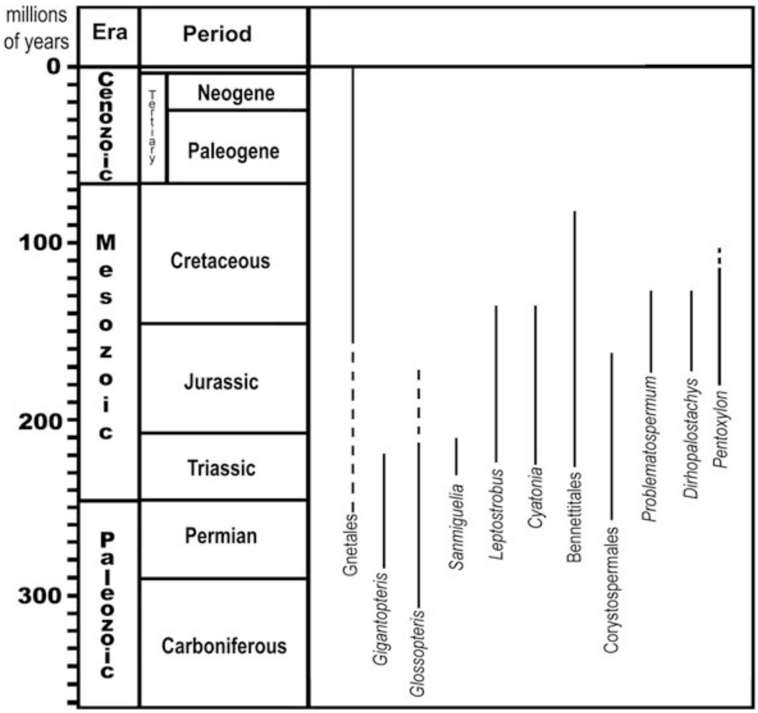

Fig. 2.1 Approximate temporal distribution of the taxa discussed in this chapter. *Dashed lines* indicate uncertainty

opposite and decussate phyllotaxy, vessel elements, circular bordered pits in protoxylem, a terminal ovule with two integuments, lack of archegonia, ribbed pollen (except for *Gnetum*) and anastomose (except for *Ephedra*) (Eames 1952; Zhang and Xi 1983; Crane 1996; Ickert-Bond et al. 2003; Maheshwari 2007). A micropylar tube is another common feature shared by these three genera, uniquely in living gymnosperms (Bierhorst 1971). Recent studies indicate that the micropylar tube is a feature seen in the Bennettitales-Erdtmanithecales-Gnetales clade (Friis et al. 2009). Gnetales appear to have had their greatest diversity in the past, and *Ephedra*-like pollen alone once accounted for up to 10–20% of palynofloral assemblage in northern Gondwana Province in the Middle Cretaceous (Brenner 1976). Gnetalean pollen grains also possibly occurred in the Permian (Delevoryas 1962; Wang 2004). Recent more megafossils most likely related to Gnetales have been found from the Early Cretaceous in South America and China (Rydin et al. 2003, 2004, 2006a; Tao and Yang 2003; Dilcher et al. 2005; Yang et al. 2005; Guo et al. 2009; Wang and Zheng 2010). Gnetales are frequently associated with other anthophytes including angiosperms in phylogenetic analyses (Thompson 1916; Crane 1985). The Gnetales are characterized by a suite of characters allying them closely to the angiosperms: eudicot-like venation, relict bisexuality, two integuments, pollen tube, vessel elements, and “endosperm” development after fertilization (Arber and Parkin 1908;

Eames 1952; Carlquist 1996; Chamberlain 1957; Martens 1971; Friedman 1990, 1991, 1992a, b; Biswas and Johri 1997; Doyle 1998; Yang et al. 2000; Rydin and Friis 2005). In addition, double fertilization, a phenomenon formerly thought restricted to angiosperms, is also found in *Ephedra* (Chamberlain 1957; Martens 1971; Friedman 1990, 1991, 1992a; Yang et al. 2000; Friedman and Williams 2004; Raghavan 2005). Despite all these similarities, however, there are still big gaps between Gnetales and angiosperms, for example, in terms of reproduction: in Gnetales the pollen grains are captured by a fertilization droplet and drawn in it to the ovule surrounded by integuments while in angiosperms pollen grains typically germinate on the stigma and sperms are conveyed to the ovule via the pollen tube (Chamberlain 1957; Eames 1961; Bierhorst 1971; Friedman 1992a, 1993; Biswas and Johri 1997; Friedman and Barrett 2008). Moreover, there are molecular data suggesting that Gnetales may actually be more closely related to Pinaceae than to angiosperms (Soltis et al. 2002; Qiu et al. 2007; Rydin and Korall 2009; For more, see Chap. 8).

2.2 Gigantopteriales

The gigantopterids (Fig. 2.2) are an enigmatic plant group from the Lower Permian to Triassic of southeastern Asia and southern North America. Their stems and cuticle have been studied anatomically (Yao and Crane 1986; Li et al. 1996; Li and Taylor 1998, 1999; Wang 1999), but reproductive organs remain elusive in spite of the reconstruction based on various fossil materials (Li and Yao 1983; Li 1992). Gigantopterid megaphylls are characterized by pinnate venation, with tertiary anastomosing veins and giving rise to higher order veins that may anastomose again and form meshes. Their leaf organization is so similar to angiosperms that Glasspool

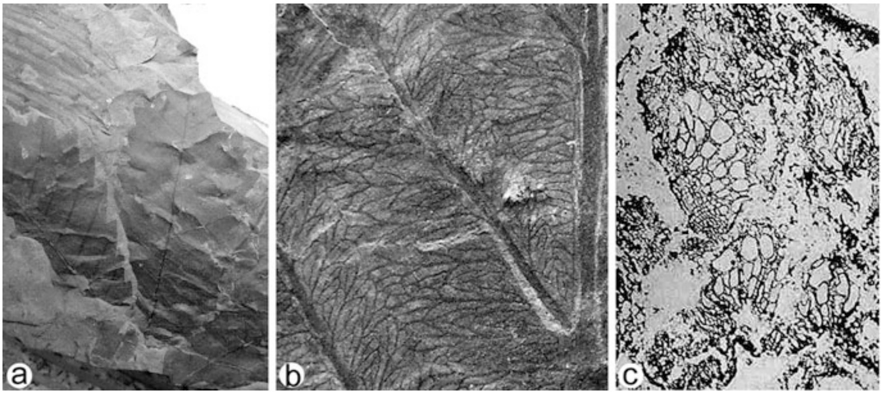

Fig. 2.2 Leaf morphology, venation and vessel elements of Gigantopterids. **A** Leaf morphology of *Gigantonoclea* (IBCAS). **B** Venation of *Gigantonoclea rosulata* (PB4969, NIGPAS). **C** Vessel elements of *Vasovinea tianii* (Courtesy of Dr. Hongqi Li)

et al. (2004) prefer to describe them using angiospermous terms although they rule out any relationship between them and angiosperms. These foliar features however were used by Asama (1982) to suggest that angiosperms in his view are derived from gigantopterids. The most intriguing feature of gigantopterids is undoubtedly that they are similar to angiosperms not only in leaf morphology and physiognomy but also in vessel elements in their wood (Li et al. 1994, 1996; Li and Taylor 1998, 1999). Oleanane, a chemical species formerly found only in extant angiosperms, has also been found in Gigantopterids (Taylor et al. 2006a). This discovery suggests a possible relationship among Gigantopterids and angiosperms as well as Bennettitales, as they are the only groups containing this chemical species (Taylor et al. 2006a). However, the hypothesized connection between Gigantopteridales and angiosperms is now largely discounted due to large time gap and lack of accurate information regarding their reproductive organs. The similarities between Gigantopterids and angiosperms may well represent large-scale convergence or parallelism (Glasspool et al. 2004).

2.3 Glossopteridales

Glossopteridales (Fig. 2.3) were mainly distributed on the Gondwanan continents (Taylor 1996; Biswas and Johri 1997; Taylor et al. 2007), although there are few, perhaps specious, reports from the northern hemisphere (Delevoryas 1969). They thrived from the Late Carboniferous to the Triassic (Middle Jurassic?) (Delevoryas 1969; Taylor 1996; Biswas and Johri 1997; Taylor et al. 2007). Common ovulate structures connected or associated with the leaves, *Glossopteris*, include *Lidgettonia*, *Denkania*, *Scutum*, *Ottokaria* and *Dictyopteridium*, and the pollen organs *Eretmonia* and *Glossotheca* with their bisaccate striate pollen of *Protohaploxypinus*-type (Taylor and Taylor 2009). *Dadoxylon* is the wood, and *Vertebraria* is the root (Biswas and Johri 1997). *Glossopteris* leaves are tongue-shaped, with an entire margin, a distinct midrib, and reticulate venation. In Glossopteridales, both pollen and ovulate structures are borne on the adaxial surface of the *Glossopteris* leaf. Unitegmic orthotropous ovules are attached either directly to the adaxial surface of a megasporophyll (Fig. 2.3b, c) or in stalked uniovulate cupules borne on a branching system (Nishida et al. 2007; Taylor et al. 2007; Taylor and Taylor 2009). Pollen sacs develop in pedicellate clusters that arise from the

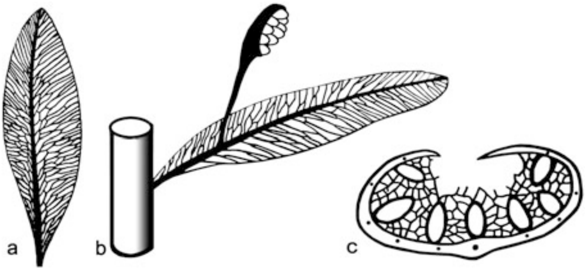

Fig. 2.3 Leaf and reproductive organ of Glossopterids. **A** Leaf. **B** Axis with a megasporophyll. **C** Cross section of cupule showing adaxial arrangement of seeds partially inrolled by the cupule

midvein of a modified leaf. The glossopterids have been suggested as potential angiosperm ancestors (Retallack and Dilcher 1981b). Theoretically, the glossopterid vegetative leaf could be homologous to an angiosperm's carpel, and the megasporophyll to the outer integument (Retallack and Dilcher 1981b; Doyle 2008). In some Glossopteridales, the margins of the megasporophyll are laterally inrolled (Nishida et al. 2007; Taylor and Taylor 2009; Fig. 2.3c), much like an under-developed conduplicate carpel of angiosperms. Among all the alternative hypotheses on carpel origin, the glossopterid-based theory is the only one that does not need to derive any carpel part de novo, and thus would be the least troublesome in morphological terms (Retallack and Dilcher 1981b). However, this interpretation is open to debate due to the differences in pollen organs, pollen grains, leaf features, and age gap between Glossopteridales and angiosperms (Retallack and Dilcher 1981b; Taylor and Taylor 2009). Moreover, the provenance of stamens and perianth are further challenges for this interpretation. Meanwhile, it has also been suggested that the Glossopteridales are the ancestors of Caytoniales based on leaf venation, pollen grains and seed structure (Krassilov 1977b).

2.4 *Sanmiguelia*

Sanmiguelia sensu lato is an enigmatic plant with large palm-like, pleated leaves and is found from the Middle to Upper Triassic of Colorado and Texas, USA (Brown 1956; Ash 1976; Tidwell et al. 1977; Cornet 1986, 1989b). The reconstructed plant includes the leaves (*Sanmiguelia*), female inflorescence (*Axelrodia*), and male inflorescence (*Synangispadixis*). *Axelrodia* includes two kinds of flowers with "carpels" bearing apical "stigmas" and enclosing pairs of basal ovules. *Synangispadixis* lacks a perianth and bears hundreds of spirally arranged microsporophylls with monocolpate pollen grains. Cornet (1989b) described the transmitting tissue, cotyledons, and developmental pattern in the fossil. Despite his and others' work, its phylogenetic position remains however both enigmatic and isolated (Friis et al. 2006). *Sanmiguelia* apparently is not closely related to any known gymnosperm or fern. It demonstrates certain similarities to monocots, such as leaf venation, ovule/seed developmental pattern, and leaf morphology. However, its relationship to other groups of plants, including angiosperms, cannot be assured until more fossils bridging the gaps between *Sanmiguelia* and other plants are found.

2.5 *Leptostrobus*

Leptostrobus (Czekanowskiales) is widely distributed in the Triassic to Cretaceous of the Laurasian continents and Australia (Liu et al. 2006b). It consists of an axis bearing numerous short-stalked, spirally arranged bivalved capsules containing many seeds (Krassilov 1977a; Liu et al. 2006b; Fig. 2.4). The capsule valves have papillate flanges (or lips), which may have functioned like stigmatic bands (Krassilov 1977a, Fig. 2.4c). Each valve bears 3–5 seeds (Liu et al. 2006b;

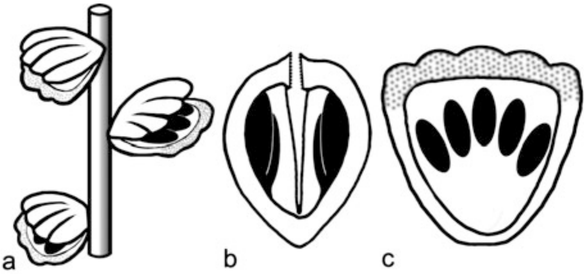

Fig. 2.4 Reproductive organ of Czekanowskiales. **A** *Leptostrobus*, showing capsules attached to an axis. **B** Longitudinal section of capsule showing two identical facing valves forming a capsule. **C** Interior view of a valve of the capsule showing seeds and flange

Figs. 2.4b, c). The flange is not seen in *Leptostrobus* species from earlier ages, therefore its presence in younger species of the genus may be derived (Krassilov 1977a). Its leaf is *Phoenicopsis*-like. Krassilov (1977a) related it to monocots based on its leaf morphology and cuticular features, although he admitted that it was hard to imagine that the coalescence of the valves could result in any known angiosperm carpel.

2.6 *Caytonia*

Caytonia is a cupulate female organ first recognized by Thomas (1925) from the Middle Jurassic of England. More materials of Caytoniales have been subsequently found in strata ranging from the Upper Triassic to Lower Cretaceous of Greenland, Poland, Canada, Siberia, Australia, Antarctic, Japan, Sweden (Harris 1933, 1940, 1964; Reymanowna 1970, 1973; Krassilov 1977a; Nixon et al. 1994; Barbacka and Boka 2000a; b; Taylor et al. 2006b), and China (Wang 2010; Fig. 2.5). Although never found physically attached, their association is so strong that it has been widely assumed that the related leaf is *Sagenopteris*. The male organ is assumed to be *Caytonanthus* with in situ monosulcate bisaccate pollen grains, *Vitreisporites* (Harris 1964; Taylor et al. 2006b; Taylor and Taylor 2009). Caytoniales have an axis bearing stalked, rounded, helmet-like cupules. Each cupule is recurved, with a lip-like projection near its base, and contains 8–30 orthotropous unitegmic ovules arranged in curved rows (Nixon et al. 1994; Taylor and Taylor 2009, Wang 2010). The cupule rim and cupule stalk form a cupule opening (Nixon et al. 1994; Fig. 2.5). The micropyles of the ovules are connected to the cupule opening via canals (Harris 1933; Reymanowna 1970, 1973). Because *Caytonia* encloses its seeds completely, Thomas (1925) initially thought that it was an angiosperm and that its cupule was equivalent to the carpel of angiosperms. Its Jurassic age also made it a perfect candidate for angiosperm ancestry (Knowlton 1925; Thomas 1925). However, later research, particularly by Harris, indicates that before fertilization the ovules of Caytoniales are exposed to the outside through canals, that the fertilization in Caytoniales is completed by drawing pollen grains through the canals to the ovules presumably in exuded fluid (a typical gymnospermous way). The seeds are

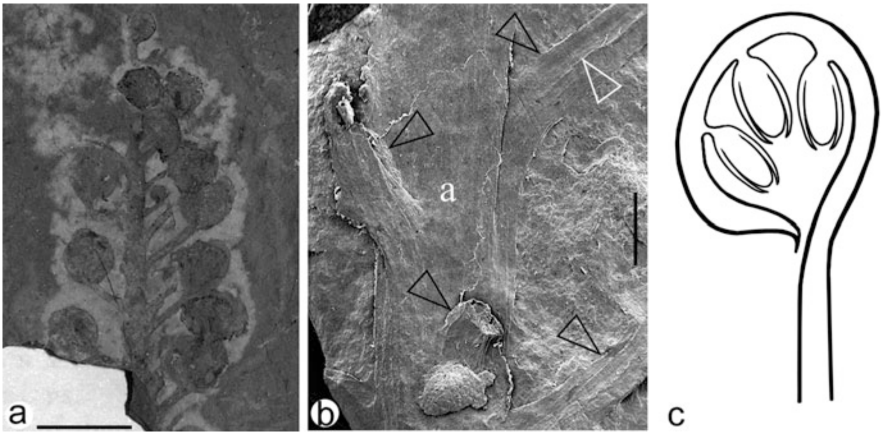

Fig. 2.5 *Paracaytonia* from the Yixian Formation (Early Cretaceous) of Liaoning, China. **A** General view of the reproductive organ. Note the multiple cupules physically connected to the same axis (GBM1, SFLBG). Bar = 1 cm. **B** Detailed view of the cupules helically arranged around the axis. Note the cupule stalks (*black arrows*) and the stub of another broken one suggesting a helical arrangement along the axis (a). Bar = 1 mm. **C** Diagram of a longitudinal section of a caytonialean cupule, showing cupule stalk, basal cupule opening, and seeds/ovules inside the cupule (from Wang 2010, courtesy of JSE)

then separated from the outside by post-fertilization plugging of the canals (Harris 1933, 1940, 1964; Reymanowna 1973; Krassilov 1977a; Nixon et al. 1994). These characters clearly place *Caytonia* in gymnosperms rather than angiosperms.

It is generally believed that the *Caytonia* cupule is derived from megasporophyll that has become folded or recurved transversely, unlike the conduplicate carpel in angiosperms which is folded longitudinally (Taylor et al. 1994; Doyle 2008; Taylor and Taylor 2009). The pollen organ, *Caytonanthus*, moreover, has 3–5 microsporangia in a group, unlike tetrasporangiate stamen in angiosperms (Nixon et al. 1994; Frohlich and Parker 2000). Nonetheless, *Caytonia* remains one of the most favored candidates for angiosperm ancestry (Krassilov 1977b; Hill and Crane 1982; Crane 1985; Doyle and Donoghue 1986a; Doyle 1998, 2006; Taylor et al. 2006b; Taylor and Taylor 2009). Since an angiospermous ovule usually has double integuments and the ovule of *Caytonia* is thought to be unitegmic, the cupule of Caytoniales is thought to be the equivalent of the outer integument in angiosperms (Crane 1986; Nixon et al. 1994; Doyle 2006, 2008). A credible relationship between Caytoniales and angiosperms clearly remains speculative until a reasonable interpretation of the de novo origin of either the carpel or outer integument is evidenced by fossils, plus reduction of seed number to one per cupule appears in the fossil record (Nixon et al. 1994; Rothwell and Serbet 1994; Rothwell et al. 2009; Taylor and Taylor 2009; Soltis et al. 2004).

The Chinese specimen of *Paracaytonia* (Caytoniales), unequivocally demonstrates that the arrangement of cupules along the axis is spiral rather than pinnate (Wang 2010; Fig. 2.5), suggesting that the so-called rachis is a true axis rather than a true rachis, as had been commonly thought (Doyle 2006, 2008; Taylor and Taylor 2009). This new information is important because many former interpretations of *Caytonia* are based on the assumed pinnate foliar nature of the whole organ, which is supposed to expand and turn into a conduplicate carpel (Doyle 2006, 2008; Taylor and Taylor 2009). Thus the Chinese material widens the gap between Caytoniales and angiosperms.

2.7 Bennettitales

Bennettitales range from the Middle Triassic to Late Cretaceous in age, including two families: the Cycadeoidaceae (with stout trunks and bisporangiate reproductive structures) and Williamsoniaceae (with slender, branching trunks, and either bisporangiate or monosporangiate strobili). Their reproductive organs have been documented from North America, Europe, Greenland, India, and China (Wieland 1899a, b, c, 1901, 1911, 1912; Harris 1944, 1967, 1969; Ye et al. 1986; Pedersen et al. 1989b; Nixon et al. 1994; Sun et al. 2001; Li et al. 2004; Crane and Herendeen 2009; Rothwell et al. 2009; Friis et al. 2009). The orthotropous ovules, sometimes with elongated funiculi, are interspersed with sterile interseminal scales on a conical ovulate receptacle at the center of their reproductive structures (Crane and Herendeen 2009; Rothwell et al. 2009). Outside of this structure, if bisexual, are microsporophylls bearing pollen sacs on their adaxial surfaces containing monocolpate pollen grains. Outermost are several whorls of bracts resembling the tepals of angiosperms (Nixon et al. 1994; Crane and Herendeen 2009; Friis et al. 2009; Rothwell et al. 2009).

The Bennettitales have been considered to be possible flowering plant ancestors because of their bisexual flower-like reproductive structures (Arber and Parkin 1908; Crane 1985; Doyle and Donoghue 1987; Nixon et al. 1994). The ovulate structure of Bennettitales is thought to be similar to an angiosperm carpel (Arber and Parkin 1907; Crane 1985; Doyle and Donoghue 1987). The presence of oleanane in Bennettitales adds further evidence to its possible relationship to angiosperms (Taylor et al. 2006a). Bennettitales, Gnetales and angiosperms are frequently grouped together in the anthophyte clade (Crane 1985; Doyle and Donoghue 1986a, b, 1987). These three groups share the minimized development of the gametophyte, together with rapid fertilization and embryogenesis after pollination (Pedersen et al. 1989b). Based on the similarities of seeds, Friis et al. (2009) proposed that Bennettitales, Erdtmanithecales, and Gnetales be grouped as the so-called BEG clade within a wider clade anthophyte. However, this interpretation faces some challenge due to possible mismatch of pollen in the reconstruction of Erdtmanithecales (Rothwell et al. 2009; Tekleva and Krassilov 2009). In addition, placement of Bennettitales in anthophytes is also questionable because of contradictory analyses and the lack of a character set for extinct taxa (Rothwell and Stockey 2002). The spatial arrangement of interseminal scales and ovules of Bennettitales appears to be too derived to be ancestral for carpels of angiosperms. The gap between Bennettitales and angiosperms is no less narrower than that between Caytoniales and angiosperms.

2.8 *Umkomasia*

The Corystospermales is a group of plants of worldwide distribution that flourished from the Late Permian to Middle Jurassic (Zan et al. 2008; Taylor and Taylor 2009). One kind of female organs in Corystospermales is called *Umkomasia* (Fig. 2.6). Based on strong evidence of association in the field, it is believed that its pollen organ is *Pteruchus*, which produces bisaccate pollen grains. The connected leaf is *Dicroidium* (Axsmith et al. 2000; Taylor and Taylor 2009). It is thought to be mainly distributed on the Gondwanan continents (Holmes 1987; Zan et al. 2008), but recent progress in palaeobotany finds more evidence of *Umkomasia* in Laurasian (Germany and China) (Kirchner and Müller 1992; Zan et al. 2008). The main axis of *Umkomasia* is borne at the apex of a short shoot, bears numerous lateral cupule-bearing axes arranged spirally or in whorls (Axsmith et al. 2000; Taylor et al. 2006b; Zan et al. 2008; Fig. 2.6). Each lateral axis bears pairs or whorls of stalked, recurved, helmet-like cupules. Unlike Caytoniales, each cupule of *Umkomasia* contains only one or two ovules, and its curved bifid micropyle usually protrudes beyond the cupule opening. The abaxial position of the ovules separates Corystospermales from angiosperms and Petriellales as well as Caytoniales, which bear adaxial ovules (Klavins et al. 2002; Taylor and Taylor 2009). Detailed comparison indicates that *Umkomasia* is unlikely to be an ancestor of angiosperms (Axsmith et al. 2000; Klavins et al. 2002), although *Pteruchus* (Corystospermales) is favored as a candidate for angiosperm ancestry by the Mostly Male Theory based on developmental genetics (Frohlich and Parker 2000; Frohlich 2003).

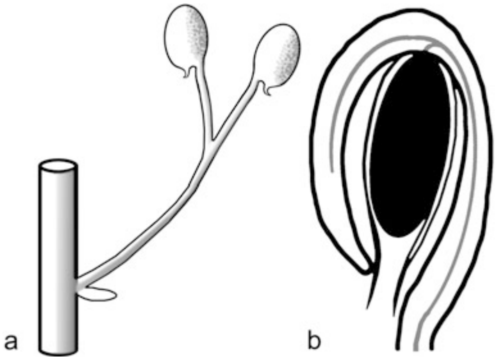

Fig. 2.6 *Umkomasia* and its details. **A** Reconstructed branch bearing a pair of cupules. **B** Longitudinal section showing cupule surrounding seeds with protruding micropyles. *Gray color* stands for vascular bundles

2.9 *Problematospermum*

Problematospermum is reported from the Middle Jurassic to Lower Cretaceous of Kazakhstan, Mongolia, and China (Fig. 2.7). It includes seeds with filamentous hairy appendages and an apical projection, all of which may fall off when mature. The elongated oval seed body has a truncated tip and a pointed base, with spikes in

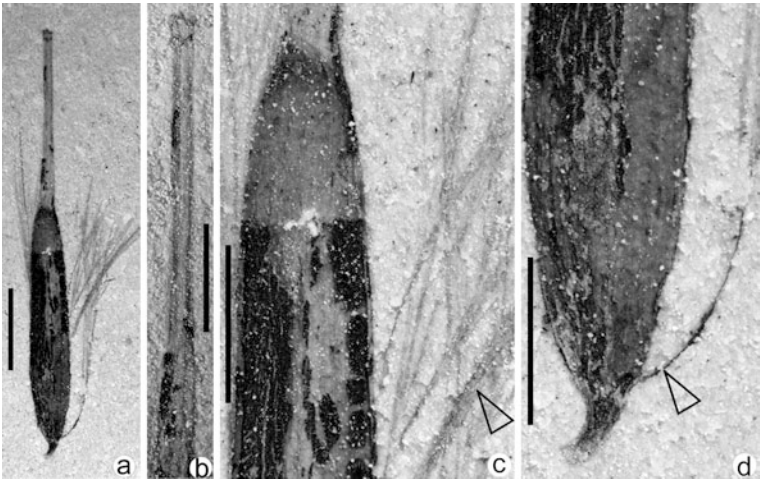

Fig. 2.7 Seeds of *Problematospermum ovale* (PB21392, NIGPAS). **A** Complete seed. Bar = 2 mm. **B** Straight apical projection. Bar = 1 mm. **C** Seed with filamentous appendages (*arrow*). Bar = 1 mm. **D** Seed body with filamentous appendages attached (*arrow*). Bar = 1 mm

rows and files. Its apical projection is straight, with a central canal. Its seed coat is composed of epidermal cells and two types of sclerified cells. Inside the seed coat is food storage tissue of parenchyma. This plant fossil has frequently been classified as an angiosperm or proangiosperm (Krassilov 1973a, b, 1977a, 1982; Liu 1988; Wu 1999). However, recent work indicates that these conclusions are inconclusive and that this plant may well bridge gaps among several groups in seed plants (for further details, refer to Wang et al. 2010).

2.10 Dirhopalostachyaceae

Dirhopalostachyaceae (the Upper Jurassic to Lower Cretaceous) has been regarded as a group of proangiosperms by Krassilov (1977a). The reproductive organ is comprised of helically attached elliptical to obovate cupules each dehiscing along a ventral suture. Each cupule has an elongated beak-like extension and a ventral suture, containing a single seed (Krassilov 1977a). Based on cuticular features, it is related to *Nilssonia*-type leaves (Krassilov 1975, 1977a). Krassilov (1977a) believes that *Dirhopalostahys* may have been derived from *Beania* by the involution of the ovuliferous shield. Based on similarities in beak, suture, external rib pattern, and/or leaf venation, Krassilov (1984) relates *Dirhopalostachys* to the capsule of the angiosperms *Trochodendrocarpus* (1977a) and *Kingdonia*. Little is known about the pollination/fertilization of this plant (Krassilov 1984), therefore it is hard to known whether or not it is truly an angiosperm.

2.11 *Ktalenia*

The ovule-baring structure named *Ktalenia* (Fig. 2.8) from the Cretaceous (Aptian) of Argentina may be the youngest one among the so-called seed ferns, which occurred at the time of the angiosperm radiation (Taylor and Archangelsky 1985). Its foliage is *Ruflorinia*. The cupules are sessile, spherical in form, recurved, with their openings pointing downward, and oppositely or suboppositely arranged along the axis. Unlike *Caytonia*, there are only one or two orthotropous seeds per cupule, with a distal nucellar beak (Taylor and Archangelsky 1985). Interestingly, *Ktalenia* demonstrates a nearly complete enclosure of ovules. Besides its abaxial ovules, *Ktalenia* is as challenging as Caytoniales to be considered as an angiosperm ancestor. Furthermore, the pre-Aptian megafossils of angiosperms, such as *Chaoyangia*, *Archaefructus*, *Sinocarpus*, and *Callianthus* (Duan 1998; Sun et al. 1998, 2001, 2002; Leng and Friis 2003, 2006; Wang and Zheng 2009, see also Chaps. 5 and 6), reduce the probability for *Ktalenia* to give rise to angiosperms, if the latter are monophyletic.

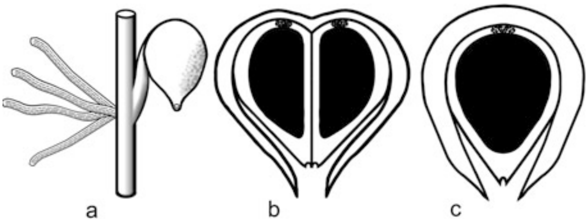

Fig. 2.8 Reconstructed *Ktalenia*. **A** Fertile axis bearing cluster of bracts at *left* and cupule at *right*. **B** Longitudinal section of a cupule containing two ovules. **C** Longitudinal section of a cupule containing one ovule

2.12 *Pentoxylales*

Pentoxylon (Pentoxylales) is named after the five wedges of secondary xylem in transverse section, resembling a cut orange, that characterize its stem. It is a Gondwanan taxon flourishing from the late Early Jurassic to Early Cretaceous in India, Australia, New Zealand, and Antarctica (Hughes 1994; Biswas and Johri 1997; Cesari et al. 1998; Bonde et al. 2004). It diversified during the Jurassic. Its foliage type is *Nipaniophyllum* with an epidermal cuticle bearing syndetocheilic stomata. The pollen organ, *Sahnia*, produces psilate monocolpate pollen grains. The ovule-bearing structures, *Carnoconites,* are clustered into a mulberry-like cone attached to the apex of a stalk, which in turn is attached to a short shoot apex (Nixon et al. 1994; Biswas and Johri 1997). Each cone comprises about 20 orthotropous, unitegmic ovules with their micropyles facing away from the cone axis (Nixon et al. 1994; Biswas and Johri 1997). *Pentoxylon* is unisexual, and thus differs from the bisexual reproductive structures of some other anthophytes. This group is regarded as isolated even within gymnosperms (Biswas and Johri 1997). Therefore it may be too specialized to be an ancestor of angiosperms.

2.13 Summary

Among these candidates for angiosperm ancestry, none of their evidence is sufficiently convincing to have become widely accepted. The main reasons are the same for all. Besides the lack of an angiosperm-like taxon (living or fossil) intermediate between these candidates and known angiosperms, they are either too derived to be an ancestor for angiosperms or lack convincing evidence of angiospermy (angio-ovuly) (see Chap. 3). These plants, at least, require further effort to be related to angiosperms.

Chapter 3
Angiosperms: Characters and Criteria

A number of characters have been used to identify angiosperms in the fossil record. Comparison between their distributions in seed plants and the scope of angiosperms indicate that none of them match that of angiosperms exactly. Based on analysis of the temporal distribution of these characters in the geological history, the author proposes that ovule enclosed at the time of pollination should be adopted as an *operational* index character for fossil angiosperms. The positive and negative sides of this criterion are discussed, and a potential way to treat possible angiospermous fossils is laid out.

3.1 Angiospermous Characters

Almost every student of biology appears to know what a flower is. But this easy-appearing question turns out to be an extremely difficult one when it comes to giving a scientific definition applicable for both living and fossil plants. Technically, a flower in the strict sense is defined as a reproductive organ of an angiosperm. If one can ascertain that a plant is an angiosperm, there is no problem calling its reproductive organ a flower. Consequently, the question is now translated into "What is an angiosperm?" This question is one for a field of science called phytotaxonomy, namely plant taxonomy.

Initially, taxonomy was the science that categorizes and puts like with like, whether they be botany, zoology, or geology. Phytotaxonomy is the branch of that science that deals with plants. Like in other branches of taxonomy, type specimens play a crucial role in it. The International Code of Botanical Nomenclature requires that a name be connected to a type. Types are the most typical examples of taxa, and all those similar to a type are grouped and placed in corresponding taxa. Preservation of holotype and various other types is still required and of crucial importance in taxonomic practice. As more and more specimens are collected, it is found that types alone cannot solve all problems in phytotaxonomy. Phytotaxonomists select certain characters of plants as features of a taxon, and further comparing and systemizing plants into groups of higher orders are based on these characters. These extracted characters are called the diagnosis of a taxon.

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Angiospermae is one of the many taxa in seed plants that phytotaxonomists have recognized in the plant kingdom. According to current understanding, there are several characters uniting angiosperms and distinguishing them from other seed plants (gymnosperms). These characters, which constitute the currently accepted diagnosis for angiosperms, include enclosed seeds/ovules, reticulate leaf venation, tectate-columellate pollen wall, double fertilization, lack of archegonia, pollen tube, vessel elements in the xylem, and certain chemical compounds (Taylor and Hickey 1992; Judd et al. 1999; Friis et al. 2005, 2006; Maheshwari 2007). These characters are frequently seen in angiosperms, but rarely in gymnosperms or ferns. If all them are seen in a plant, it is safe to declare it as an angiosperm. However, nature is never so simple as we assume. Not all of these characters are present in all angiosperms, and not all plants with some of these characters are angiosperms. Actually, there are several gymnosperms, and even some ferns, with one or more of these characters, and none of the above characters is unique to angiosperms.

3.1.1 *Leaf Venation*

As reticulate leaf venation is a rarity in gymnosperms or ferns but a common character in angiosperms (Doyle and Hickey 1976; Doyle 1977; Taylor and Hickey 1990; Li 2003; Archangelsky et al. 2009), thus, unsurprisingly, it is frequently used as an identifier for angiosperms. This character, related to the efficiency of material transport within plant bodies, may have contributed to the success of angiosperms in their struggles to compete against their rivals. However, equally complex reticulate venation is also seen in *Gnetum* (Gnetales) (Arber and Parkin 1908; Chamberlain 1957; Martens 1971; Biswas and Johri 1997) and some ferns (Potonie 1921; Kryshtofovich 1923; Shen et al. 1976; Sun 1981, 1993; Li et al. 1994; Li and Taylor 1998; Glasspool et al. 2004). In fact, the similarity between *Gnetum* and eudicots is so close, they are frequently hard to distinguish from one another. In addition, examination of the fossil record finds that reticulate leaf venation has been reported in several non-angiospermous ferns and gymnosperms, including Dipteridaceae, Gigantopteriales, Caytoniales, Glossopteridales, and Bennettitales (Potonie 1921; Kryshtofovich 1923; Thomas 1925; Harris 1940, 1964; Chamberlain 1957; Sporne 1971; Shen et al. 1976; Retallack and Dilcher 1981b; Sun 1981, 1993; Ye et al. 1986; Hughes 1994; Li et al. 1994; Li and Taylor 1998; Glasspool et al. 2004). It is the reticulate venation, at least partially, in these groups that has led some workers to infer a possible relationship between angiosperms and Gigantopteriales, Caytoniales, Glossopteridales, as well as Bennettitales (Thomas 1925; Eames 1961; Retallack and Dilcher 1981b; Asama 1982; Crane 1985). Conversely, not all angiosperms have such venation. For example, monocots, a group of plants including grasses, on which most people rely to survive in this world, do not have reticulate leaf venation, and reticulate venation is lacking in at least several basal angiosperms, such as *Cabomba*, *Ceratophyllum*, and fossil *Archaefructus*. It appears that the presence or absence of reticulate venation in a plant can neither ascertain nor negate an affinity to angiosperms.

3.1.2 Vessel Elements in the Xylem

Vascular plants are distinguished from non-vascular plants by their special and efficient water conducting system, the vascular bundle. The evolution of the land plants is, besides other aspects, reflected in the organization and composition of the vascular bundle. During the past 400 million years, the composition of the vascular bundle in higher plants has undergone a series of innovations. The most advanced stage of vascular element evolution is the occurrence of vessel elements. The wide diameter and perforation plate of vessel elements demonstrate an efficiency superior to tracheids in water transportation. These vessel elements undoubtedly give those bearing these characters an advantage over their rivals, especially when water is a key limiting ecological factor. Angiosperms are one of the groups that take advantage of such a character. Historically, vessels have evolved independently in several distinct categories of the Tracheophyta: Selaginellales, Filicales, Gnetales, monocots, dicots, and some fossil group of unknown affinity, such as Gigantopterids (Bailey 1944; Eames 1952; Chamberlain 1957; Eames 1961; Martens 1971; Sporne 1971; Cronquist 1988; Li et al. 1996; Carlquist 1996; Li and Taylor 1999). Also, many basal angiosperms, including *Amborella*, do not have vessel elements (Eames 1961; Doyle 2008). Therefore the occurrence of vessel elements does not ensure an angiospermous affinity since it is neither exclusive nor universal to angiosperms.

3.1.3 Closed Carpel, or Enclosed Ovule/Seed

Angiosperms were originally defined by having seeds that are enclosed (Hill and Crane 1982) since it is exactly what the word “angiosperm” means (Harper 2001). A closed carpel provides angiosperms an added protection against predation and harsh environments including desiccation, as well as a self-incompatible system, and adds a pre-zygotic selection in addition to the post-zygotic one, which is common in other seed plants (Taylor and Taylor 2009; Doyle and Donoghue 1986a). All these functions give angiosperms an advantage over their gymnospermous rivals in the competition. If this character had been unique to angiosperms, recognizing an angiosperm would be much easier. Unfortunately, some of gymnosperms also have evolved similar strategies to ensure the opportunity for their seeds and consequent offspring to survive harsh competition. According to Hill and Crane (1982) and Tomlinson and Takaso (2002), some of the conifers have demonstrated the same tendency to enclose and protect their seeds after pollination. Parallel to this, some fossil gymnosperms, such as Caytoniales and Glossopteridales, as well as some seed ferns, also have demonstrated the same tendency to protect their ovule/seed (Thomas 1925; Harris 1933, 1940, 1964; Chamberlain 1957; Reymanowna 1970, 1973; Krassilov 1977a; Taylor and Archangelsky 1985; Holmes 1987; Kirchner and Müller 1992; Nixon et al. 1994; Biswas and Johri 1997; Barbacka and Boka 2000a, b; Taylor et al. 2006b; Nishida 2007; Maheshwari 2007; Zan et al. 2008; Taylor and Taylor 2009). At the same time, not all angiosperms have their seeds/ovules physically enclosed, including members of the

Amborellaceae, Schisandraceae, Austrobaileyaceae, and Trimeniaceae (Endress and Igersheim 2000a, b). Furthermore, carpels in *Reseda* (Resedaceae) (Marilaun 1894; Hill and Crane 1982; Cronquist 1988) and *Delphinium consolida* (Ranunculaceae) (Baillon 1880; Puri 1952) remain open throughout their whole development. Many of the basal angiosperm groups have their ovule protected from the outside only by a layer of secretion (Endress and Igersheim 2000a). This situation is not so different from those seen in Gnetales, in which the pollination drop usually draws the pollen grains to the ovule or sometimes the pollen grains may germinate in the stylar canal some distance away from the nucellus (Johri and Ambegaokar 1984). Furthermore, some angiosperm (*Butomopsis lanceolata*) may even have its pollen grains germinating on the surface of the ovule (Johri and Ambegaokar 1984). Considering all these, it appears that the protection of seeds is a general trend of evolution in seed plants, and that this protection reaches its highest level in most, although not all, angiosperms by the physical enclosure of the ovule, although it is hard to draw a line between gymnosperms and angiosperms in this term.

3.1.4 Bitegmic Ovule

The so-called integument is a protective layer of tissue surrounding an ovule. Its existence can be traced back to the earliest ovules/seeds of the Devonian (Arnold 1938). It is widely accepted that ovules in angiosperms generally have two integuments (bitegmic), and unitegmic condition (with only one integument) in angiosperms is taken as being derived from a previously bitegmic condition. The number of integuments in angiosperms may actually vary from one to as many as four (Eames 1961). The detailed forms and arrangement of integuments are variable, and such variations are frequently used to classify seed plants. Besides in angiosperms, two integuments also occur in Gnetales and some Cycadales (Hill and Crane 1982) although there is some controversy about the nature of the outer integument in these cases. The homology for angiosperms' outer integument in gymnosperms is still an open question (see Chap. 8 for further information). The cupule of *Caytonia* is frequently compared to the outer integument of angiosperms, but this comparison faces the problem of deriving carpels (for further information, see Chaps. 2 and 8). Although many believe that the earliest angiosperms had bitegmic ovules, this promising hypothesis remains speculative since bitegmic ovules have yet to be observed in early fossil angiosperms. Owing to limitations of preservation, it would increase the difficulty identifying a fossil angiosperm, if bitegmic ovule were taken as an identifier of angiosperms. Consequently, this character cannot, at least at present, be used as the index character of fossil angiosperms although it can be safely applied in most instances to living plants.

3.1.5 Double Fertilization

Double fertilization was discovered in 1898 by Nawaschin (Raghavan 2005). In its most frequently used definition, it designates the process during which one male nucleus fuses with an egg nucleus while a second one fuses with two polar nuclei in the female gametophyte within the ovule (Friedman 1992a). Double fertilization, resulting in the formation of a (usually) triploid endosperm tissue (for exceptions, see Williams and Friedman 2002), has been taken as ubiquitous among angiosperms, and is treated as an important difference between angiosperms and gymnosperms in developmental, reproductive and survival strategies. Therefore double fertilization and triploid endosperm have frequently been taken as a unique defining characteristic of flowering plants (Friedman 1992a). However, within angiosperms, double fertilization does not occur in *Cortaderia jubata* (Gramineae) (Johri and Ambegaokar 1984), Podostemaceae (Raghavan 2005; Maheshwari 2007) or *Calycanthus* (Stevens 2008). At least for the time being, whether double fertilization occurs in all basal angiosperms is still an open question (Friedman and Williams 2004). Moreover, multiple fertilization events within a single ovule are not unique to angiosperms (Martens 1971; Friedman and Williams 2004; Raghavan 2005), and may occur among various groups of gymnosperms, such as *Ephedra* and *Abies* (Chamberlain 1957; Martens 1971; Friedman 1990, 1991, 1992a; Yang et al. 2000; Friedman and Williams 2004; Raghavan 2005).

Even if this character were considered a touchstone for angiospermy, confirming its actual existence in fossil plants would be an insurmountable challenge for palaeobotanists, at least for the time being, due to preservation.

3.1.6 Tetrasporangiate Anther

A tetrasporangiate anther designates a pollen-bearing unit that has four pollen sacs, although frequently, when mature, two of them become fused into one, giving the appearance of two pollen sacs. Most living angiosperms have tetrasporangiate anthers and this kind of pollen organ is never seen in gymnosperms to this time (Taylor and Hickey 1992; Judd et al. 1999; Maheshwari 2007). It is also true, however, that there are certain variations in terms of the number of pollen sacs per anther in angiosperms. Eames (1961) mentions the existence of anthers with only one or two pollen sacs in angiosperms. While the presence of the tetrasporangiate anthers may strongly suggest that the bearer is an angiosperm, it is clear from these considerations that lack of such an anther does not necessarily mean that the bearer is not an angiosperm. This character therefore is not exclusive enough to be an index character for angiosperms.

3.1.7 Pollen Tube

Pollen tube is a tubular channel that grows out from the pollen grain and transfers the male nuclei to the ovule, especially in angiosperms, so that fertilization may then take place. The function of pollen tube in angiosperms is believed to be related to the enclosure of ovules by carpels, which protect ovule against desiccation, predation, and self-pollination (providing an incompatibility barrier) (Taylor and Archangelsky 1985). The germination of the pollen and growth of the pollen tube require a favorable external physical and biological environment, which is related to the genetics and physiology of the plant. Their coupling increases the advantage of angiosperms over their rivals because of enhanced outcrossing. However, there are exceptions to this generalization. On one hand, structures apparently very similar to typical angiosperm pollen tube have been observed in some Ginkgoales, Cycadales, *Callistophyton*, Coniferales, Glossopteridales, Gnetales, probably in Bennettitales (Bierhorst 1971; Biswas and Johri 1997; Crane 1985; Fernando et al. 2005; Nishida et al. 2003, 2004; Stockey and Rothwell 2003; Taylor and Taylor 2009). In Cycadales, however, the pollen tube has a haustorial function, i.e. it functions as a holdfast to supply nutrition for the development of the gametophyte (Norstog 1990; Biswas and Johri 1997). The pollen tube in Palaeozoic seed ferns may well have performed a similar function (Rothwell 1972). On the other hand, pollen grains have been found in stylar canal or germinating on the ovule in some angiosperm, suggesting a "gymnospermous way" of pollination in an unquestionable angiosperm (Johri and Ambegaokar 1984). Considering the overlap of characters among vascular plants, the presence of a pollen tube does not appear to be a synapomorphy of angiosperms because a pollen tube may be a common character shared by many groups, including angiosperms.

3.1.8 Tectate-Columellate Pollen Grains

Tectate-columellate pollen wall structure is usually seen in angiosperms. Such a character might be related to entomophily and self-incompatibility of angiosperms during the pollination, which promotes crossbreeding and speciation in angiosperms and may have contributed to their rapid radiation during the Middle Cretaceous. At first glance this kind of pollen grain wall structure appears distinct and limited only to angiosperms, and it seems safe to make the claim that fossil angiosperms have occurred in certain strata based on the presence of such pollen grains. However, palaeobotanical practice in the past decades indicates that such a character cannot be accepted as a sign of angiosperms universally applicable in the fossil record. Pollen grains with such a wall structure have been reported from strata of pre-Cretaceous age (Cornet 1989a; Cornet and Habib 1992; Zavada 1984; Pocock and Vasanthy 1988; Hochuli and Feist-Burkhardt 2004; Maheshwari 2007; Archangelsky et al. 2009). Many such pollen grains are indistinguishable from angiosperms even after careful examination under a TEM. However, they are still regarded as enigmatic gymnosperms due to a lack of information about the mother plant (Friis et al. 2005, 2006). Moreover, tectate-columellate structure has been seen in *Equisetoporites chinleana* (Triassic), *Eucommiidites* (Triassic-Cretaceous) and *Classopollis* (Triassic-Cretaceous) (Zavada 1984). Although the author does not exclude the possibility that these pollen records may signal the presence of angiosperms, it appears that such kind of angiosperm record based on this character alone has met some resistance in palaeobotany. In the meantime, such kinds of pollen wall must be a result of prolonged evolution and, according to the trends in pollen evolution, early angiosperms may well have not had any such advanced pollen wall structures (Zavada 1984). Therefore, even if this character in the fossil record were a mark of the existence of angiosperms, its presence could not designate the earliest record of angiosperms. To the contrary, it would signify that there must have been angiosperms in older strata. Probably due to this complicated situation, the presence of triaperturate pollen grains is taken as the sign of a true angiosperm by some scholars (Hughes 1994), but this character is not an ideal proxy for early angiosperms.

3.1.9 Developmental Pattern

The formation of nutritional storage tissue in seeds follows different patterns in angiosperms and gymnosperms. In gymnosperms it is derived from the female gametophyte, which typically forms before pollination (pre-fertilization allocation of nutrients to the embryo-nourishing tissue, according to Friedman 2008). In angiosperms the endosperm does not form until after pollination. This manner of endosperm development in angiosperms does not waste too much nutrition on ovules that may not be pollinated or later abort, as is frequently seen in gymnosperms. For example, cycadalean ovules accumulate much nutrition, but may not ever be pollinated at all and thus waste much nutrition (Cronquist 1988). This economic strategy might have contributed partially to the success of angiosperms in competition against their gymnospermous peers. Cornet (1989b), working on *Sanmiguelia*, has attempted to use its developmental pattern as evidence for its angiospermous identity. Although this seems to be a reasonable inference, it should be kept in mind that this pattern may not be exclusive to angiosperms. For example, the pollination in Bennettitales appears to have occurred when the ovule was small (Pedersen et al. 1989b), implying that the endosperm or perisperm may not have started forming before pollination, i.e. as in angiosperms. A developmental pattern like that of angiosperms is also seen in *Gnetum* (Arber and Parkin 1908). Therefore the once-thought angiosperm-specific endosperm developmental pattern appears to have been adopted by some gymnosperms. Recent study on a basal angiosperm, Hydatellaceae, suggests that the plant reserves a certain amount of nutritional tissue for its embryos even before pollination, a typical gymnospermous trait (Friedman 2008). At least many caryophyllaceous plants have perisperm instead of endosperm as food storage (Boke 1968; Cronquist 1988; Judd et al. 1999). Therefore the scopes of angiosperms and gymnosperms overlaps in this term, so it is not universally valid to use such a character to identify an angiosperm, especially from the fossil record.

3.1.10 Chemical Species

The presence or absence of various chemical compounds, including secondary metabolites, DNA, RNA, and proteins, is frequently used to determine relationships among plants at various levels in phytotaxonomy (Judd et al. 1999). For example, betalains are restricted to the Caryophyllales while flavonoids are distributed throughout the embryophytes (Judd et al. 1999). The taxonomic value of chemical compounds varies. Needless to say, DNA fragments have been intensively sequenced to extract phylogenetic plant information. However, labile chemical compounds such as DNA, RNA, and proteins are usually not applicable when fossil materials are dealt with. More applicable for palaeobotany are relatively stable chemical compounds present in plants. Some chemical compound, such as syringyl lignin, formerly considered to be limited to angiosperms, was recently found to be present in *Selaginella* of Lycophyta (Weng et al. 2008). Similarly, oleanane, formerly thought restricted to angiosperms, has been found in Palaeozoic and Mesozoic non-angiospermous plant fossils (Taylor et al. 2006). The variable value and difficulty of extracting information on chemical compounds in fossil plants makes them unlikely to be a safe index character of angiosperms.

3.2 Criterion for Criteria

We need a standard or a criterion to distinguish a fossil angiosperm from other seed plants (Hill and Crane 1982; Maheshwari 2007). A criterion is "a standard on which a judgment can be based" (Berube et al. 1985). A standard is "an acknowledged basis for comparing or measuring" (Berube et al. 1985). If a criterion needs to be established for something, the criterion must be widely accepted, open to access, strict and applicable. A criterion should not be a secret. It has to be acknowledged to the public or at least related colleagues.

A criterion has to be specific, not multiple or composite. If a criterion were based on several characters or an assemblage of characters, sooner or later a case would appear that only a subset of the assemblage occurs in a plant. What do we do then? Either accepting or rejecting it would be criticized by someone, and this would cast suspicion on the reliability of the definition. To avoid such a potential dilemma, selecting a definition based on a single specific character is of pivotal importance.

3.3 Criterion for Fossil Angiosperms

It is apparent from the foregoing that several characters have been utilized to diagnose angiosperms, but none can be used as a touchstone for angiosperms. The presence of all these characters together, as in living plants, can easily confirm the identity of most angiosperms since most living angiosperms are unequivocal angiosperms displaying the character assemblage typical of angiosperms. It appears ironic that botanists cannot agree with each other on the definitions of a flower and an angiosperm (Bateman et al. 2006). The situation becomes more complicated when you face angiosperms in their early history. Clearly there must be a time when there was little distinction between angiosperms and gymnosperms. The above angiospermous characters may well have been scattered in several unrelated plant groups. Using all of these characters to identify an angiosperm would only result in no angiosperms. This partially explains the sudden appearance of angiosperms, which is a misleading impression of angiosperm history partially resulted from an ignorance of evolution. Technically, preservation is rarely sufficiently good enough to be able to recover all these characters from a fossil. A compromised way is to select important features that are detectable in fossils as index characters for angiosperms, and use these index characters as proxies for the existence of angiospermy in a plant.

Even if we were to make such a compromise, however, challenge still exists. Which character should be included in the list of index characters? If more than one, which has higher priority? Unfortunately, palaeobotanical practice has shown that answering these two questions does not help solving the problem, instead it widens the gaps between different schools or scholars. Many times the criterion for angiosperms is ad hoc. To answer the question whether or not a fossil is an angiosperm, palaeobotanist can only use the characters preserved in the specimen under examination. It is not surprising that people working on leaves prefer reticulate leaf venation, those working on anatomy prefer vessel elements, those working on mesofossils prefer reproductive characters, and palynologists prefer pollen wall structure. This multiple-criteria-status has led to controversy, even chaos, in the attempt to define early angiosperms. Current study of early angiosperms is one of the most controversial fields in palaeobotany. The origin of such controversy is the existence of multiple criteria applied to early angiosperms. To expel the controversy dogging this research, aligning with one or another authority does not help. As said above, the field needs a widely accepted, open-access, strict, applicable criterion for identifying early angiosperms.

Many people prefer to have more characters to increase their confidence in certain statement. This normal thinking works only when the key character is assured. Marginal characters help less than assumed. For example, *Gigantopteris* has three characters (reticulate venation, vessel element, and oleanane) shared with angiosperms, but it is not an angiosperm. On the contrary, *Archaefructus* initially only has enclosed seeds (Sun et al. 1998) and it is accepted as an angiosperm. It is true that later research finds more characters and increases the confidence. But the initial acceptance is based on this single feature. From the negative side, *Caytonia* is rejected as an angiosperm also based on a single character: pollen grain within the cupule. In both cases the decision centers on one key feature, ovule enclosed or not. Although this is the first time that this criterion is proposed explicitly, it has been applied to identify fossil angiosperms in palaeobotanical practice for long time (Sun et al. 1998; Leng and Friis 2003, 2006). The number of characters should be considered, but its value is of secondary consideration.

Reproductive characters or floral features should be the candidates from which to sieve such a criterion since “reproductive traits represent adaptations” and “adaptation commonly contributes to floral diversity” (Harder and Johnson 2009). To reach the final goal, we should begin with an analysis of the geological history regarding how angiosperms acquired their characters. Evolutionarily, all characters in organisms, from molecular, cellular to morphological, have undergone a process from barely apparent to fully expressed. This is clear to all students of palaeontology. Living angiosperms are a transient snapshot of prolonged evolution, and they are not the concluding point of the past evolution but a starting point for future evolution. The characters that appear stable in living plants are simply snapshots of the on-going evolution that has lasted more than billion years. The origin and development of a character in plants is a function of time. Strictly speaking, two, not to mention several, characters cannot occur simultaneously in the same plant (Doyle 2008), even though they may appear so in the fossil record. Therefore it is plausible to assume that the above-discussed angiospermous characters have been acquired one after another as in Fig. 3.1 (Hill and Crane 1982; Stuessy 2004; Maheshwari 2007; Doyle 2008), if they are present in the same plant today. With this in mind, not all the characters acquired at different times can be used as index characters to determine when angiospermy came into existence in the geological record. Otherwise the controversy will last forever. Therefore a single valid character is badly needed. According to the Tomlinson and Takaso (2002), the only consistent difference between angiosperms and gymnosperms is angio-ovuly. Careful readers may also have noticed that *a physically enclosed ovule alone is a sufficient, although not necessary, character to identify an angiosperm*. Since all ovules in angiosperms are exposed at least once during development, timing has to be taken into consideration: status at pollination is of critical significance. Except for the case of secretion sealing, for the sake of accuracy, *a physically enclosed ovule at pollination appears to be an optimal and sufficient criterion*, although enclosure by secretion, if proven, can also be included.

This criterion is of course not a perfect choice and it is only an *operational* criterion for fossil angiosperms, but it seems apparent that it is superior to other candidates. Although this criterion is not applicable on some true angiosperms that either have other angiospermous characters or have their carpels closed by secretions, the positive side is that this will make the recognized list of fossil angiosperms above suspicion. Triaperturate pollen grains are the most competitive candidate for such index character because their presence can also ensure the existence of

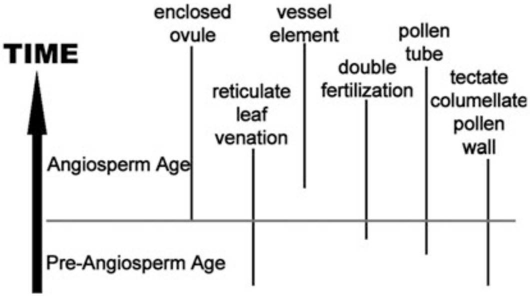

Fig. 3.1 A possible scenario for the acquisition of characters typical of angiosperms in the geological history. All these characters could not be acquired at once in a plant. Picking a specific index character for angiosperms is conducive to minimizing controversy among scholars. The author prefers to take a physically enclosed ovule as the index character for angiospermy. The figure does NOT reflect the actual occurrence of these features in the geological history

angiosperms. However, since the core feature of angiosperms is angio-ovuly, the author prefers enclosed ovules as the index feature. Since palaeobotanists studying early angiosperms are more concerned with which IS, rather than which IS NOT, an angiosperm, this criterion may function well as an *operational* index character for fossil angiosperms. In the following chapters, the author will use this criterion to identify early angiosperms. All those plants with some of the other above-listed characters will be placed either in groups with possible angiospermous affinities or in groups of other seed plants depending on available information. This treatment does NOT imply that any plant without enclosed ovules belongs to gymnosperms. Finally, besides this criterion, more characters, especially those of plants in various developmental stages, are always welcome and helpful for *bona fide* determination.

Chapter 4
Background for the Plant Fossils

Most of the fossil materials documented in this book are from the Jurassic and Cretaceous of northeastern China. In this chapter, the author describes the geological and palaeobiological backgrounds in this region, which is very helpful to complete the understanding of the plant fossils to be documented in the later chapters. The Yixian Formation and Jiulongshan Formation are by far the most productive strata for early angiosperms, and, therefore, they are dealt with some details in this chapter. The geological background and age of the formations are briefly summarized. Species list and assemblages in various faunas and floras are given. For those not interested in details of the fossil floras and faunas, please feel free to skip certain sections in this chapter.

4.1 Stratigraphy

Escaping much tectonic activities during the Mesozoic, the western and middle parts of North China were relatively stable terrestrial basins, while the eastern part of North China was more tectonically active. Except a narrow zone in eastern Heilongjiang that received marine sediment, most areas in Northern China received terrestrial deposition during the Mesozoic. According to the regional sedimentology and biostratigraphy, North China can be divided into five regions: Xinjiang, Qilian, Ordos, Northeast China, and North China. Among them, the Northeast China region includes Heilongjiang Province, Jilin Province, Liaoning Province, Beijing Municipality, northern part of Hebei Province, and most of Inner Mongolia. This region can be further subdivided into six sedimento-tectonic zones: North Hebei-Western Liaoning, Erlian-Yinshan, Xing'an, Songliao, Eastern Liaoning-Eastern Jilin, and Eastern Heilongjiang (Deng et al. 2003). Most fossils documented in this book are from the Northern Hebei-Western Liaoning zone in Northeast China region (Fig. 4.1).

The Jurassic strata are represented mainly by fluvial and swampy coal-forming facies in Northeast China (Deng et al. 2003). During this time, there were also multiple cycles of volcanic activity. Palaeogeographical study indicates that there was a large lake in the Beipiao area of western Liaoning. The strata

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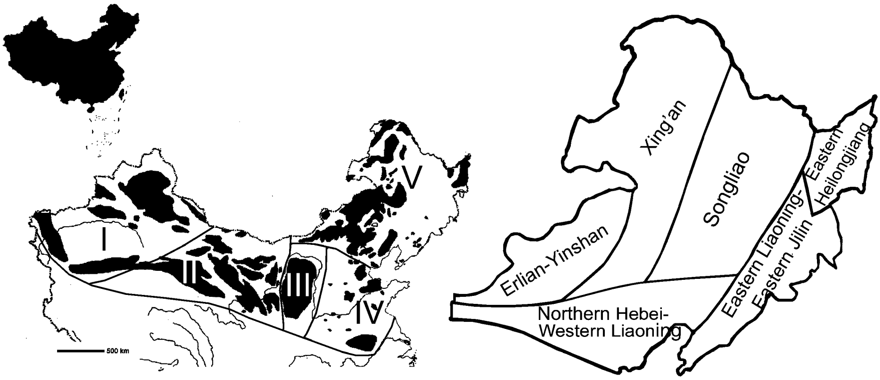
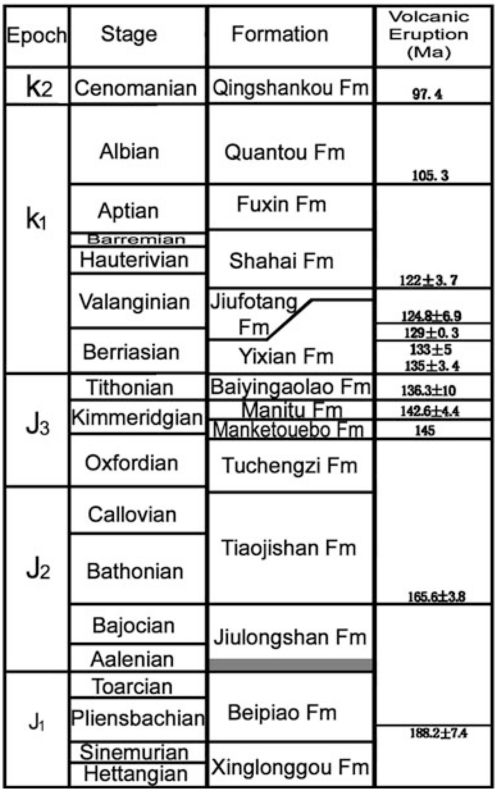


Fig. 4.1 Geographical distribution of the Jurassic strata (including Early Cretaceous Yixian Formation) in China. *Upper left* is a map of China. *Lower-left* shows the five regions in North China. *Right* shows the six zones in Northeast China (after Deng et al. 2003)

developed in this area are continuous and abundant in fossils, and can be divided into, in ascending order, the Xinglonggou Formation and Beipiao Formation (Lower Jurassic), Jiulongshan Formation (=Haifanggou Formation) and Tiaojishan Formation (=Lanqi Formation) (Middle Jurassic), Tuchengzi Formation (Upper Jurassic), and Yixian Formation (Lower Cretaceous), which is overlain by the Jiufotang Formation (Fig. 4.2) (Deng et al. 2003).

The Middle Jurassic Jiulongshan Formation is outcropped in the Beipiao, Jinyang, Kezuo, Jianchang, Niuyingzi-Guojiadian, Lingyuan-Shisanjiazi, and Ningcheng areas (Fig. 4.3). Its local equivalent in Liaoning, called the Haifanggou Formation, is well developed in the Beipiao area, while its local equivalent in Inner Mongolia is called the Daohugou Formation (Fig. 4.6). For the sake of simplicity and consistency, in the following text all of these equivalent local stratigraphic strata are referred as the Jiulongshan Formation. The Jiulongshan Formation rests on the Beipiao Formation, and is overlain by the Tiaojishan Formation in western Liaoning (Figs. 4.2, 4.4). The basal part of the formation includes alluvial deposition of yellowish poorly sorted, angular conglomerate and sandstone interrupted by volcanic breccia and tuff, with plant stem impressions. The lower member of the formation is comprised of yellowish conglomerate, volcanic breccia, tuff, and greenish shale, with abundant plant stem fossils and insect fossils. The middle member of the formation is comprised of shallow lacustrine sediment of green-yellowish, grey-yellowish, grey shale, siltstone, sandstone, and tuff, with abundant plant, insect, and bivalve fossils. The upper member of the formation is comprised of alluvial sediments and pyroclasts, with fragmental plants and silicified wood (Deng et al. 2003). The formation is yielded a large number of fossils, including conchostracans, ostracodes, bivalves, insects, vertebrates, and plants (Pan 1983; Kimura et al. 1994; Wang et al. 1997; Ji and Yuan 2002; Ren et al. 2002; Zhang 2002, 2006,

Fig. 4.2 The stratigraphic column of the Jurassic and Cretaceous strata in western Liaoning and adjacent regions (after Xu et al. 2003)



Epoch	Stage	Formation	Volcanic Eruption (Ma)
K2	Cenomanian	Qingshankou Fm	97.4
K1	Albian	Quantou Fm	105.3
	Aptian	Fuxin Fm	
	Barremian	Shahai Fm	
	Hauterivian		122±3.7
	Valanginian	Jiufotang Fm	124.8±6.9
	Berriasian	Yixian Fm	129±0.3 133±5 135±3.4
J3	Tithonian	Baiyingaolao Fm	136.3±10
	Kimmeridgian	Manitu Fm Manketouebo Fm	142.6±4.4 145
	Oxfordian	Tuchengzi Fm	
J2	Callovian	Tiaojishan Fm	
	Bathonian		165.6±3.8
	Bajocian	Jiulongshan Fm	
	Aalenian		
J1	Toarcian	Beipiao Fm	
	Pliensbachian		188.2±7.4
	Sinemurian	Xinglonggou Fm	
	Hettangian		

2007a, b, c; Zhang et al. 2007, 2008, 2009; Shen et al. 2003; Zheng et al. 2003; Li et al. 2004; Liu et al. 2004; Ji et al. 2005; Wang et al. 2005, 2007b, c; Zhang and Lukashevich 2007; Zhou et al. 2007; Huang et al. 2008; Liu and Ren 2008; Liang et al. 2009; Shih et al. 2009; Wang and Ren 2009; Wang and Wang 2010). The age of the Jiulongshan Formation is bracketed by those of the overlying volcanic rocks in the Tiaojishan (Lanqi) Formation, which have been isotopically dated as 160.7±0.4 Ma old, and the underlying Xinglong Formation, which has been isotopically dated as 190–200 Ma (there is no dateable volcanic rock in the Beipiao Formation) (Deng et al. 2003; Chen et al. 2004; Gao and Ren 2006; Chang et al. 2009b). According to the palaeomagnetic and isotopic dating as well as biostratigraphic data, the Jiulongshan Formation can be correlated to the Aalenian-Bajocian (164–175 Ma) (Deng et al. 2003).

The Yixian Formation rests unconformably on the Tuchengzi Formation, and is overlain by the Jiufotang Formation (Figs. 4.2 and 4.5) (Wang et al. 2004). It is composed of dark grey to black, grey and purplish-red andesites, basalts, greyish-green, greyish-yellow, and dark grey to black tuff, tuffaceous sandstone, grit and sandy shale, silty mudstone, shaly tuffaceous silty mudstone and siltstone, sandstone, and

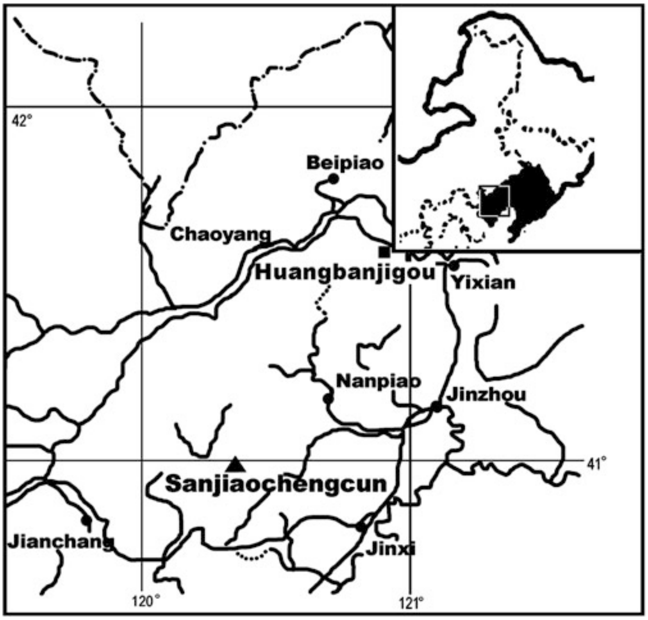


Fig. 4.3 Geographical locations of Sanjiaocheng Village (triangle, 40°58′N, 120°21′E) and Huangbanjigou (square, 41°12′N, 119°22′E) in western Liaoning Province, which is shown as the black area in the inset map of northeast China (modified from Wang et al. 2007b)

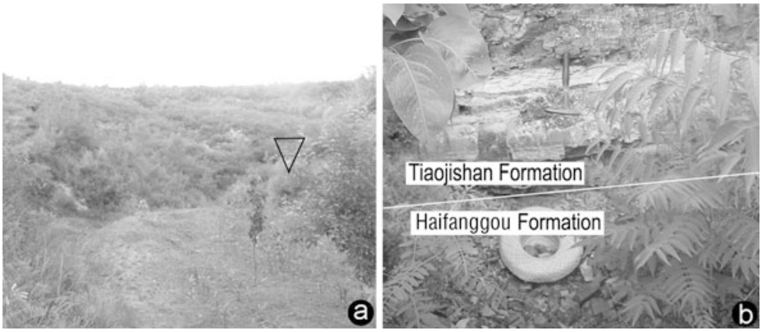


Fig. 4.4 The Jiulongshan Formation. **A** Outcrop of the Jiulongshan Formation (=Haifanggou Formation) near Sanjiaocheng Village, Jinxi, Liaoning, China. **B** Boundary between the Jiulongshan (Haifanggou) Formation and the overlying Tiaojishan Formation. Courtesy of AGS

basal tuffaceous conglomerate (Wang et al. 2004; Sha 2007; Wang et al. 2007a). It is the lowest of the three formations in the Jehol Group, which includes the Yixian Formation, Jiufotang Formation and Fuxin Formation in ascending order (Sha 2007). The Yixian Formation is widely distributed in western Liaoning, eastern Inner Mongolia, northern Hebei, and southern Mongolia (Wang et al.

Fig. 4.5 Outcrop of the Yixian Formation near Huangbanjigou in Beipiao, Liaoning, China

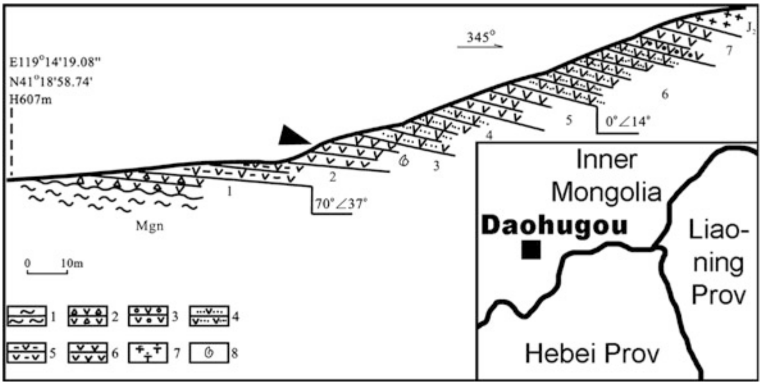


Fig. 4.6 The geographical position of Daohugou Village (*square* in the inset, 41° 19′N, 119° 14′E) in Inner Mongolia, China. Note its position close to the borders between Inner Mongolia, Liaoning and Hebei Provinces. Layer 3 (*black triangle*) in the geological section is the major fossil yielding stratum (modified from Tan and Ren 2009, courtesy of Science Press)

2004). It has yielded abundant charophytes, plant fossils, conchostracans, ostracods, shrimps, insects, gastropods, bivalves, fishes, amphibians, reptiles, birds, and mammals (Wang et al. 2004; Sha 2007). The fossil fauna is characterized by *Eosetheria-Lycoptera-Ephemeropsis trisetalis* (Wang et al. 2004). Radiometric and palaeomagnetic dating of the Yixian Formation indicates an age of around the Barremian-Aptian transition, and previous studies gave an age ranging from 136.2 Ma (Hauterivian) to 118.12 Ma (Middle Aptian). Since radiometric dating of zircon from tuff in the overlying Jiufotang Formation has indicated an age of 120.3 Ma (Early Aptian) (He et al. 2004) and a recent ^{40}Ar/^{39}Ar dating indicates that the age of the Yixian Formation is between 129.7±0.5 and 122.1±0.3 Ma (Chang et al. 2009a), the Yixian Formation must be mainly Barremian. This determination agrees with the biostratigraphic data (Sha 2007) and other isotopic dating (Swisher et al. 1999, 2002; Deng et al. 2003; Peng et al. 2003; He et al. 2004).

4.2 Faunas

The western Liaoning area is famous for its abundant fossil resources, which have provided invaluable materials for palaeontological studies of this region. Following are brief summaries of various fossils found in the Jiulongshan Formation and Yixian Formation, the strata yielding the plant fossils documented in this book.

4.2.1 The Jiulongshan Fauna

In this region, conchostracans are distributed in all threes members of the Jurassic in this region and especially widespread in the Middle Jurassic. The Jiulongshan Formation yields the *Euestheria ziliujingensis* conchostracan fauna, including 5 species in 2 genera (Deng et al. 2003; Huang et al. 2006, see Appendix 10.3.1.1 for the species list).

Ostracodes are also distributed in all three members of the Jurassic in this region, occurring rarely in the Lower Jurassic, abundantly but with little diversity in the Middle Jurassic, and abundantly and diversified in the Upper Jurassic. In the Jiulongshan Formation, only several species in two genera are known, referred as *Darwinula sarytirmenensis-D. magna-Timiriasevia* assemblage, including 5 species in 2 genera (Deng et al. 2003, see Appendix 10.3.1.2 for the species list).

Bivalves are very abundant in the Jurassic of this region, including three faunas, warm and humid *Unio-Margaritifera-Yananoconcha-Ferganoconcha* fauna, warm and arid *Psilunio-Eolamprotula-Cuneopsis-Pseudocardinia* fauna, and semi-warm-humid to semi-hot-arid *Arguniella-Sphaerium-Mengyinia* fauna. The Jiulongshan Formation has yielded 9 species in 4 genera (Deng et al. 2003, see Appendix 10.3.1.3 for the species list).

Although gastropods are abundant in North China, they are missing in the Lower and Middle Jurassic of western Liaoning (Deng et al. 2003).

Due to their short life cycle, strong adaptability, rapid spreading and strong evolutionary capability, insects become good index fossils for stratigraphic correlation of Jurassic terrestrial strata. Insect fossils are rare in the Lower Jurassic, abundant in the Middle Jurassic, and very abundant and diversified in the Upper Jurassic. The Jiulongshan Formation yields the *Samarura-Necrocercopis* insect assemblage, including at least 19 orders: Ephemeroptera, Odonata, Blattaria, Orthoptera, Dermaptera, Grylloblattodea, Plecoptera, Psocoptera, Hemiptera (including Heteroptera), Megaloptera, Rhaphidioptera, Neuroptera, Mecoptera, Coleoptera, Trichoptera, Diptera, Hymenoptera, Archostemata, and Lepidopetra (Huang et al. 2006; Tan and Ren 2009). The formation has yielded 134 species in 108 genera (Wang 1987a; Deng et al. 2003; Huang et al. 2006, 2008a, b, c, 2009; Huang and Nel 2007a, b, 2008a, b; Petrulevicius et al. 2007; Zhang 2007a, b, c; Zhang and Lukashevich 2007; Nel et al. 2007, 2008; Lin and Huang 2008; Lin et al. 2008; Selden et al. 2008; Wang and Zhang 2009a, b; Wang et al. 2009a, b, c; Fang et al. 2009; Tan and Ren 2009, see Appendix 10.3.1.4 for the species list).

Vertebrate fossils are rare in the Lower Jurassic, but rich in the Middle and Upper Jurassic in North China. The Jiulongshan Formation has yielded abundant fossils of fish, salamander, pterosaur, and mammal, including 11 species in 11 genera (Deng et al. 2003; Ji et al. 2005; Huang et al. 2006, see Appendix 10.3.1.5 for the species list).

4.2.2 *The Yixian Fauna*

The Yixian Formation has yielded rich conchostracan fauna, including 113 species in 14 genera (Wang 1987b; Deng et al. 2003; Wang et al. 2004; Li et al. 2007, see Appendix 10.3.2.1 for the species list).

The Yixian Formation has yielded abundant and diversified ostracode fauna, called *Cypridea* (*Ulwellia*) *sihetunensis-Cypridea* (*C.*) *liaoningensis-Timiriasevia jianshangouensis* ostracode assemblage, including 63 species in 18 genera (Deng et al. 2003; Wang et al. 2004, see Appendix 10.3.2.2 for the species list).

The Yixian Formation has yielded the *Arguniella-Sphaerium* bivalve fauna (Jiang et al. 2007). The fauna is abundant but monotonous generically and endemic with *Sphaerium*, including 10 species in 3 genera (Yu et al. 1987; Jiang et al. 2007; Sha 2007, see Appendix 10.3.2.3 for the species list).

Gastropods are abundant in the Yixian Formation, including 12 species in 8 genera (Yu 1987; Deng et al. 2003, see Appendix 10.3.2.4 for the species list).

The Yixian Formation has yielded abundant fossil insects, forming the *Aeschnidium-Manlayamyia* insect assemblage, including 126 species in 94 genera (Deng et al. 2003; Wang et al. 2004; Huang and Lin 2007; Lin et al. 2007; Liu et al. 2006a, 2007b; Zhang et al. 2007; Huang and Nel 2009; Wang et al. 2009c, see Appendix 10.3.2.5 for the species list).

The Yixian Formation has yielded abundant vertebrate fossils, including 61 species in 53 genera (Smith and Harris 2001; Deng et al. 2003; Zhang and Wang 2004; Wang et al. 2004; Ji et al. 2005; Liu et al. 2007, 2008; Wang et al. 2007d; see Appendix 10.3.2.6 for the species list).

4.3 Floras

4.3.1 *The Jiulongshan Flora*

In North China, vascular plants are well-developed in the Lower and Middle Jurassic and reach their peak in diversity during the Middle Jurassic (Deng et al. 2003). The Lower Jurassic flora is often referred as the *Neocalamites-Cladophlebis* flora, the Middle Jurassic one as *Coniopteris-Phoenicopsis* flora (Deng et al. 2003). The Jiulongshan Formation belongs to the Middle Jurassic, and its flora is dominated by Cycadales and Bennettitales, followed by Filicales, Ginkgoales, Coniferales, Equisetales, Lycopodales, and rare Angiospermae (Zhang and Zheng 1987), including 140 species in 57 genera (Pan 1977; Zhang and Zheng 1987; Wang et al. 1997; Deng et al. 2003; Li et al. 2004; Wang et al. 2007b, c; Zhou et al. 2007; Wang and Wang 2010; Zheng and Wang 2010; Wang et al. 2010; see Appendix 10.4.1 for the species list).

4.3.2 The Yixian Flora

The Yixian Formation has yielded abundant plant fossils, and is particularly famous for its early angiosperms, including *Chaoyangia*, *Archaefructus*, *Sinocarpus* and *Callianthus* (Duan 1998; Sun et al. 1998, 2001, 2002; Leng and Friis 2003, 2006; Ji et al. 2004; Wang and Zheng 2009). The flora of the Yixian Formation is referred as the *Otozamites turkestanica-Brachyphyllum longispicum* assemblage, including Coniferales, Bennettitales, Cycadales, Filicales, Ginkgoales, Czekanowskiales, Gnetales, Equisetales, Bryophytes, Lycophytes, Angiospermae, and Caytoniales, in descending order of abundance. The documented plant fossils include 151 species in 75 genera (Wu 1999; Sun et al. 2001, 2002; Leng and Friis 2003, 2006; Ji et al. 2004; Wang et al. 2004; Zheng and Zhou 2004; Yang et al. 2005; Liu et al. 2006b; Wang and Zheng 2009, 2010; Guo et al. 2009; Wang 2010; Wang et al. 2010; see Appendix 10.4.2 for the species list).

Chapter 5
Flowers from the Early Cretaceous

Fossil angiosperms from the Early Cretaceous are of special interest because currently the earliest widely-accepted angiosperms are from this age. *Chaoyangia*, *Archaefructus*, *Sinocarpus*, and *Callianthus* are four representative angiosperms from the Yixian Formation (125 Ma, Early Cretaceous). Their early age, distinct morphology, and reproductive features not only display an aspect of early angiosperms, but also, if monophyly of angiosperms is assumed, strongly suggest that the origin of angiosperms must have occurred even earlier.

There have been numerous reports of fossil angiosperms from the Aptian to the Cenomanian, too many to list in this book. Mesofossils especially numerically increase the multitude of angiosperms in the Early Cretaceous, as Friis, Crane and their colleagues documented. Searching for fossil angiosperms in strata younger than the Barremian (the Early Cretaceous) shows little promise in providing insight on angiosperm origin. It is the goal of this chapter to document those from the pre-Aptian age, with emphasis on female reproductive organs since other organs cannot provide a definite answer to the question of whether or not a fossil plant is an angiosperm. The early angiosperms from the Yixian Formation (Early Cretaceous) in China include *Chaoyangia*, *Archaefructus*, *Sinocarpus*, and *Callianthus*. This does not mean that other fossil plants have no relationship to angiosperms, but that their affinities need further evidence to confirm according to the definition proposed in this book before being accepted.

5.1 *Chaoyangia*

5.1.1 Previous Studies

Chaoyangia from the Yixian Formation (Early Cretaceous) was initially reported to be an angiosperm by Dr. Shuying Duan (Fig. 5.1a) in Chinese in 1997 and English in 1998. The specimens, including two facing parts of the same inflorescence, were collected by Mr. Shikuan Liang (Fig. 5.1b) in the early 1990s. Although it was taken as an earliest angiosperm at that time, published in the Chinese Science Bulletin, and attracted certain attention, its affinity was challenged and undervalued, especially

X. Wang, *The Dawn Angiosperms*, Lecture Notes in Earth Sciences 121,
DOI 10.1007/978-3-642-01161-0_5,

Fig. 5.1 Dr. Shuying Duan (**A**), the author of the first paper describing *Chaoyangia*, and Mr. Shikuan Liang (**B**), the collector of *Chaoyangia*, holding the holotype. Figures 5.1–5.10 all relate to the holotype

after the description of the so-called "first flower", *Archaefructus*, was published by Sun et al. (1998) in *Science*. In their paper, Sun et al. related *Chaoyangia* to a poorly understood fossil taxon, *Gurvanella*, and further with *Welwitschia* (Gnetales). Since then *Chaoyangia* has been repeatedly mentioned and interpreted in various ways in the literature despite the fact the holotype specimens were rarely visited and serious investigation was rarely undertaken (Guo and Wu 2000; Sun et al. 2001; Zhou et al. 2003; Krassilov et al. 2004; Friis et al. 2005, 2006; Rydin et al. 2006b; Krassilov 2009). Since 1998 many more specimens of *Chaoyangia*, including isolated infructescences and physically connected parts, have been collected. Unfortunately, the information in these specimens is rarely explored and the affinity of *Chaoyangia* remains unresolved.

5.1.2 Misunderstanding and Clarification

Chaoyangia has been clouded by uncertainty ever since Sun et al. (1998) designated *Chaoyangia* a junior synonym of *Gurvanella* and further related it to *Welwitschia* based on "the ribbed stems, opposite branching, and winged fruits or seeds". Based on current knowledge, treating *Chaoyangia* as a relative of *Welwitschia* appears overemphasizing the taxonomic significance of the opposite branching pattern and ribbed stems. In citing a paper by Crane (1996) and Sun et al. (1998) wrote that "many members of Gnetales, found in the Mesozoic, are characterized by oppositely placed leaves, branches, and reproductive organs". Sun et al. (2001) held the same point of view and did not provide further evidence for their treatment. Careful comparison between Crane (1996) and Sun et al. (1998, 2002) indicates that Crane listed eight (rather than three) characters as potential synapomorphies of Gnetales, but warned that none of these characters was diagnostic of Gnetales (S50-S51, Crane

1996). Apparently, Sun et al. (1998, 2001) did not pay sufficient attention to Crane's warning and related *Chaoyangia* to Gnetales by cherry-picking two out of eight non-diagnostic characters to assign a plant to a taxon, a chancy taxonomic practice. Treating a plant, especially a fossil plant, requires attention to all preserved characters, which are valuable and the only solid basis for its identification.

The characters, including urceolate receptacle, hairs on its surface, monocolpate pollen grain, spatial relationship between female and male flowers, three carpels in the receptacle, morphology of the male flower, and seed in a spacious ovary, seen in *Chaoyangia* have never been seen in the Gnetales or other gymnosperms (Figs. 5.2–5.14). Important features of the Welwitschiaceae, such as well-defined cone, polyplicate or spinulose pollen grain, and winged seeds, have never been seen in *Chaoyangia*. In *Welwitschia* the winged seeds are sandwiched between bracts and never attached terminally on a branch, and the two wings (if there were wings in *Chaoyangia*) should surround a single seed rather than 3 seeds, as in *Chaoyangia*. The wing-like structure around the infructescences of *Chaoyangia* is an artifact of degaging to expose the hairs in Fig. 5.5a. The so-called wing in *Chaoyangia* has no actual boundary (Figs. 5.3j–r, 5.4a, b, 5.6a, 5.7a, b, and 5.11a–f, i), as would be expected in a typical wing. The appearance of hairs on the surface of the infructescences (Figs. 5.7b, 5.13g–i) indicates that the hairs are scattered on the surface of the spherical infructescences rather than deployed in two dimensional wing. Also, a wing is unlikely to be partially preserved, as in Fig. 5.11h. Placing *Chaoyangia* between *Welwitschia* and *Ephedra*, per se, reflects the dilemma Zhou et al. (2003) and Rydin et al. (2006b) faced. Similarly, the flipping placement of *Chaoyangia*, in Welwitschiaceae (Dilcher et al. 2005; Sun et al. 1998) or Ephedraceae (Yang et al. 2005), by the same person also reflects the lack of both evidence and confidence

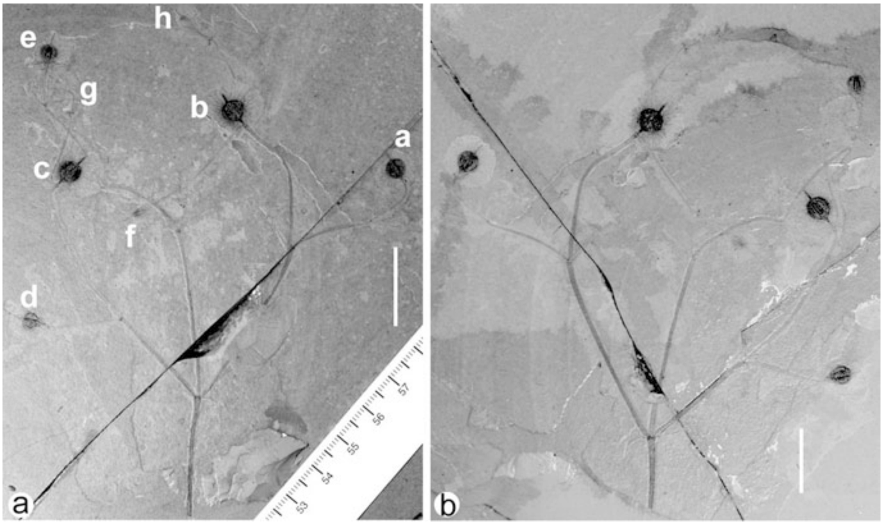


Fig. 5.2 The holotype of *Chaoyangia*. The flowers/infructescences are labeled with *letters*. **A** and **B** are two facing parts of the same specimen (9341a&b, IBCAS)

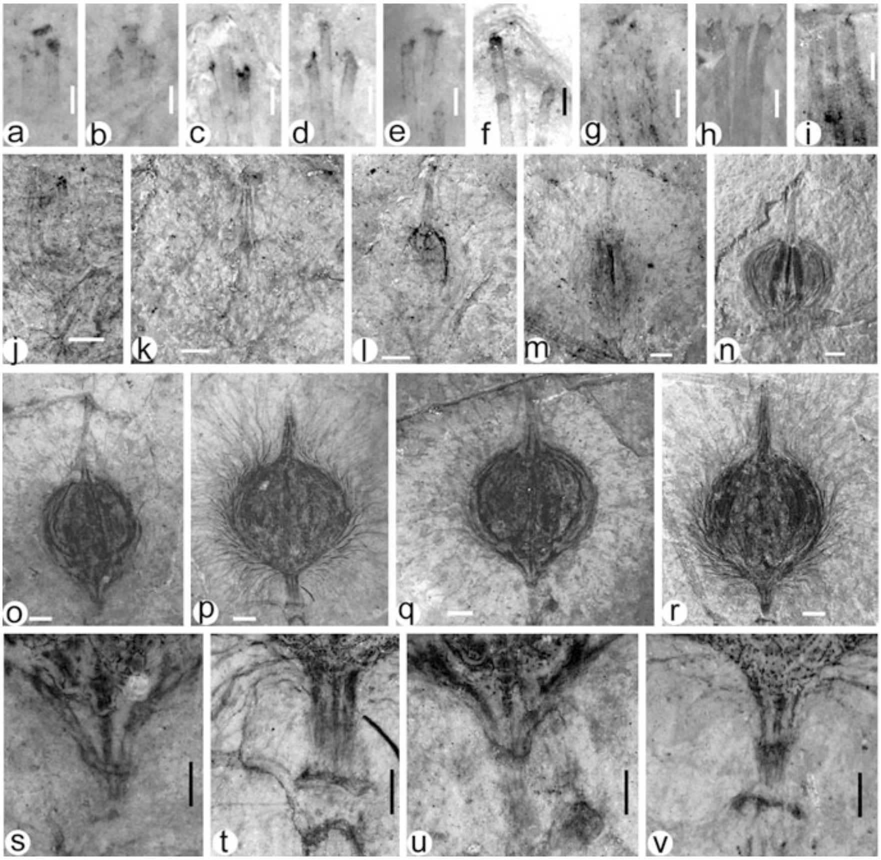


Fig. 5.3 Details of the styles, flowers/infructescences. **A**–**I** Styles of the flowers/infructescences labeled i, g, h, f, e, d, b, a, and c, in that order, in Fig. 5.2a. Note the lobed stigmas in b, e and h. Bar = 0.2 mm. **J**–**R** The flowers/infructescences labeled i, g, h, f, e, d, b, a, and c, in that order, in Fig. 5.2a. Bar = 1 mm. **S**–**V** The stalks of the flowers/infructescences labeled d, b, a, and c, in that order, in Fig. 5.2a. Bar = 0.5 mm

in the placement. The micropylar tube remains free-standing in the Gnetales (Yang et al. 2003, 2005; Yang 2007; Friis et al. 2009; Wang and Zheng 2010). In contrast, in mature infructescences of *Chaoyangia* the styles are appressed against each other by hairs on the receptacle (Figs. 5.5a, 5.13b, and 5.14c). In short, *Chaoyangia* shares too few characters of taxonomic significance and demonstrates too many differences to be related to any element in Gnetales.

At present, many palaeobotanists think that *Gurvanella* is equivalent to *Chaoyangia* (Sun et al. 2001; Zhou et al. 2003; Krassilov et al. 2004; Krassilov 2009). This situation is partially due to the strong influence of Sun et al.'s *Science* paper, partially due to the mistreatment by Krassilov, the author of *Gurvanella*. According to the original publication (Krassilov 1982), *Gurvanella* has a "concave stigma" and a "wing" around the fruit. *Chaoyangia,* in contrast, has three distinct stigmas on the style terminals and hairs scattered over the entire infructescence

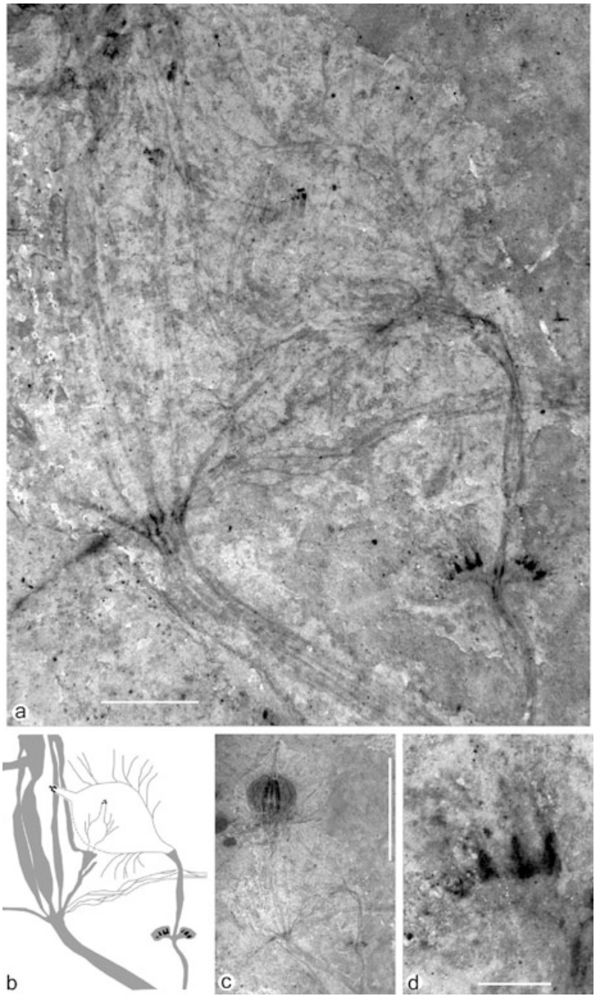


Fig. 5.4 Details of connected floral parts. **A** Details of the lower central portion in **C**. Note the connection between the male flower at the lower right and its female flower at *upper center*, and that there is another smaller flower overlapping the larger female flower. Bar = 2 mm. **B** Line-drawing of **A**. **C** Detailed view of the flowers e and g in Fig. 5.2a. Its *lower central portion* is shown in detail in **A**. Bar = 1 cm. **D** Detailed view of male flower in **A**. Note the *dark material* in the pollen sacs. Bar = 0.5 mm

surface. These two differences alone are enough to distinguish *Chaoyangia* and *Gurvanella*, in addition to bisexuality *vs* unisexuality, respectively, recognized recently. The inadvertent mixing of these two taxa is also partially due to the poor quality printing of the paper by Duan (1998). It is unfortunate that Krassilov et al. (2004) conflated *Chaoyangia* and *Gurvanella* in spite of the distinctions between these two taxa. Krassilov's inconsistency is not realized by most palaeobotanists, and even a specialist who once reviewed a paper on *Chaoyangia* was misled to believe that *Chaoyangia* and *Gurvanella* were the same thing and rejected

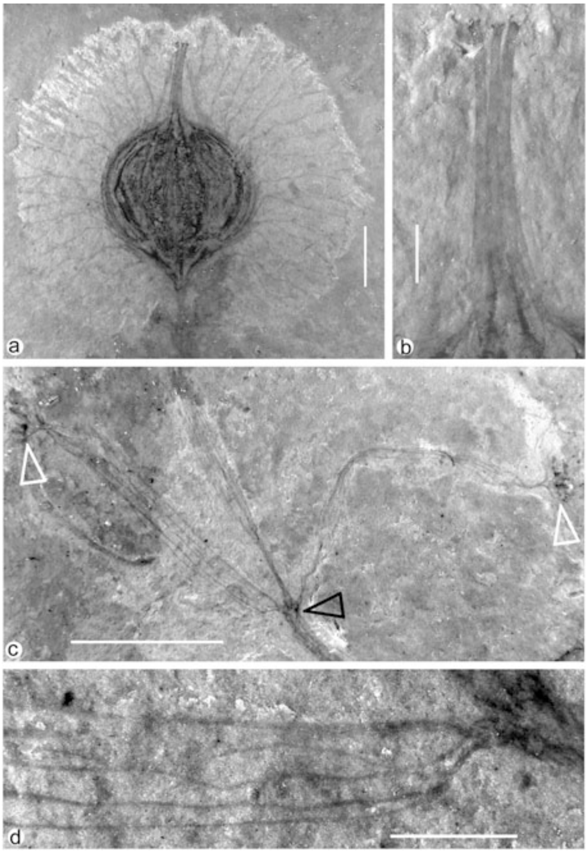


Fig. 5.5 Female flower a in Fig. 5.2b. **A** Whole female flower. Note the receptacle enclosing the ovaries, forked hairs on its surface, and hairs in their early stage forming an envelope around the style. Bar = 2 mm. **B** Three straight styles at *top*, and dark stigmas on the terminal of the styles. Bar = 0.5 mm. **C** Portion of the branches below female flower a. Note the conspicuous joint (*black arrow*), the main branch (*lower center*) giving rise to a fleshy branch (*upper center*) with two fleshy lateral branchlets with parallel ribs, plus two male flowers (*white arrows*) attached to the lateral branchlets. Bar = 5 mm. **D** Nearly parallel vascular bundles on the fleshy lateral branch. Bar = 1 mm

any further modification. Actually, the truth may be revealed by simply putting Krassilov's publications (1982, 2004, 2009) side by side. The International Code of Botanical Nomenclature stipulates that a taxon is connected to a type. Therefore, although the author of *Gurvanella*, Krassilov and his coauthors do not have the authority to change the definition of *Gurvanella*, published in 1982, to conform to their publication on *Gurvanella* in 2004, the latter of which, in this author's opinion, is invalid.

5.1.3 New Information

Recent investigation of *Chaoyangia* reveals male flowers, enclosed seeds, young female flowers with well-defined styles, and physically connected male and female flowers on the same branch. These features suggest that *Chaoyangia* was a pioneer monoecious angiosperm although these features have been poorly represented or ignored in the previous studies. In this book, they are the documenting foci for *Chaoyangia*.

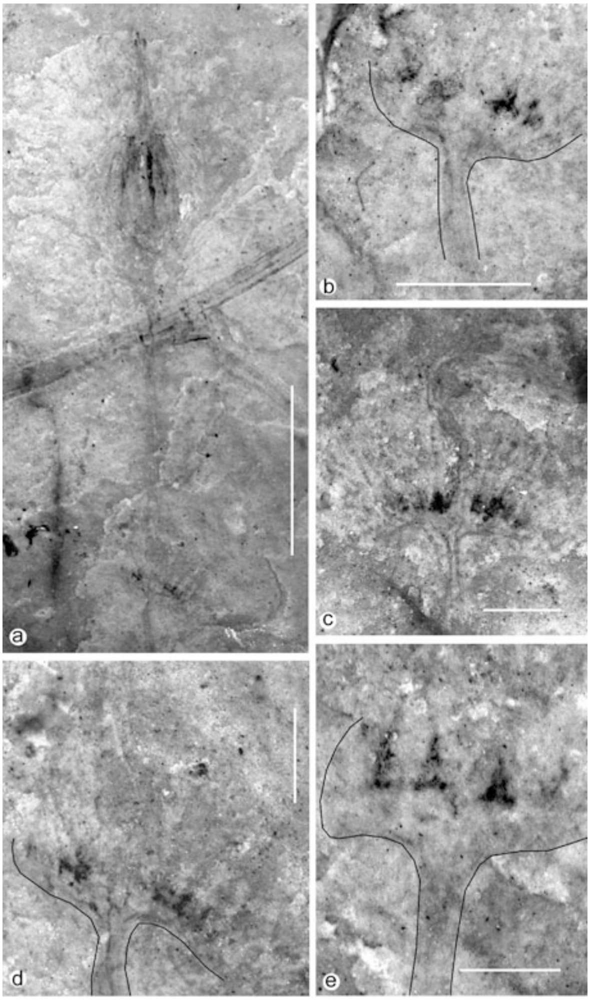


Fig. 5.6 Male flowers and its connection to female flower. **A** Female flower f in Fig. 5.2a (*top*) and its connection to its male flower (*bottom*). Bar = 5 mm. **B** Another male flower. Note its outline and relationship to the branch. Bar = 1 mm. **C** Side view of two male parts oppositely attached to a branch. Note the vertical branch (*bottom*), two opposite male parts, rigid upward pricks, and pollen sacs (*dark regions*). Bar = 1 mm. **D** Detailed view of the male flower in **A**. Note its outline and relationship to the branch. Bar = 1 mm. **E** Tangential view of a male part. Note the branch (*bottom*), outline of the male part (*dotted line*), and three or four triangular pollen sacs (*dark regions*). Bar = 0.5 mm

5.1.3.1 Physically Connected Male and Female Flowers

Physically connected parts of fossil plants are always welcome because they bear information that helps to clarify description and classification. This is why palaeobotanists yearn to find whole plant fossils. In the case of *Chaoyangia*, the best preserved specimen is the holotype initially described by Duan in 1997 and 1998. This specimen includes connected branches, leaves, female flowers, and male flowers, the last was not recognized with certainty in the initial documentation and was only briefly mentioned, with reservation, by Duan (1998) because she could not ascertain this relationship at that time due to a technical reason: the contrast between the specimen and matrix sometimes is too weak to be graphically recorded. Current technology has allowed better documentation of these features and the male flower

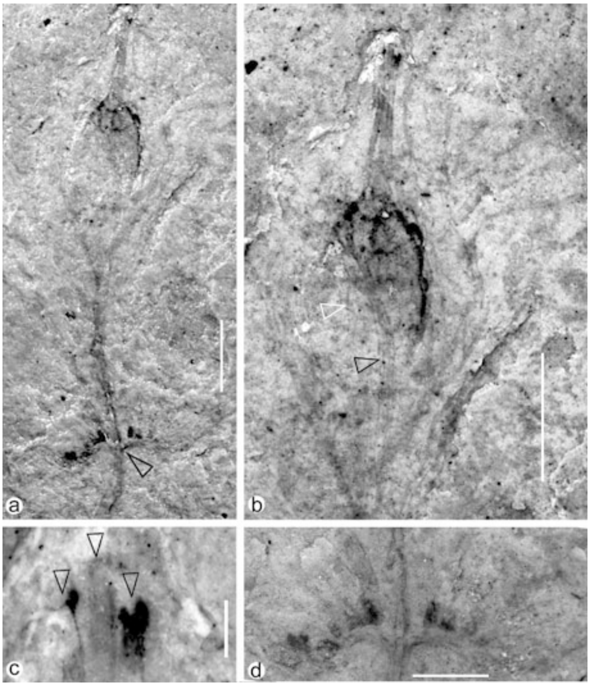


Fig. 5.7 Connected female flower and male flower. **A** Whole flower. Note the physical connection between the female flower (*top*) and male flower (*bottom*). Bar = 2 mm. **B** Detailed view of the female flower. Note the styles on the *top*, hairs (*white arrow*) on the surface, and a ribbed branch (*black arrow*) overlapping the flower. Bar = 2 mm. **C** Detailed view of style terminals (stigmas). Note the dark material on the stigmas (*arrows*). Bar = 0.2 mm. **D** Detailed view of male flower in **A**. Note the opposite arrangement of the two parts along the branch, and dark relics of the pollen sacs. Bar = 0.5 mm

was finally identified. As seen in Figs. 5.4, 5.6a, and 5.7a, the male and female flowers are physically connected.

In Fig. 5.4c there is a conspicuous female flower under which are other connected parts, shown in detail in Fig. 5.4a. In the lower-left portion of Fig. 5.4a there is a joint that connects a branch to its lower right, and several branches and a leaf to its upper and right. The branches would be hard to see if they had no longitudinal parallel ribs/vascular bundles. To the upper right of the joint, there is a branch bearing a female flower, which is the smallest and most immature one in the plant. The outline of this flower is not clearly preserved but the stigmas at the terminals of the styles are conspicuous due to their dark coloring. On the right side of Fig. 5.4a, from the bottom up, there are a branch, a male flower, another branch, and a female flower. The female flower has a better defined outline with sparse hairs and it overlaps with the above described small female flower. Just like the small flower, this more mature flower has conspicuous stigmas. Its connected male flower is composed of two parts oppositely arranged along the branch, and its pollen sacs are preserved as dark clusters (Fig. 5.4d). This interpretation is better depicted in the line drawing in Fig. 5.4b.

The physical connection between male and female parts/organs is further confirmed by more examples seen in the same physically connected specimen. Figure 5.6 and a clearly demonstrate the physical connection once more. Based on these pictures, it can be safely said that *Chaoyangia* is monoecious, not dioecious, as previously thought. The morphologies of these male flowers, similar to

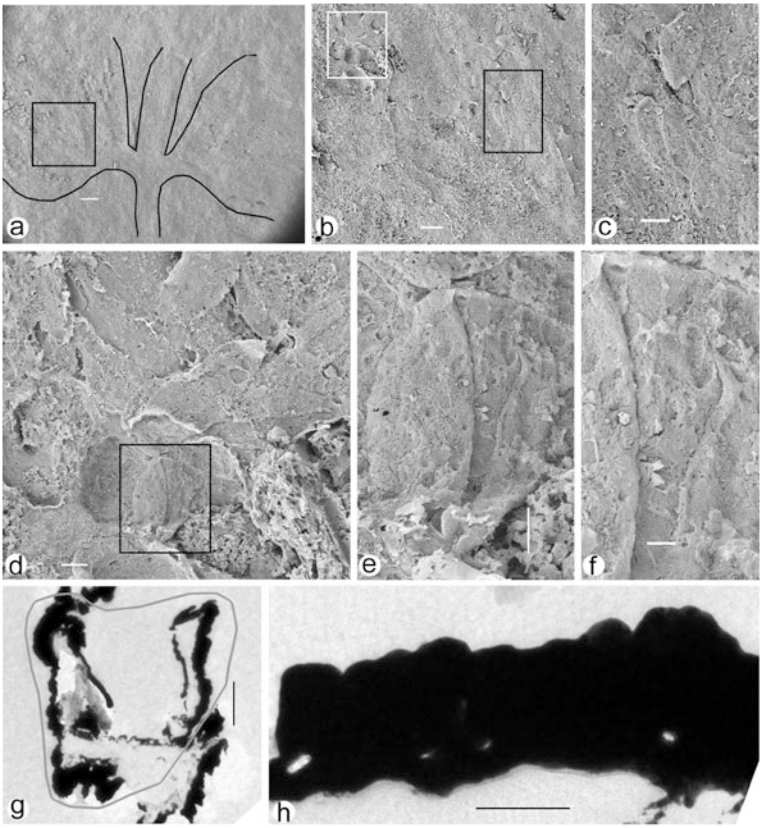


Fig. 5.8 In situ monocolpate pollen grains. **A** SEM view of the male flower shown in Fig. 5.7d. Note the outline of the flower and branch. Bar = 0.2 mm. **B** Detailed view of the rectangular region in A. Bar = 50 μm. **C** In situ pollen grains in the black rectangle in B. Bar = 20 μm. **D** In situ pollen grains in the white rectangle in B. Bar = 10 μm. **E** One of the in situ pollen grains, in rectangle in D. Note its monocolpate form. Bar = 5 μm. **F** Details of the pollen sculpture. Bar = 2 μm. **G** TEM view of an in situ pollen grain. Note the different thickness of the pollen wall in the aperturate and non-aperturate regions. Bar = 500 nm. **H** Detailed view of the non-aperturate pollen wall. Note the lacunae outlining the top of the foot layer. Bar = 200 nm

those, isolated or connected, preserved in the same specimen (Fig. 5.5c white arrows; Fig. 5.6b, c, e), suggest the common existence of male flowers and demonstrate their scope of morphological variation. This reinforces Duan's statement, tentative at that time, and also narrows the scope about nature and affinity of *Chaoyangia*.

5.1.3.2 Young Female Flowers

Due to technical difficulty and weak contrast between the specimen and the sedimentary matrix, Duan (1998) was not able to document the young female flower

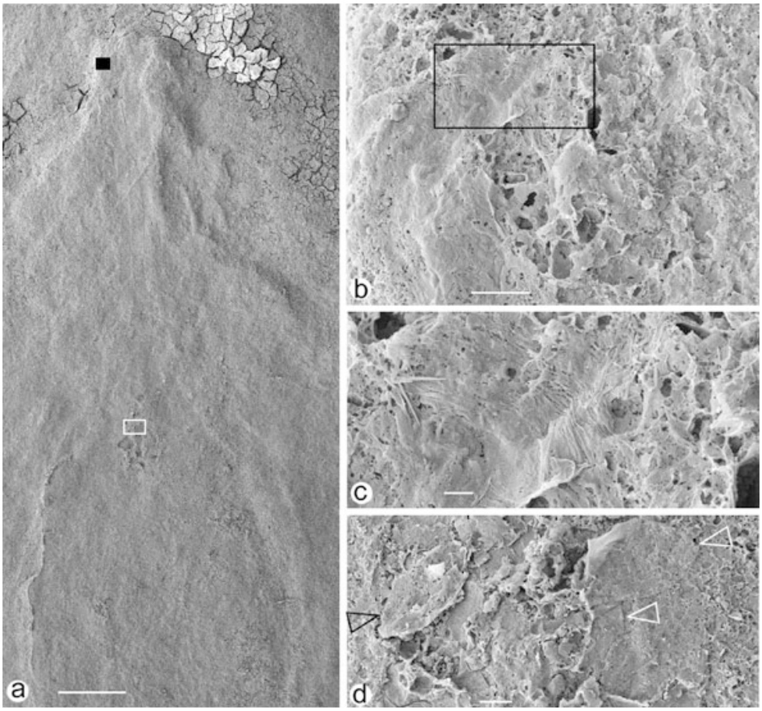


Fig. 5.9 Details of the female flower shown in Fig. 5.7b. **A** Top half of the female flower. Note the elliptic outline of the ovary portion (*bottom*) and elongate styles (top). Bar = 0.5 mm. **B** Detail of the stigma in the *black rectangle* in **A**. Bar = 10 μm. **C** Detail of the rectangle in **B**. Note the relics of the sticky material on the surface of the stigma. Bar = 2 μm. **D** Pollen pellet seen at the base of the styles in rectangular region in **A**. Note the pollen grains (*arrows*). Bar = 10 μm

of *Chaoyangia* in detail although she documented more mature female flowers that had more conspicuous styles and hairs. These more mature female flowers are very similar to the subsequently found isolated infructescences of *Chaoyangia* and, presumably, opened the door to later misunderstandings. Scholars have used these isolated parts as proxies of *Chaoyangia*. The young female flowers in *Chaoyangia* are important in several aspects: (1) when preserved on the same branch as more mature ones, young flowers shed light on the early development of the plant; (2) the conspicuous dark material on the stigmas of young flowers becomes less evident in mature ones; and (3) the sticky secretory material, which may be related to pollination, can only be seen in young female flowers. Therefore new information on young female flowers is of critical importance for a better understanding of *Chaoyangia*.

Figures 5.3j–n, 5.4a, b, 5.5a, b, 5.6a, and 5.7a, b show young female *Chaoyangia* flowers in different developmental stages. The subtle difference between young and more mature female flowers (Figs. 5.3o–r and 5.5a, b), plus isolated infructescences

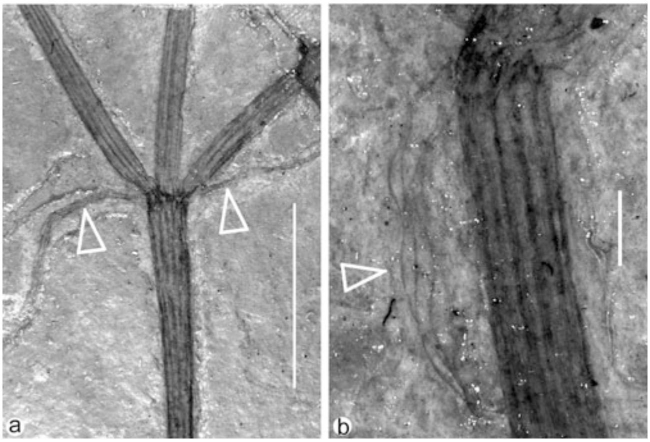


Fig. 5.10 Branches and leaves. **A** Typical opposite branching pattern. Note the subtending leaves (*arrows*) and longitudinal ribs on the branch. Bar = 1 cm. **B** Details of leaf venation. Note the near-parallel veins with rare interconnections (*arrow*), as well as longitudinal ribs on the branch. Bar = 1 mm

(Fig. 5.11a–f), represent a continuous developmental spectrum of female flowers in *Chaoyangia*. This becomes the basis on which the development of the plant is inferred later.

5.1.3.3 Styles and Stigmas

Styles and stigmas are features of angiosperms. Recognizing them in fossil plants requires extra care, however, because the micropylar tubes in Gnetales, Bennettitales and Erdtmanispermales (all gymnosperms) may appear similar (Chamberlain 1957; Bierhorst 1971; Biswas and Johri 1997; Yang 2007; Friis et al. 2009, Crane et al. 2009; Rothwell et al. 2009). Micropylar tubes in Bennettitales, Erdtmanispermales, Welwitschiaceae and Gnetaceae (the latter two in Gnetales) are always solitary, never in groups of three (Chamberlain 1957; Bierhorst 1971; Biswas and Johri 1997; Yang 2007; Friis et al. 2009; Crane et al. 2009; Rothwell et al. 2009), as in *Chaoyangia*. Therefore these groups can be excluded from consideration hereafter. Micropylar tubes in *Ephedra* (Ephedraceae) may be in group of more than one (Yang 2007) and thus easier to be confused with styles of angiosperms. However, micropylar tubes in *Ephedra* are relatively shorter, with pointed tips, sometimes entangled while the styles in *Chaoyangia* are very elongate, with rounded or lobed tips, and always distinct in the flower. *Chaoyangia* is further alienated from *Ephedra* by its linear leaves, hairy infructescences, male flower, and in situ monocolpate pollen grains (Figs. 5.3o–r, 5.4a, 5.8, 5.10, and 5.11). There is some sticky secretory material on the terminal of the style (stigma), especially in young flowers of *Chaoyangia* (Fig. 5.9a–c). This feature may be related to pollination in *Chaoyangia*, as in other angiosperms.

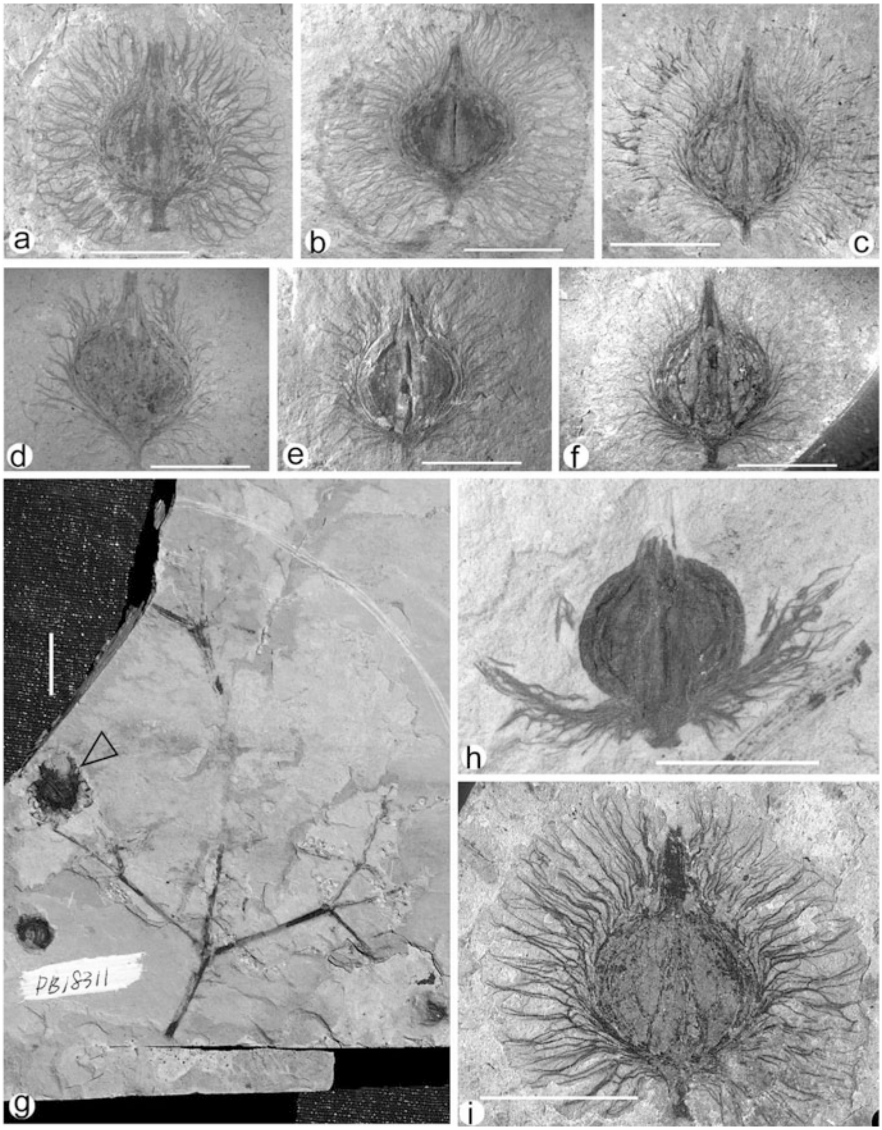


Fig. 5.11 Isolated infructescences and those connected by branches. Note that the styles are eclipsed by the enclosing by hairs, and the dense hairs on the surface of the infructescence. **A** Isolated infructescence. PB18178. Bar = 5 mm. **B** Isolated infructescence with hairs around. PB18176. Bar = 5 mm. **C** Isolated infructescence. PB18310. Bar = 5 mm. **D** Isolated infructescence. Note the relatively sparse hairs around the infructescence. PB18183. Bar = 5 mm. **E** Isolated infructescence. Note the rigid receptacle around the infructescence. PB18181. Bar = 5 mm. **F** Isolated infructescence. PB18180. Bar = 5 mm. **G** Branch connected with infructescences. Note the opposite branching pattern. Bar = 1 cm. **H** Isolated infructescence. Note the hairs in the upper portion of the infructescence have fallen off. PB21389. Bar = 5 mm. **I** Isolated infructescence. CNU-Plant-2008-001a. Bar = 5 mm

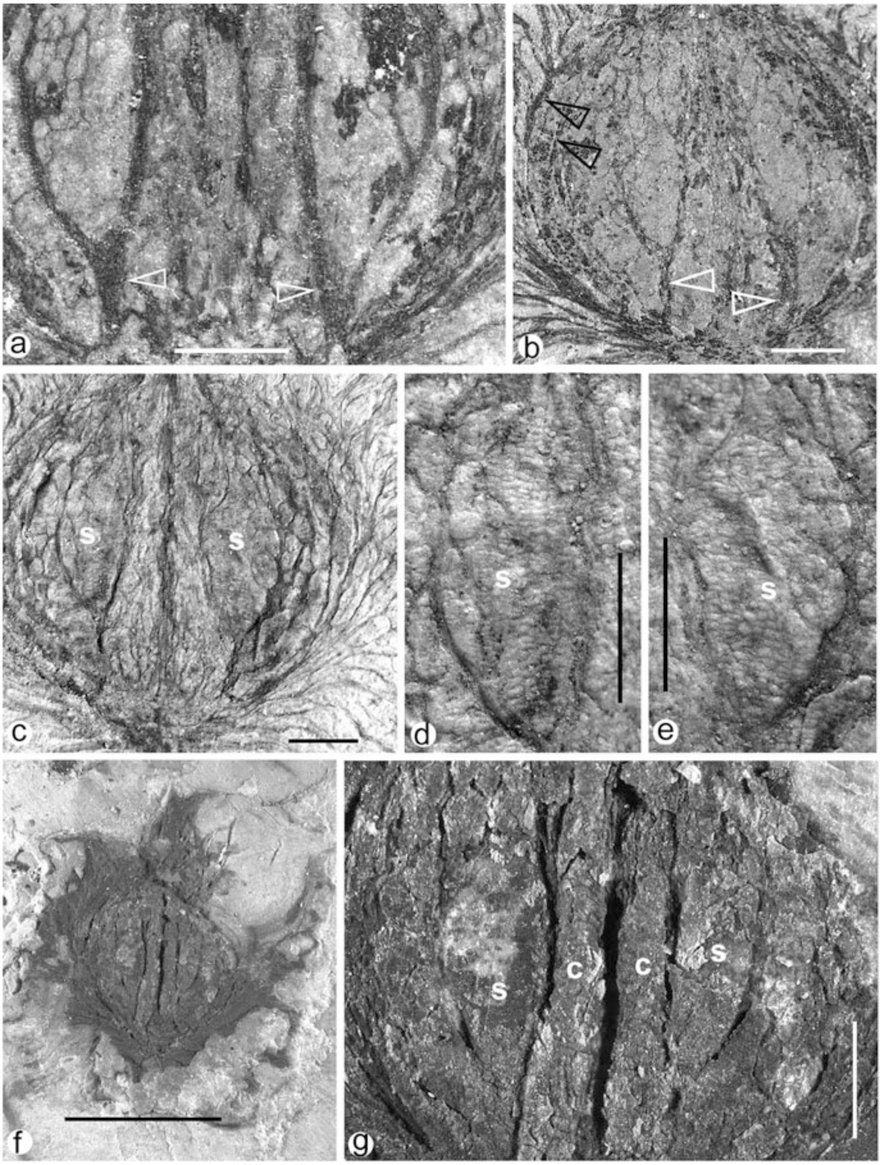


Fig. 5.12 Details within the infructescences. **A** Detailed view of the infructescence in Fig. 5.11f. Note the vascular bundles (*arrows*) corresponding to ovule/seed in other infructescences. Bar = 1 mm. **B** Detailed view of the infructescence in Fig. 5.11i. Note the vascular bundles (*arrows*) corresponding to ovule/seed in other fruits. Bar = 1 mm. **C** Detailed view of the infructescence in Fig. 5.11c. Note the seeds (S) and the vascular bundles at their bases. Bar = 1 mm. **D&E** Detailed views of two seeds in **C**. **F** Infructescence (*black arrow* in Fig. 5.11 g) with in situ seeds. Bar = 5 mm. **G** Details in the infructescence shown in **F**. Note the distance between the ovary walls (**C**) and seeds (S), borders of the seeds, ovary wall covering the seed in the upper region, and gap between two ovaries. Bar = 1 mm

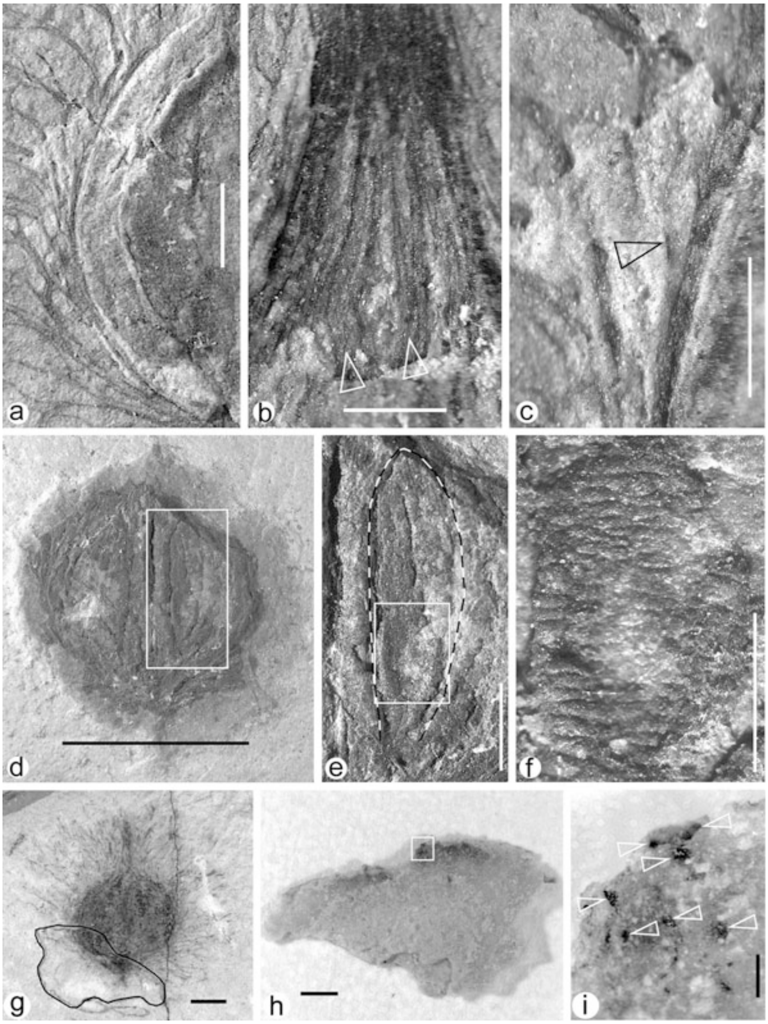


Fig. 5.13 Infructescence and in situ seed. **A** Details of the infructescence shown in Fig. 5.11e. Note the receptacle of uniform thickness and bearing hairs on its surface. Bar = 1 mm. **B** Hairs (*arrows*) forming an envelope around the style, visible after removing the styles. Bar = 0.5 mm. **C** Detailed view of the hairs on the receptacle surface. Note the rigid outer surface of the receptacle, a hair just arising from the receptacle (black arrow), adjacent hairs on different planes (out of focus). Bar = 0.5 mm. **D** Another infructescence with in situ seeds. Note that most of the hairs have been shed or abraded. PB18312. Bar = 5 mm. **E** The rectangular region in **D**. Note the profile of the seed (zebra line). Bar = 1 mm. **F** Ripples on the seed coat, enlarged from the rectangle in **E**. Bar = 0.5 mm. **G** An infructescence split through the center. Note the lower-left portion (*white line*) is detached from the main infructescence. Bar = 2 mm. **H** The reverse side of the detached portion in **G**. The *rectangular region* is detailed in **I**. Bar = 1 mm. **I** Traces of several hairs (*arrowed* organic material) embedded in the sediments. Bar = 0.1 mm

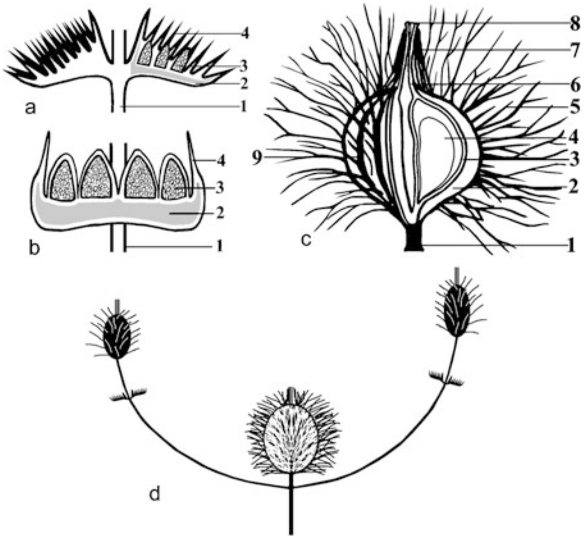


Fig. 5.14 Idealized diagrams of male flower, female flower, and inflorescence. **A** Side view of two stamens, right one partially dissected to show inner details. Note the opposite arrangement of male floral parts along the branch (1), foliar structure (2) supporting pollen sacs (3) on its adaxial surface, and upward pricks (4) along the margin of the foliar structure. **B** Tangential view of a male floral part, with the foreground half removed to show inner details. Note the branch (1) in the background, foliar structure (2) supporting pollen sacs (3) on its adaxial surface, and upward pricks (4) along the margin of the foliar structure. **C** Female flower with the front-right quarter removed to show the inner details. Note the stalk (1), receptacle (2), ovary (3) with seed/ovule (4) inside, hairs (5), style (6), hair envelope (7) surrounding the styles, stigma (8), and longitudinal ribs (9) on the receptacle. **D** The arrangement of the male and female flowers in the inflorescence

5.1.3.4 Male Flowers

Previously, the male flowers of *Chaoyangia* were poorly understood. It was only tentatively mentioned in Duan's (1998) paper. Later publications (Sun et al. 1998, 2001; Guo and Wu 2000; Sun et al. 2001; Zhou et al. 2003; Krassilov et al. 2004; Friis et al. 2005, 2006; Rydin et al. 2006b) have never mentioned the existence of male flowers/parts in *Chaoyangia*. Until recently, the male flowers of *Chaoyangia* had been ignored completely. New careful investigation indicates that the holotype of *Chaoyangia* indeed has male flowers, isolated or in physical connection with the female flowers (Figs. 5.4, 5.5c, 5.6, and 5.7). The male flowers of *Chaoyangia* usually subtend the female flowers, and are less conspicuous in the preservation (Figs. 5.4a, b, 5.6a, and 5.7a). A male flower is composed of two symmetrical parts oppositely arranged along a branch (Figs. 5.4a–d, 5.5c, 5.6, and 5.7). Each part includes a foliar structure supporting pollen sacs on its adaxial surface and upward pricks along its margin (Figs. 5.4, 5.5c, 5.6, and 5.7). The pollen sacs are conical in form, containing dark material (Figs. 5.4d, 5.5b–e, and 5.7d). In situ pollen grains extracted from the dark material in pollen sacs are monocolpate (Fig. 5.8a–f). TEM observation indicates that the pollen wall has no laminated layer, as is frequently seen in gymnosperms, has no evident columellae layer, and has a few lacunae just above the foot layer (Fig. 5.8g, h). The pollen wall has different structure and composition in aperturate and the non-aperturate regions (Fig. 5.8g, h).

5.1.3.5 Enclosed Ovules/Seeds

In general, angiosperms are defined by their enclosed seeds although a stricter definition is based on enclosed ovules (see Chap. 3 for details). Seeds of *Chaoyangia* were rarely considered until recently. New investigation indicates that there are three seeds/ovules in the ovaries that are surrounded by a receptacle. This is especially evident in isolated infructescences (Figs. 5.11, 5.12, and 5.13d–f). These seeds are situated in a spacious ovary and they have horizontal ripples on their surface. They are enclosed by ovary walls (= carpels), which are connected to the styles and in turn enveloped by the receptacle. The positions and outlines of these seeds correspond well to the vascular bundles in the base of the ovaries (Figs. 5.11–5.12, 5.13d–f). It is worth mentioning that these seeds do not occupy the whole space in the ovary, instead there is a gap between the seed coat and ovary wall, an inconceivable phenomenon for gymnosperms, in which the seeds are surrounded by other immediately adjacent tissues. Pellets of pollen grains, with a diameter greater than that of the styles, have been seen at the bottom of those styles, suggesting that the pollen grains cannot pass through the styles even if the latter had internal canals. Considering all features of the styles and pollen grains, there is no canal allowing pollen transfer, as in Gnetales, in the styles of *Chaoyangia* and the seeds are completely enclosed by the carpels in *Chaoyangia*. It is noteworthy that the stigmas in young flowers that have no trace of seeds are conspicuous due to the dark coloring of probable secretory material and they are most likely in a receptive state. This implies that pollination in *Chaoyangia* is performed when the ovules in the ovaries of young flowers are completely enclosed, which satisfies the criterion for angiosperms as stated in Chap. 3.

5.1.4 Emended Diagnosis

Chaoyangia Duan emend. Wang
Type species: *Chaoyangia liangii* Duan emend. Wang

Emended diagnosis: Dichasial bisexual flowering branch, with linear leaves. Branch with parallel longitudinal ribs and rare interconnections. Leaf with parallel veins and rare interconnections. Male flower, consisting of two parts, attached to the branch laterals below female flowers. Each part including a foliar structure, with numerous pollen sacs sessile on its adaxial surface and upward pricks along its margin. In situ pollen grain monocolpate. Female flower terminal, with an urceolate receptacle bearing forked hairs on its surface and enclosing three ovaries. Three carpels inserted on central bottom of receptacle, each forming an ovary at the bottom and a straight slender style with a terminal stigma. A single ovule inserted to ovary bottom. Fruit indehiscent. Seed single, enclosed in a fruit, attached to the base of the fruit. Hairs likely shed in mature infructescences.

5.1.5 Description

Chaoyangia liangii Duan emend. Wang
(Figures 5.2–5.14)

Synonyms: *Chaoyangia liangii* Duan, Duan (1998, pp. 14–20, Figs. 1–4)
Chaoyangia liangii Duan, Wu (1999, p. 22, Pl. XIV, Figs. 1,1a, 2,2a, 4,4a, Pl. XV, Figs. 2,2a)
Gurvanella exquisita Sun, Zheng et Dilcher, Sun et al. (2001, pp. 107–108, 207–208, Pl. 24, Figs. 7, 8, Pl. 25, Fig. 5, Pl. 65, Figs. 2–11)
Gurvanella sp. Zhou et al. (2003, p. 812, Figs. 6b–d)
Gurvanella dictyoptera Krassilov, Krassilov et al. (2004, p. 705, Fig. 10B)
Gurvanella dictyoptera Krassilov, Krassilov (2009, p. 1273, Fig. 6)
Diagnosis: (Same as that of the genus).

Description: Currently known specimens of *Chaoyangia* include the holotype and numerous specimens, isolated or connected with other parts, discovered later. The holotype is approximately 13 cm long and 11 cm wide, including physically connected male and female flowers of various maturity, preserved on two facing slabs of sandstone (Fig. 5.2). Another physically connected specimen including branch and infructescence is approximately 8 cm long and 7 cm wide (Fig. 5.11g). All other specimens are isolated infructescences and more mature than the holotype (Fig. 5.11a–f, h, i).

The holotype is monoecious, with compound dichasium and evident joints (Figs. 5.2 and 5.10). At the joints, each lateral branch is subtended by a leaf and oppositely arranged (Figs. 5.2, 5.10, and 5.11g). The branches are more or less contracted immediately above the joint (Fig. 5.10a). Branches of various orders are 0.3–1.6 mm wide, with 4–6 parallel longitudinal ribs on its visible half surface and rare connections between the ribs (Figs. 5.4a, 5.5c, d, 5.6a, and 5.10). Most branches are rigid and straight (Figs. 5.2, 5.10, and 5.11g), while some younger branches appear fleshy (Fig. 5.5c, d).

The leaves are linear, with parallel veins and occasional interconnections (Fig. 5.10a, b).

Below some young female flowers are male flowers (Figs. 5.4, 5.6a, d, and 5.7). Each male flower has two parts oppositely arranged along the branch (Figs. 5.4a, b, d, 5.6b–d, 5.7d, 5.8a, and 5.14a, d). Each male part is 1.5–2.5 mm thick, 1.4–1.7 mm long and 1.3 mm wide, and includes a foliar structure, pollen sacs and numerous marginal pricks (Figs. 5.4a, b, d, 5.6b–e, 5.7d, 5.8a, and 5.14a, b). The pricks are arranged along the margin of the foliar structure, close to vertical, up to 1.1 mm long (Figs. 5.6c, 5.7c, and 5.14a, b). The pollen sacs are about 200 μm wide and 450 μm high, triangularly shaped, and sessile on the adaxial surface of the foliar structure (Figs. 5.4a, b, d, 5.6b–d, 5.7d, 5.8a, and 5.14a, b). The in situ pollen grains are monocolpate, elliptical, 32–51 × 20–36 μm, rough-surfaced in nonaperturate region, relatively smooth in aperturate region, usually in clumps (Figs. 5.8a–f and 5.9d). The pollen wall is homogeneous, uneven in thickness, with no columellae, thin and nonsolid in aperturate region (Fig. 5.8g, h).

Female flowers are terminal on the branches, elongated to globular in form depending on maturity (Figs. 5.2, 5.3j–r, 5.4c, 5.5a, 5.6a, and 5.7a, b). Each female flower has a stalk at the bottom, a central unit in the middle, and terminates in three styles (Fig. 5.3). Each stalk is 1.2–1.8 mm long, 0.2–0.6 mm in diameter, and appears to have three distinct parts when young (Fig. 5.3s–v). The central unit is 1.4–6.3 mm high and 0.6–5.2 mm wide, elongate to globular in form (Figs. 5.2, 5.3j–r, 5.4c, 5.5a, 5.6a, and 5.7a, b). Each mature central unit includes an urceolate receptacle covered with forked hairs and three closed carpels (Figs. 5.3n–r, 5.4c, 5.5a, 5.11a–f, h, i, 5.12, 5.13, and 5.14c, d). The hairs are 20–180 μm wide and up to 3 mm long, forked, tapering to the tip, and are scattered over the infructescence surface (Figs. 5.3j–r, 5.4a, b, 5.5a, 5.6a, 5.7a, b, 5.11a–f, i, 5.12c, 5.13a, c, g–i, and 5.14c, d). Hairs are sparse and less forked, not surrounding the style in young flowers (Figs. 5.3j–r, 5.4a, b, 5.5a, 5.6a, and 5.7b), but become dense and more forked, forming an envelope surrounding the styles at maturity (Figs. 5.11a–f, i, 5.12c, 5.13a, c, and 5.14c, d). Some hairs may be shed from mature infructescences (Figs. 5.11h and 5.13d). The mature receptacles are almost uniformly 0.6 mm thick (Figs. 5.12b, 5.13a, and 5.14c). Each carpel base is fixed to the central base of the receptacle (Fig. 5.12), forming an ovary at the base and a style at the top (Figs. 5.3j–r, 5.4a, b, 5.5a, 5.6a, 5.7a, b, and 5.14c). Mature ovary wall is 0.8–1.2 mm thick, with coarse horizontal ripples (Figs. 5.12, 5.13a, d, and 5.14c). Styles are 0.5–3.1 mm long and 67–107 μm wide, straight and slender, corresponding to the three ovaries in the receptacle (Figs. 5.3a–i, 5.5b, 5.6a, and 5.7a, b). Styles are distinct when young (Figs. 5.3a–i, 5.5b, 5.6a, and 5.7a, b), but appressed against each other by the surrounding hairs when mature (Figs. 5.11a–f, i, 5.13b, and 5.14c). Stigmas are terminal on style, expanded, lobed or not, probably secretory, conspicuous in young flowers due to their dark color (Figs. 5.3a–i, 5.4a, b, 5.5b, 5.6a, 5.7b, c, and 5.9a, c). Pellets of pollen grains are also found near the base of the styles (Fig. 5.9d). An ovule/seed is attached to the ovary base by a funiculus (Figs. 5.12a–e and 5.14c). Seeds are 2.8–3.6 mm long, 0.65–1 mm wide, with fine horizontal ripples, much smaller than the ovary cavities, corresponding the ovules outlined by vascular bundles in position, enclosed in but separated from ovary walls (Figs. 5.12 and 5.13d–f).

Holotype: 9341.

Further specimens: PB18309-18312, PB19176-19178, PB19180-19181, PB19183, PB21088-21090, PB21389, B0082, CNU-Plant-2008-001a&b.

Holotype locality: Huangbanjigou, Shangyuan, Beipiao, Liaoning, China (41°12′N, 119°22′E).

Further locality: Yingwoshan, Toudaohezi, Yixian, Liaoning.
Stratigraphic horizon: the Yixian Formation (about 125 Ma), equivalent to the Barremian, Lower Cretaceous.
Depository: 9341, in IBCAS; PB18309-18312, PB19176-19178, PB19180-19181, PB19183, PB21088-21090, PB21389, in NIGPAS; B0082, in IVPP; CNU-Plant-2008-001a&b, in CNU.

5.1.6 Development

Thanks to the physically connected young and mature organs in the holotype of *Chaoyangia*, it is possible to learn about the development of this pioneer angiosperm. These physically connected flowers demonstrate a transitional spectrum in morphologies of branches, male flowers, and female flowers in young and mature organs.

Branches of *Chaoyangia* demonstrate a consistent branching pattern and all have similar longitudinal ribs. However, younger branches exhibit certain difference than older ones, being relatively fleshy, with more distantly spaced longitudinal ribs, while the older branches are more rigid, slender, straight, with more closely spaced longitudinal ribs. The younger branches usually bear immature female and male flowers, while more mature female flowers appear on the older branches.

Male flowers are only borne on young branches. They are composed of two opposite parts arranged along the branch. Younger male flowers demonstrate more irregular forms, their pollen sacs and pricks are less evident, while older male flowers have more regular forms, their pollen sacs are more conspicuous and in regular form, their pricks are straight and pointing upward.

Female flowers demonstrate changes in several aspects, including size, amount of hair, receptacle, styles, and hairy envelope around styles. The female flowers are much smaller and elongate in shape when young. They become increasingly bigger and close to round in shape as development progresses. The mature female flowers show little difference in shape from the infructescence. Young female flowers have sparsely spaced, weakly developed, barely visible, simple hairs on their surface while the mature female flowers have densely spaced, well developed, very conspicuous forked hairs on their surface. In addition, hairs in young female flowers are not associated with the styles, while hairs in mature female flowers tend to form an envelope surrounding the styles, completely eclipsing the latter. In mature infructescences, some of the hairs may be shed. Receptacle is barely visible in young female flowers, but becomes a rigid spherical covering of uniform thickness surrounding the fruits in infructescences. The most invariable feature of the female flowers is the morphology and dimension of the styles, which are visible in the youngest observed female flowers, and like in mature flowers, the styles are straight. The stigmas of young female flowers are especially conspicuous due to their dark color in contrast to the poor preservation of the styles. The stigmas in mature female flowers are less conspicuous because styles in mature female flowers and infructescences are preserved in similar conditions, the contrast between stigmas and styles becomes weak, and stigmas and styles are usually eclipsed by the surrounding hairs.

The above described progress from young to mature flowers reveals the morphological changes that *Chaoyangia* normally undergoes during its development. This allows us not only to learn about its development, but to help to identify related fossils.

5.1.7 Pollination

Pollen pellet seen at the base of the style in a young female flower (Fig. 5.9d) is indistinguishable from those in situ in the pollen sacs (Fig. 5.8b–f). The dimensions of the pollen pellet is close to or greater than the width of the style, implying that it could not pass through a canal in a micropylar tube, as in the BEG clade, if the styles in *Chaoyangia* were actually micropylar tubes. The presence of these pollen pellets between the carpels implies that the pollination in *Chaoyangia* may have been assisted by animals, since studies on extant as well as fossil materials all relate clumped pollen grains to zoophily (Bierhorst 1971; Hu et al. 2008). This is in agreement with the conclusion drawn by Ren (1998) on pollination based on insect fossils from the Yixian Formation.

5.1.8 Affinity

5.1.8.1 Morphological Data

Recent study brings several new or overlooked characters of *Chaoyangia* to light, including monoecism (Figs. 5.2, 5.4, 5.6a, d, 5.7, and 5.8), male flower (Figs. 5.4, 5.6, 5.7d, and 5.8), in situ monocolpate pollen (Fig. 5.8), in situ seed/ovule in ovary (Figs. 5.12 and 5.13d–f), secretory, lobed, expanded stigmas (Figs. 5.3a–i, 5.5b, 5.7c, and 5.9), three straight, long styles (Figs. 5.3a–i, 5.5b, 5.6a, and 5.7c), hairs scattered over the female flower/infructescence (Figs. 5.3j–r, 5.7b, 5.13a, c, g–i, and 5.14c), and receptacle enclosing carpels (Figs. 5.5a, 5.12b, and 5.13a). The secretory material (Fig. 5.9a–c) on the stigma of *Chaoyangia* appears similar to that seen in extant plants (*Brasenia*, Fig. 1e, Endress 2005, *Nelumbo*, Fig. 2g, Hayes et al. 2000), suggesting that pollination in *Chaoyangia* might be very close or identical to those in some angiosperms. The styles in small (thus young) flowers (Fig. 5.4a, b) imply that the closure of the carpel occurs quite early, probably also well before pollination since many bigger flowers appear still receptive (Figs. 5.3a–h, 5.7c, and 5.9). The styles in *Chaoyangia* are in groups of three, straight and distinct (at least during early development), showing no evidence of a central canal (Figs. 5.3a–i, 5.5b, 5.6a, and 5.7c), which, if present, could have been preserved in fossils (Wang and Zheng 2010, Wang et al. 2010). They are indistinguishable from those in angiosperms, and are unlike the three usually pointed, sometimes entangled, micropylar tubes in *Ephedra* (Figs. 354–355, Chamberlain 1957, Figs. 1b, d, Yang et al. 2003), or single micropylar tube in *Welwitschia* and *Gnetum* (Figs. 26-8d, 26-4a, Bierhorst 1971). Seeds in *Chaoyangia* are enclosed in the ovary wall, and the ovary wall and the seed coat are distinct with a gap in between (Figs. 5.12 and 5.13d–f). It is implausible to interpret the “seed coat” here as either “carpel wall” or “ovary wall” considering that there are still two additional layers outside (the ovary wall and the receptacle). Therefore these characters, especially seed enclosed in an ovary and carpel closed before pollination, unequivocally place *Chaoyangia* in angiosperms.

The newly identified male flowers, plus the female flowers, indicate that *Chaoyangia* was monoecious, unlike previously thought (Duan 1998; Sun et al. 1998, 2001, 2002; Guo and Wu 2000; Zhou et al. 2003; Krassilov et al. 2004; Rydin et al. 2006b). The floral organization in *Chaoyangia* is unique and not directly comparable to any extant angiosperms. However, the female flowers of *Chaoyangia* demonstrate certain similarities to those in some Laurales. Their form, position, symmetry, receptacle form and appendages, position of carpels, and slender exserted style are comparable to those in Monimiaceae, e.g. *Atherosperma moschatum* (p. 89, Fig. 20.5, Takhtajan 1969) and *Monimia rotundifolia* (p. 34, Fig. 1b, c, Heywood 1979) (Table 5.1). Between the two, *Monimia rotundifolia*’s receptacle has a much-narrowed opening at the top, more similar to *Chaoyangia*. However, the leaf venation and numerous carpels per receptacle, plus other characters (Table 5.1) in these two monimiaceous elements defy concluding that there is a close relationship between Monimiaceae and *Chaoyangia*. It is possible that their similarities are a result of convergence rather than synapomorphies.

The in situ boat-shaped, medium-sized, monocolpate pollen of *Chaoyangia* has no laminated endexine (Fig. 5.8g, h). This set of pollen features strongly supports the concept of ancestral angiosperm pollen proposed by Walker and Walker (1984), except for a lack of psilate sculpture, and favor their evolutionary map for angiospermous pollen. The most primitive pollen grain is supposed to be columellaless, and columella is weakly developed in living primitive angiosperms (Walker 1976; Walker and Skvarla 1975). Compared to those of living primitive angiosperms, *Chaoyangia*’s pollen grain has incipient lacunae developing and thus does not appear to be the most primitive type for angiosperms, implying that the time of origin is even earlier than the Yixian Formation age of 125 Ma. The lack of laminated layer in the endexine, a character of angiosperms (Hill and Crane 1982), reinforces the angiospermous identity of *Chaoyangia*.

Chaoyangia has well-defined styles (Figs. 5.3a–i, 5.5b, 5.6a, and 5.7c). The latest study on floral features indicates that a well-defined style is derived (Endress and Doyle 2009; Williams 2009). The well defined styles with secretory stigma in *Chaoyangia* are indisputably not the most primitive type in angiosperms. The co-occurrence of the assumed primitive (poorly defined styles in *Archaefructus* and *Sinocarpus*) and derived characters (well-defined styles in *Chaoyangia* and *Callianthus*) in the Yixian Formation angiosperms rejects the hypothesis that the Yixian Formation yields the earliest angiosperms. *Chaoyangia* and other angiosperms (including *Archaefructus*, *Sinocarpus*, and *Callianthus*, Sun et al. 1998, 2001, 2002; Leng and Friis 2003, 2006; Ji et al. 2004; Wang and Zheng 2009) demonstrate diversified angiospermous reproductive strategies, suggesting that angiosperms already had undergone a certain period of evolution before and

Table 5.1 Comparison among *Chaoyangia* and other seed plants

	Chaoyangia	*Atherosperma moschatum*	*Monimia rotundifolia*	*Gurvanella*	*Ephedra*	*Welwitschia*
Leaf	Linear	Elliptical	Orbicular	?	Triangular	Strap-like
Leaf venation	Parallel	Pinnate	Pinnate	?	Parallel?	Parallel
Phyllotaxy	Opposite	Decussate	Decussate	?	3 in a whorl	Decussate
Joint/internode	+	–	–	?	+	+?
Sexuality	Bisexual?	Unisexual	Unisexual	Unisexual?	Unisexual?	Unisexual?
Flowering branch	Compound dichasium	Decussate	Compound dichasium	?	Compound strobilus	Compound strobilus
Pollen organ	Below female one, sessile pollen sacs	Independent of the female, anther on filament	Independent of the female, anther on filament	?	Independent of the female? sporangia on filament	Independent of the female? sporangia on staminal tube
Pollen organ arrangement	2, opposite	2, opposite	4 in a whorl	?	1–6 in bract axil, in compound strobilus	6 in bract axil, in compound strobilus
Pollen sacs	On the adaxial of a foliar structure	With a short filament	With a filament	?	In axil of bract, on a filament	In axil of bract, on staminal tube
Pollen grain	Monocolpate	Colpate	Inaperturate	?	Inaperturate, polyplicate	Monoaperturate, polyplicate
Female flower position	Terminal	Axillary?	Terminal	?	Axillary in compound cone?	Axillary in compound cone
Female flower form	Globular	Globular	Globular	Flattened	Triangular in cross section	Flattened
Female flower symmetry	Radial	Radial	Radial	Bilateral	Bilateral	Bilateral
Receptacle	Urceolate	Urceolate	Urceolate	N/A	N/A	N/A
Female flower appendage	Forked hairs	Hairs	Hairs	Lateral wing?	N/A	Lateral wing

Table 5.1 (continued)

	Chaoyangia	*Atherosperma moschatum*	*Monimia rotundifolia*	*Gurvanella*	*Ephedra*	*Welwitschia*
Female flower stalk	Short with an enlarged base	Long	Long	?	N/A	Short with an enlarged base
"Carpels"	3 in a whorl, free	Numerous, free	Numerous, free	2?	1(–3) ovuliferous unit in a whorl	1 ovuliferous unit
"Carpel" position	In receptacle	In receptacle	In receptacle	?	In bract axil	In bract axil
Ovulate part tip	3 long styles	∞ long styles	∞ long styles	1 style	1 micropylar tube	1 micropylar tube
"Stigma"	Lobed, expanded, secretory	?	?	Funnel-shaped	Tubular, secretory	Tubular, secretory

*1. "stigma" includes stigma in angiosperms and micropylar tube tip in BEG clade. 2. "carpel" includes carpel in angiosperms and ovuliferous unit in Gnetales.

had reached a certain level of diversity as early as the Barremian (Early Cretaceous), and that the origin of angiosperms may be much earlier than that. This conclusion is in agreement with a recently raised hypothesis on angiosperm origin based on megafossils as well as palynology (Zavada 1984, 2007, Hochuli and Feist-Burkhardt 2004; Wang et al. 2007b, c; Wang and Wang 2010), and helps to bridge the gap between the fossil record and molecular data (Moore et al. 2007), which have often been at odds.

5.1.8.2 Cladistics

To test the hypothesis on the phylogenetic position of *Chaoyangia* and its relationship to other seed plants, a data matrix was built on the basis of the morphological matrices of Doyle and Endress (2000) and Sun et al. (2002): 11 morphological characters (No. 2–8, 10–12 and 14) in the data matrix of Sun et al. (2002) and 108 morphological characters in the data matrix of Doyle and Endress (2000) were added to the matrix in the original order. Then four new morphological characters (namely seed/ovule enclosed or not, floral symmetry, double fertilization, and micropylar tube) were inserted at the beginning. A total of 46 and 47 characters are coded for *Chaoyangia* and *Archaefructus*, respectively. For the list and status of these morphological characters, refer to Appendix 10.1 and 10.2.

In addition, DNA sequences of *atp*B, *18S*, and *rbc*L were compiled from GenBank (for details see Table 5.2). These sequences were aligned using Clustalx1.83 (Thompson et al. 1997) and adjusted manually. Analyses based on the molecular matrix showed no significant difference from that given by APG (2003), and this constituted the basis for APG's results as constraints in the remaining analyses.

Since the focus of this analysis was the phylogenetic position of *Chaoyangia* relative to seed plants, only 28 taxa in basal angiosperms or basal eudicots, 8 taxa in four major gymnosperms groups (Cycadales, Ginkgoales, Coniferales, Gnetales), and 2 fossil taxa (*Chaoyangia, Archaefructus*) were included in the matrix.

The combined matrix (morphological plus molecular) included 38 taxa with 123 morphological and 4,654 molecular characters. The morphological data, molecular data, and combined data were analyzed using Paup 4.0 beta10 to reconstruct the phylogeny (Swofford 2002). Analyses with backbone, various other constraints according to the APG (2003), and with inclusion or exclusion of certain fossil or living taxa were performed on morphological and combined data. Reconstruction of all the most parsimonious (MP) trees was accomplished using a Paup 4.0 beta10 with heuristic search of 1,000 replications, with TBR swapping and multrees in effect. One of nine constrained morphological MP trees is shown in Fig. 5.15.

When the gymnosperms are constrained as a monophyletic group as ((*Cycas*, *Bowenia*, *Zamia*), (*Ginkgo*, (*Pinus*, (*Ephedra*, *Gnetum*, *Welwitschia*)))) and two other monophyletic lineages are constrained as (*Hydatella*, *Brasenia*) and (*Euptelea*, *Platanus*, *Trochodendron*, *Xanthorhiza*, *Sabia*) according to recent molecular results (Bowe et al. 2000; Chaw et al. 2000; Magallon and Sanderson 2002; Soltis et al. 2002; APG 2003; Burleigh and Mathews 2004; Saarela et al. 2007). All nine trees,

Table 5.2 DNA sequence accession numbers for the taxa used in the cladistic analysis

	Access number		
Taxon	rbcL	atpB	18S
Acoruscalamus	M91625.2	AJ235381.2	L24078
Amborella trichopoda	L12628.2	AJ235389.1	U42497.1
Aristolochia macrophylla	L12630.2	AJ235399.1	AF206855.1
Asarum canadense	L14290.1	U86383.1	L24043.1
Austrobaileya scandens	L12632.2	AJ235403.1	U42503.1
Bowenia serrulata	L12671.1	AF469654.1	/
Brasenia schreberi	M77031.1	AJ235418.1	AF096693.1
Calycanthus floridus	L14291.1|	AJ235422.1	U38318.1
Canella winterana	AJ131928.1	AJ235424.1	AF206879.1
Ceratophyllum demersum	M77030.1	AJ235430.2	U42517.1
Chloranthus japonicus	L12640.2	AJ235431.2	/
Chloranthus multistachys	/	/	AF206885.1
Cycas taitungensis	AP009339.1	NC_009618.1	D85297.1
Degeneria vitiensis	L12643.1	AJ235451.1	AF206898.1
Ephedra tweediana	L12677.2	AJ235463.1	/
Ephedra sinica	/	/	D38242
Eupomatia bennettii	L12644.2	AJ235473.1	AF469771.1
Euptelea polyandra	L12645.2	U86384.2	L75831.1
Ginkgo biloba	AJ235804.1	DQ069344.1	D16448.1
Gnetum gnemon	L12680.2	AF187060.1	U42416.1
Gyrocarpus sp.	L12647.2	/	/
Gyrocarpus americanus	/	AJ235487.1	AF206923.1
Hedyosmum arborescens	L12649.2	AJ235491.1	AF206925.1
Idiospermum australiense	L12651.2	AJ235500.1	AF206937.1
Illicium parviflorum	L12652.2	U86385.2	L75832.1
Liriodendron tulipifera	X54346.1	AJ235522.1	AF206954.1
Pinus thunbergii	D17510.1	D17510.1	/
Pinus elliottii	/	/	D38245.1
Piper betle	L12660.2	AJ235560.1	AF206992.1
Platanus occidentalis	L01943.2	U86386.2	U42794.1
Sabia sp.	L12662.2	/	/
Sabia swinhoei	/	AF093395.1	L75840.1|
Saruma henryi	L12664.1	AJ235595.1	L24417.1
Saururus cernuus	L14294.1	AF093398.1	U42805.1
Schisandra sphenanthera	L12665.2	AJ235599.1	/
Schisandra chinensis	/	/	L75842.1
Spathiphyllum wallisii	AJ235807.1	AJ235606.2	AF207023.1
Trithuria submersa	DQ915188.1	AJ419142.1	/
Trochodendron aralioides	L01958.2	AF093423.1	U42816.1
Welwitschia mirabilis	AJ235814.1	AJ235645.1	AF207059.1
Xanthorhiza simplicissima	L12669.2	AF093394.1	L75839.1
Zamia pumila	AY056557.1	AF188845.1	M20017.1

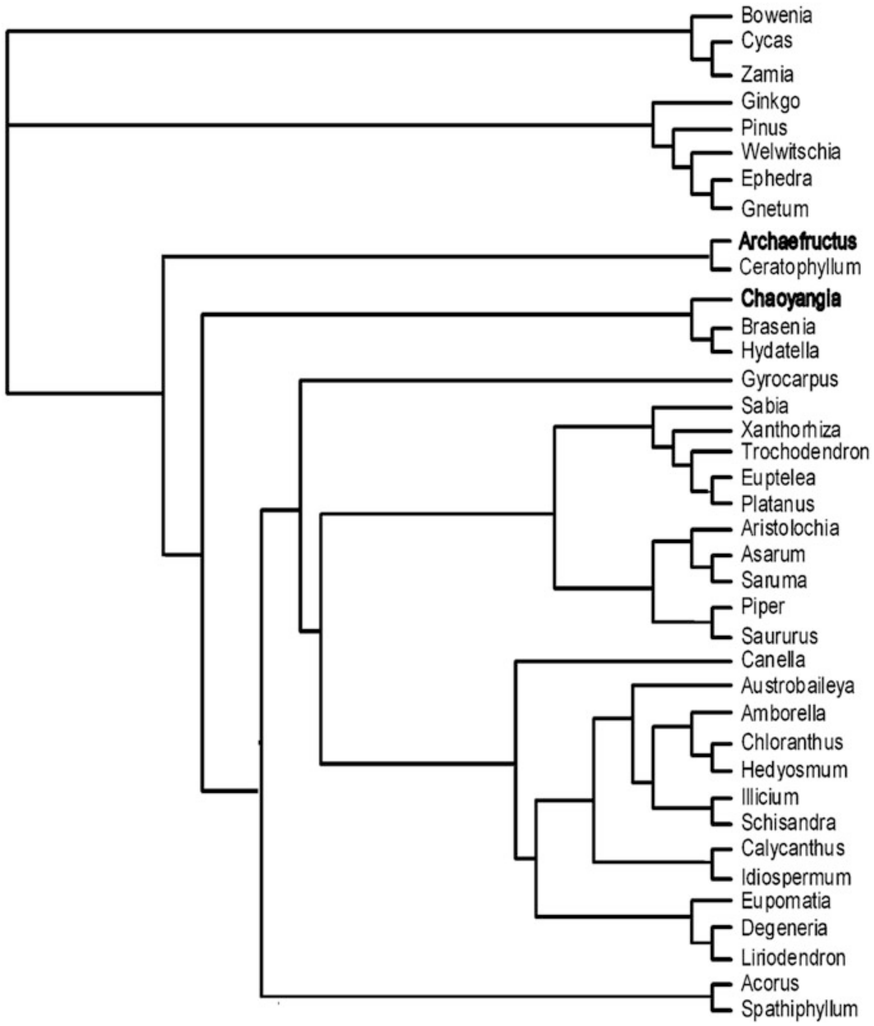


Fig. 5.15 Possible phylogenetic relationship among *Chaoyangia*, *Archaefructus*, and other seed plants, inferred based on morphological data. The relationships among living plants are fixed according to APG (2003)

produced by heuristic search of 1,000 replications, indicate that *Archaefructus* plus *Ceratophyllum* is the first branch followed by a lineage of *Brasenia* together with *Hydatella*. *Chaoyangia* becomes the third branch in six of the nine trees, and in the other three trees, (*Chaoyangia*, (*Brasenia*, *Hydatella*)) is the second branch (Fig. 5.15). Excluding *Archaefructus* under this circumstance does not affect the position of *Chaoyangia*, except that *Chaoyangia* becomes the third branch preceded by *Ceratophyllum* and (*Brasenia*, *Hydatella*) in all twelve trees. Furthermore, if *Hydatella* is excluded from the analysis by the same constraint, only one MP tree is produced from 1,000 heuristic searches, and this tree indicates that *Archaefructus* and *Chaoyangia* are the first and second branches, respectively, although *Brasenia* is now attracted toward the eudicots. This result is in line with the outcome of others based on other types of data (Crepet et al. 2004; Endress and Doyle 2009).

Since *Chaoyangia* demonstrates an affinity close to *Hydatella* based on morphological data, further constrained analyses were performed to examine the relationship among the ANITA species and the two fossil taxa. When the large groups above ANITA are constrained as ((Chloranthaceae, Magnoliids), (Ceratophyllaceae, (Monocots, Eudicots))) according to molecular results (Penaflor et al. 2007), all six trees indicate that *Archaefructus* takes the first branch followed by (*Brasenia*, (*Chaoyangia*, *Hydatella*)) and (*Amborella*, *Austrobaileya*, (*Illicium*, *Schisandra*)) as the second and third branch, respectively. If the *Archaefructus* and *Amborella* are fixed at the base, and the large groups above ANITA are also constrained as previously, *Archaefructus*, *Amborella*, and (*Austrobaileya*, (*Illicium*, *Schisandra*)) hold the first to third positions followed by (*Brasenia*, (*Hydatella*, *Chaoyangia*)).

The analyses (especially the constrained ones) based on morphological data strongly support a close affinity between *Chaoyangia* and *Hydatella*, as evidenced by 30 out of 123 morphological characters (namely, character No. 1–2, 4, 6–10, 12–15, 20, 41, 43–45, 53–54, 74–76, 79–80, 82–84, 87, 97, 108) shared between the two taxa. It seems unlikely that the basal position of *Chaoyangia* is spurious due to morphological homoplasy because the basal position of *Chaoyangia* remains stable even after the exclusion of *Hydatella* from the analysis, even though *Brasenia* is attracted toward eudicots under this condition.

Above all, in all the analyses, *Chaoyangia* is closely related to *Hydatella* while *Archaefructus* is frequently placed basalmost in angiosperms (Fig. 5.15). Considering the well-supported phylogenetic framework given by APG, (*Brasenia*, (*Chaoyangia*, *Hydatella*)) most likely composes the third branch after *Amborella* and *Archaefructus* in angiosperms.

This outcome supports the conclusion that *Archaefructus* is the basal-most angiosperm, as proposed by Sun et al. (2002). The basal positions for both fossil taxa are in accordance with their early age. It appears that phylogeny will be better reconstructed if the advantages of fossil taxa, which bear more historic information, and extant taxa, which have more molecular and morphological characters, are combined.

5.1.9 Problem Unsolved

Although its holotype is quite large, no one has yet seen a whole plant of *Chaoyangia*. The root and stem have yet to be discovered, and its leaves are not well preserved. Consequently, there are still a number of uncertainties, such as the rest of its anatomy, as well as its habitat and ecology. It is hoped that future exploration will reveal more aspects of this interesting fossil plant.

5.2 *Archaefructus*

5.2.1 Archaefructus, *a Great Discovery*

Archaefructus may be the most famous fossil plant of the past decade. It was excavated from the Yixian Formation outcrop near Huangbanjigou, Beipiao, Liaoning, China, published in 1998 by Sun et al. in *Science*, and it immediately caught the attention of media worldwide. Because of its early age, Sun et al. called *Archaefructus* the "First Flower". People from various disciplines, ranging from professional botanist to forensic professor from police academy, interpreted the discovery of *Archaefructus* from their own perspectives. It is not surprising that *Archaefructus* becomes the most controversial fossil plant in history.

As an angiosperm, *Archaefructus* attracted so much attention for the following reasons: (1) It was initially claimed as a Jurassic angiosperm; (2) It was the "First Flower"; and (3) It was supposed to represent the primitive state of early flowers. Sun et al. (1998) initially claimed that *Archaefructus* was a 145 Ma old fossil plant. Considering that the enigma of angiosperm origin has perplexed botanists for more than a century, it is not surprising that, when a "Jurassic angiosperm" was found, many people exclaimed that the so-called mystery of angiosperm origin was finally close to being solved. Anything that is number one deserves people's attention. The title "First Flower" also excited many people. Later progress in stratigraphy indicated, however, that the age of *Archaefructus* is close to 125 Ma (Dilcher et al. 2007). Whether or not *Archaefructus* is a Jurassic angiosperm now appears settled. According to the traditional orthodoxy, the conduplicate carpel of *Magnolia* is taken as the archetypal carpel. The carpels *Archaefructus* happened to be of this type (Sun et al. 1998, 2001, 2002), fitting in the expectations of many botanists, who got excited by this discovery of long-wanted fossil evidence. However, this concept is challenged by recent research on angiosperm phyolgeny (Qiu et al. 1999; Soltis et al. 2004, 2008) and fossil plants (*Xingxueanthus* and *Schmeissneria* from the Jurassic) (see Chaps. 6 and 8). It should also be kept in mind that *Archaefructus* was published after *Chaoyangia*, an angiosperm uncovered from the same locality (see above for details).

Since 1998, a total of three species have been published in the genus, namely *Archaefructus liaoningensis* (Sun et al. 1998), *A. sinensis* (Sun et al. 2002), and *A. eoflora* (Ji et al. 2004). All demonstrate similar assemblages of characters: dissected leaves, bisexual reproductive axes, clusters of 1–3 stamens, and carpels/fruits with single rows of ovules/seeds (Sun et al. 1998, 2002; Ji et al. 2004).

Archaefructus liaoningensis, the first species, was found near Huangbanjigou, Beipiao, Liaoning, China, and the specimen is incomplete. According to the latest research, *A. liaoningensis* may be described as follows. Main fertile shoots commonly have lateral fertile shoots. Lateral shoots are borne in the axils of leaves. The main fertile shoot is subtended by a leaf. Main shoots up to 85 mm long and 3 mm wide basally. Fruits are attached by pedicles. Fruits are larger basally, each containing two to four seeds, with finger-like prominences extended about 1 mm above its apex. The fruits are derived from conduplicate (?) carpels. Both main and lateral shoots terminate in numerous fruits. Fruits are crowded at the shoot apex and decrease in size distally. Fruits near the apex have only two seeds. Seeds are obliquely orientated in the fruits, attached to the abaxial (?) side. Seeds may overlap each other or be distinct within the fruits. Epidermal cells are rectangular to polygonal, about 25–45 μm by 12–20 μm. Anticlinal cell walls are sinuous and cutinized. Ten to twelve short stalks are located below a 15 mm-long fruit zone. These stalks usually have two (one to three) stamens. Stamens are deciduous as the shoot matures. A stamen consists of a short filament and a basifixed anther. The anthers may have two distinct parallel thecae, each containing two longitudinal pollen sacs. The in situ pollen is more or less elliptic. The pollen appears monosulcate with a verriform or fossulate/rugulate exine pattern. The leaves, attached or associated, are small, pinnately dissected three to four times. Multiple vascular strands are observed in the petiole. A leaf frequently subtends a central or lateral fertile shoot, and may be deciduous. Leaf petiole is about 10 mm long. Leaves are pinnately branched, with oppositely to alternately arranged leaflets, further dissected into rounded terminal lobes. (After Sun et al. 2002, and modified according to Ji et al. 2004).

Archaefructus sinensis, the second species in the genus, is based on a specimen of a more complete plant. Specimens are excavated from Beipiao and Lingyuan, Liaoning, China. *A. sinensis* may be described as follows. Plants are herbaceous, 30.1 cm long by 17 cm wide. Reproductive axes are subtended by vegetative shoots. Main axes are 3 mm wide basally, narrowing gradually upward to 1 mm wide. Roots are poorly developed, consisting of a primary and few lateral roots. Leaves are dissected two to five times, and their petioles vary in length. Basal leaves have long petioles and those near reproductive organs have short petioles. Ultimate leaf segments have rounded lobes about 2 mm long by 0.3 mm wide. Lateral branches diverge from the main stem at an angle of 30–35°. Each lateral branch has a terminal fertile portion. Fertile axes terminate in numerous small carpels, which are subtended by several short, blunt, helically arranged stalks, each bearing two stamens. Carpels are small when anthers mature. Carpels are helical, whorled, or opposite in arrangement. Carpels mature into elongate follicle-like fruits containing 8–12 seeds. A stamen consists of a short fine filament and a broad long anthers ending with a prominent tip. No petals, sepals, or bracts are seen. (After Sun et al. 2002, and modified according to Ji et al. 2004).

Archaefructus eoflora (Fig. 5.16), the third species in the genus, is based on a specimen of a whole plant. It is excavated from Sihetun, Beipiao, Liaoning, China. According to Ji et al. (2004), the stratum yielding this fossil plant is below those yielding *A. liaoningensis and A. sinensis,* implying this species is older than the above two species in the same genus. Ji et al. (2004) provided a very detailed description of the specimen. According to Ji et al. (2004), *Archaefructus eoflora* is different from *A. sinensis*, which is a whole plant, in several characters. (1) In shoot system, *A. eoflora* has a pseudo-indeterminate rhizome-shoot system with lateral fertile shoots growing out from the rhizome top, while *A. sinensis* has a "lateral branch system" with lateral branches originating from the axils of leaves inserted on a stem with long internodes. (2) In shoot organization, *A. eoflora*'s secondary

Fig. 5.16 Reconstruction of *Archaefructus eoflora*. From Ji et al. (2004), with permission from Dr. Qiang Ji and AGS

branches exhibit a determinate developmental pattern, while those of *A. sinensis* exhibit indeterminate developmental pattern. (3) Two vegetative shoots that emerge directly from the top part of the rhizome in *A. eoflora* are never seen in *A. sinensis*. (4) *A. eoflora* has bract-like structures subtending the male section or a lateral fertile branch on the main shoot, even covering the fertile bud, while there is no such leafy structure in *A. sinensis*. (5) *A. eoflora* has a shorter carpellate section (only about 1 cm long), while *A. sinensis'* carpellate section is much longer (up to 3 cm long). (6) *A. eoflora* has fewer (4–8) seeds per carpel than *A. sinensis* (8–12 seeds).

The study of *A. eoflora* reveals some information overlooked, or deemed uncertain in previous studies (Ji et al. 2004). *A. eoflora* and *A. sinensis* each has two carpels/fruits and one stamen borne on the lowest carpellate stalk, therefore Ji et al. called it the oldest known bisexual organ of angiosperms (Ji et al. 2004). The ovules/seeds of *A. eoflora* are orthotropous with their funiculi attached to the carpel midvein, i.e., laminar placentation and their micropyles (seed apices) facing toward the carpel tip. This information was added to the genus diagnosis in the emendation of Ji et al. (2004).

5.2.2 Controversies over **Archaefructus**

Despite three papers documenting *Archaefructus*, there are still controversies about these interesting fossil plants. The controversies focus on three issues. (1) is their age the Jurassic or Cretaceous; (2) do they have a flower or inflorescence; and (3) is their status (leaf, carpel) primitive or derived.

Since first published the age of *Archaefructus* has been a focus of debate in stratigraphy. The strata of the Yixian Formation have been repeatedly dated by various scientists, and the results range from 147 Ma (the Late Jurassic) to 105 Ma (the Early Cretaceous) (Peng et al. 2003; Wang et al. 2004). The debate became less heated after Dilcher et al. (2007), one of the groups favoring an earlier age for *Archaefructus* and the Yixian Formation, accepted 125 Ma as the age of the Yixian Formation. It should be kept in mind that the Yixian Formation includes a series of strata and its age should not be a point, rather a range in time. Recent study dated the overlying Jiufotang Formation to 120.3 Ma (He et al. 2004), and the below fossil yielding layer to 125–127 Ma (Peng et al. 2003). A recent ^{40}Ar/^{39}Ar dating indicates that the age of the Yixian Formation is between 129.7±0.5 and 122.1±0.3 Ma (Chang et al. 2009a), the Yixian Formation must be mainly Barremian.

As for *Archaefructus* bears whether flowers or inflorescences, there was a heated debate between the Dilcher-led group (Sun et al. 1998, 2001, 2002) and the Friis-led group (Friis et al. 2003, 2005, 2006). Each group cited many references and evidence to support its own claim, but neither gained a wide acceptance. The author thinks that this controversy, although interesting and well-reasoned, is not necessary: flower and inflorescence are two concepts that botanists abstracted from living angiosperms while unaware of the existence of fossil angiosperms. The two terms are mutually exclusive and discrete in living plants. If Darwinism is correct, then there should be a transition between various forms of organs and organisms, so so-called concepts, especially those based only on living plants, should be applied with an awareness that they are like names of colors in the spectrum: there are limited names/concepts but an infinite number of statuses to describe. Therefore forcing *Archaefructus'* reproductive organ into either category, flower or inflorescence, is like forcing a round peg into a square hole. This is not the first time palaeobotanists face such a situation: a century ago they had tried placing seed ferns into either ferns or seed plants. Ji et al. (2004) and Rudall et al. (2009) share a similar point of view on this. Rudall et al. (2009) think that "flower" is an oversimplistical term because reproductive organs in many early angiosperms, for example, Hydatellaceae, may have combined features of both flower and inflorescence. The author thinks that the best thing we can do is to depict and document *Archaefructus* as it is and let people understand it in their own way depending on their research background.

There are two interpretations on the leaf morphology of *Archaefructus*. One, that its leaf looks like those of some ferns, suggesting its primitiveness and possible seed fern ancestors (Sun et al. 1998), and the other, that its leaf is derived and specially adapted to an aquatic habitat, like *Cabomba* and *Ceratophyllum* (Friis et al. 2003). Current knowledge does not allow the author to favor either opinion.

The carpel of *Archaefructus* was initially claimed as primitive (Sun et al. 1998, 2001, 2002). This sounded reasonable only when it was assumed that *Magnolia* is the archetype of angiosperms. However, progress in angiosperm phylogeny in the past decade consistently indicated that *Amborella* rather than *Magnolia* is the basal-most angiosperm, implying that an ascidiate rather than a conduplicate carpel is the most primitive in angiosperms, and that intermediate between the fully-closed carpel in angiosperms and open ovuliferous unit in gymnosperms is a carpel sealed by secretion. This would mean that *Archaefructus* is more derived than Sun et al. (1998, 2001, 2002) assumed. If correct, it can be inferred from current knowledge that *Archaefructus* occurring 125 Ma ago is derived from a more primitive ancestor that must have existed long before. This inference is buttressed by an unexpected high diversity in the Yixian Formation and by early angiosperms from the Jurassic documented in Chap. 6.

The phylogenetic position of *Archaefructus* within angiosperms has been the focus of debate for the past decade. Sun et al. (1998) claimed it as the earliest angiosperm, and further reinforced this conclusion in 2002 based on cladistic analysis of morphological and molecular data. Their placement was frequently blamed on the miscoding of several characters, which, however, if "correctly coded", may not necessarily change the final conclusion. But it is true that Sun et al. (2002) included only limited morphological characters in their matrix. Recent cladistic work, including more morphological data and angiosperm phylogeny constrained as APG (2003), suggests that *Archaefructus* is indeed the basal-most clade in angiosperms, assuming that cladistics reveals the truth and that there are no Jurassic angiosperms. However, the last two assumptions may not be true. First, cladistics is an idealistic method because it assumes that the evolution is optimal and the most parsimonious. Recent ideas on evolution call for attention to that evolution is a suboptimal, but good-enough option under certain historical contexts (Dorit 2009). Therefore a cladistic conclusion that usually is unconditional or independent of historical background should be accepted with caution and be considered a reference rather than the ultimate truth. Thinking inertia and background should be integrated in the future cladistic analyses. Furthermore, recent progress in palaeobotany indicates that indeed there were angiosperms in the Jurassic (see Chap. 6). However, their influence on the tree of angiosperms is unknown at this time.

5.2.3 Diagnosis After Emendation

Since it was first published, the diagnosis of *Archaefructus* has been revised and updated several times (Sun et al. 1998, 2001, 2002; Ji et al. 2004). This brings its diagnosis more accurate and closer to completion. The following is the one summarized by Ji et al. (2004): Aquatic herbaceous plants with primary root and/or rhizome; reproductive axes forming a lateral branching system or a pseudo-indeterminate system associated with a main inflorescent axis in a cymose pattern. Reproductive axes branched or unbranched, proximally bearing petioles that hold pinnately-dissected leaves with lobes further divided 3–6 times into linear to slightly spatulate lobes, and distally bearing protogynous bisexual reproductive organs, including staminate section with helically arranged clusters of stamens and carpellate section with helically arranged carpels. Stamen clusters with 1–3 stamens on each peg-like stalk. Each stamen with a short filament, a dithecal tetrasporangiate anther, and a connective tip. Carpels/fruits commonly solitary, but occasionally in pairs on a short pedicle. Sometimes, bisexual cluster/flower with 1–2 carpels and one stamen. Orthotropous ovules in one row attached on the abaxial side inside each carpel. Fruits maturing distally (after Ji et al. 2004).

5.2.4 Ecology of Archaefructus

Based on the completely preserved specimen that even includes the original soil, Ji et al. (2004) reconstructed the ecology of *Archaefructus*. The preservation of roots, rhizome, and leafy shoots, including multiparted bisexual floral and fruit organs in different developmental stages, makes *Archaefructus eoflora* one of the most completely preserved plants. It is preserved in a tuffaceous claystone, associated with complete fish (*Lycoptera davidi*) and some unrelated fascicular needle-like leaves, implying a low hydrodynamic lacustrine environment. The original soil mass attached to its rhizome indicates that the plant was not transported far away from its habitat, which was probably close to or in an aquatic ecosystem. This is in agreement with Sun et al. (2002) and with the hypothesis that early angiosperms would be herbaceous with fast growth and reproduction, and thus would prevail over other plants (Taylor and Hickey 1990, 1992, 1996). The analysis of the subterraneous axis of *Archaefructus eoflora* suggests that this early angiosperm was a perennial herb and it was buried just before abscission of the fertile shoots. The lower parts of the shoots of *A. eoflora* bear the larger dissected leaves with longer petioles, while the upper leaves, smaller and less dissected, have short petioles. The upper leaves have a thin cuticle not observed on lower leaves. All of these characters suggest that *A. eoflora* might grow in water, with its floral parts extended above the surface, just like an extant emergent aquatic herb. Sun et al. (2002) also have given a similar reconstruction.

5.2.5 The Discovery of Archaefructus

In 1996, Mr. Zhiping Zhang, then an employee at the Nanjing Institute of Geology and Palaeontology, collected three specimens, including a specimen that later was identified as *Archaefructus liaoningensis*, from local people in Liaoning Province. Mr. Zhang presented the specimens to Dr. Ge Sun who was a research professor at the Institute. Dr. Sun received them and did not pay much attention before putting them in his drawer. Days later when Dr. Sun had time to check out the specimens, he was immediately attracted and excited by one of the three specimens, which "was a very strange fossil". "The fossil was unlike anything Sun Ge had ever seen before. At the top of two simple branches were structures that appeared to enclose seeds" (Hamilton 2007). The follicles preserved on the specimen are arranged along a branch, somehow looking like fruits of Legume. This is an exciting new feature never seen before in a fossil plant. Dr. Sun invited Dr. Zhekun Zhou at the Yunnan Institute of Botany to join the research. However, there was something bothering about this specimen: the original stratum information was missing! This was unacceptable for scientific publication. To ascertain the stratigraphy related to this fossil plant, Dr. Sun asked for help from Dr. Shaolin Zheng. Dr. Zheng was a palaeobotanists and stratigrapher in Shenyang, the capital city of Liaoning Province. Dr. Zheng was familiar with almost every single stratum in Liaoning. Under the request from Dr. Sun and with the limited clue from the sedimentary rock, Dr. Zheng and his wife, Dr. Wu Zhang, started their searching in western Liaoning. After 1 month digging in the now-famous village Huangbanjigou, Dr. Zheng and Zhang not only found the original stratum yielding *Archaefructus* but also measured the geological section and collected more specimens of *Archaefructus*. "After months of analysis, Sun Ge decided to share it with a fellow botanist in the United States" (Hamilton 2007). "Sun Ge brought the fossil to his longtime friend and colleague David Dilcher, of the University of Florida, for another opinion" (Hamilton 2007). Dr. Dilcher was one of the leading palaeobotanists working on early flowers. At the first glance Dr. Dilcher was fascinated by the specimens. Through the cooperation among the authors, Sun et al. managed to publish their result in *Science* on November 27, 1998. This became a masterpiece in palaeobotany. The news of this great discovery was soon spread all over the world.

5.3 *Sinocarpus*

Sinocarpus decussatus was uncovered from the Yixian Formation (Early Cretaceous) outcrop at Lingyuan and Beipiao, Liaoning, and Ningcheng, Inner Mongolia, all in China (Leng and Friis 2003, 2006; Dilcher et al. 2007). *Sinocarpus* and its associated leaves were documented by Leng and Friis (2003, 2006). Although initially reported in association, the relationship between the leaf and fruit of *Sinocarpus* was recently confirmed by Dilcher et al. (2007).

Like *Archaefructus*, as an early angiosperm, *Sinocarpus* is not free from controversy. Dilcher et al. (2007) thought that *Sinocarpus* was a junior synonym for *Hyrcantha*. They emphasized the similarities shared between these two taxa, including the terminal clustering of multiple carpels, partial basal fusion of individual carpels, the attachment and orientation of the seeds, the nature of stem branching and long slender stems (Dilcher et al. 2007). It is true that there are such similarities shared between them, but the carpels of *S. decussatus* are almost twice as long, have twice the number of ovules/seeds per carpel, and the ovules/seeds are larger than those of *Hyrcantha karatscheensis* (Dilcher et al. 2007). Some features documented by Krassilov et al. (1983) for *Hyrcantha* are never seen in *Sinocarpus*: (1) The stamen seen in *Hyrcantha* is, at the very least, missing in *Sinocarpus* (Dilcher et al. 2007). Dilcher et al. (2007) did not mention the stamen of *Sinocarpus* in their diagnosis and description. However, in a talk given at the 10th Mesozoic Terrestrial Ecosystem Symposium held in Spain in 2009 and in Dilcher et al. (2007), they mentioned the possibility of stubs at the bases of the carpels being relics of stamens. But it should be kept in mind that this was only a guess, and not yet a fact. (2) The "terminal scar" or "broad notch" at the tips of the gynoecia in *Hyrcantha* (Krassilov et al. 1983) is never seen in *Sinocarpus*, which has terminal crests instead. (3) No seed information is provided in the original publication on *Hyrcantha* (Krassilov et al. 1983). (4) The "compound ternate leaves" (Krassilov and Volynets 2008) of *Hyrcantha* at least appear different from those associated or attached to *Sinocarpus* (Leng and Friis 2006; Dilcher et al. 2007). These make the comparison with *Sinocarpus* hard to be convincing. Apparently, how to weigh the above similarities and differences is a challenge. The Dilcher et al. (2007) paper contained an error: on the p. 9371 are two completely different interpretations for the same structure in Fig. 1c (reaction tissue formed after insect feeding or egg-laying *vs* micropyle of ovule/seed). Whichever interpretation is correct, this appears to be a headache for the authors. This kind of minor error makes their point of view self-conflicting and leaves room for someone to cast doubt on the authors' attitude.

The following diagnosis of *Sinocarpus* was combined from Leng and Friis (2006) and Dilcher et al. (2007): Plant erect, with one to two main slender stems arising from a short taproot. Stems with alternating secondary branches at the dilated nodes. Nodes enlarged, encircled by thin sheathes (ocrea) and may be associated with or attached to small serrate margined leaves. Main axis and lateral branches of compound infructescence slender, with dilated or slightly dilated nodes with lateral units in a decussate arrangement or a combined arrangement of alternate and opposite branching. Infructescence compound, ebracteolate or possibly bracteolate. Pedicels of infructescences long and slender. Receptacle of flower small, probably slightly dome- to cone-shaped. Perianth present and perianth parts apparently free. Androecium not observed. Gynoecium superior and syncarpous basally, composed of (3-) 4 carpels in a whorled arrangement and fused along the ventral side for about half of their length. Each carpel contains two rows of anatropous ovules/seeds borne along ventral marginal linear placentae; each row with about 10 seeds. Seeds laterally flattened, sometimes embedded in an amorphous tissue. Seed surface smooth, without ornamentation other than faint outlines of epidermal cells.

5.4 *Callianthus*

5.4.1 *Previous Studies*

Erenia stenoptera Krassilov is a fossil taxon that was established based on material from the Early Cretaceous in Mongolia (Krassilov 1982). According to the original description, *Erenia* is a small (2 mm × 2 mm), stalked, winged fruit with bilocular endocarp and funnel-shaped, sessile stigma (Krassilov 1982). Wu (1999) described a specimen from the Yixian Formation outcrop at Huangbanjigou, Beipiao, Liaoning, China that is now found to be a infructescence of *Callianthus*, and named it *Erenia stenoptera* Krassilov. At first glance, the smooth membraneous wing and elliptical bilocular endocarp of *Erenia* might appear comparable to the fleshy envelope and two fruits in the "hip" of *Callianthus*. Probably due to these similarities and a dearth of specimens for more comprehensive study, Wu (1999) named this specimen *Erenia stenoptera* and this conclusion was later repeated in a monograph on the Jehol biota (Wu 2003).

5.4.2 Misunderstanding and Clarification

"*Erenia stenoptera* Krassilov", described by Wu (1999, Pl. XVI, Figs. 5,5a; 2003, Fig. 243), is from the holotype locality of *Callianthus*. Despite the superficial similarities mentioned above, the characteristic "funnel-shaped, sessile" stigma of *Erenia* is far different from the divergent papillate styles (stigma) in *Callianthus*. This character alone is enough to distinguish *Erenia* from *Callianthus*. Furthermore, *Callianthus* is distinguished from *Erenia* by its larger size, distinct stamens and tepals, and lack of a "stalk-avoiding" wing. The consistent differences between *Callianthus* (one complete flower and six infructescences examined) and *Erenia* suggest that they are two distinct fossil plants. Therefore the fossil formerly described as "*Erenia stenoptera* Krassilov" by Wu (shown in Fig. 5.25a, b) should be assigned to *Callianthus dilae* because it shares, besides the same locality, almost exactly the same gynoecium and infructescence morphology as the latter.

5.4.3 New Information

A recent study by Wang and Zheng (2009) is based on a more completely preserved specimen that has several floral parts physically connected. This study yields the following new information.

5.4.3.1 Physically Connected Male Floral Parts, Female Floral Parts and Tepals

Compared to previously reported flowers from the Yixian Formation, *Callianthus* is unique in its flower-like organization, composed of physically connected female floral parts, male floral parts, tepals, and pedicel. These floral parts are arranged center to periphery in the order listed above. This spatial order of floral parts resemble a typical angiosperm flower. In contrast, the arrangement of floral parts in *Chaoyangia* does not look like that in typical angiosperms, *Archaefructus* and *Sinocarpus* do not have all necessary floral parts to be typical angiospermous flowers. Therefore it is not surprising that *Callianthus* was claimed as the earliest normal flower (Wang and Zheng 2009).

5.4.3.2 Female Floral Parts

Wang and Zheng (2009) interpreted the central dark materials in Fig. 5.17a, b as two carpels/fruits, for the following reasons. (1) Two papillate styles at the top of the female floral parts are unlike the glabrous micropylar tube of Gnetales, which otherwise may look like styles in angiosperms (Yang 2007); (2) They are composed of two hemi-globular forms in the central position in the flower, a position expected for carpels/fruits in angiosperms; (3) They are physically connected to stamens, perianth, and pedicel; (4) The stamens, which are missing when mature (Figs. 5.25 and 5.26), are positioned peripheral to the carpels/fruits, an arrangement typical of angiosperms; (5) Their positions and morphology correspond closely to two fruits in other fossil infructescences (Figs. 5.25 and 5.26); (6) If the fleshy envelope were

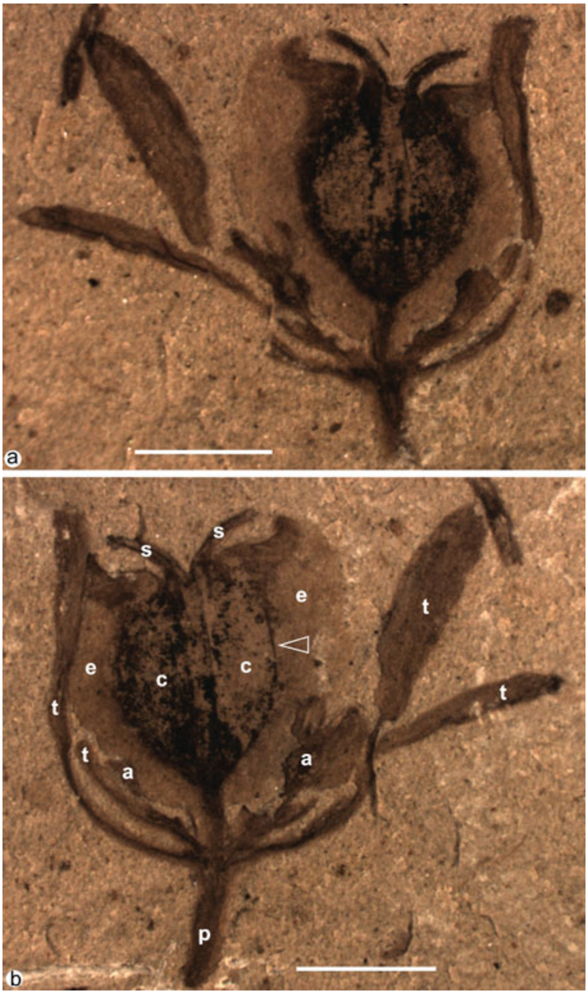
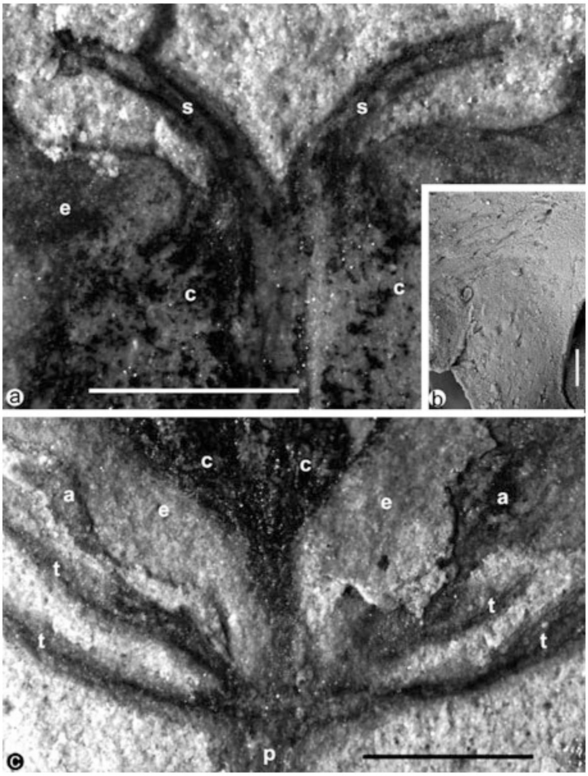


Fig. 5.17 Two facing parts of the same flower of *Callianthus*. Note the pedicel (p), tepals (t), stamens and anthers (a), fleshy envelope (e), carpels (c), their styles (s), and the abaxial vascular bundle of the carpel (*arrow*). Figures 5.17–5.24 are about the holotype (PB21047, NIGPAS). Bar = 2 mm. Courtesy of JIPB

Fig. 5.18 Styles and arrangement of floral parts. **A** The divergent styles. Note the relationship between the fleshy envelope (e), carpels (c) and styles (s). Bar = 1 mm. **B** Style surface covered with papillae scars of variable sizes. Bar = 10 μm. **C** The arrangement of the pedicel (p), tepals (t) in two cycles, stamens (a), fleshy envelope (e), and carpels (c). Bar = 1 mm. Courtesy of JIPB



compared to the outer integument, there would be two carpels/fruits per "hip" rather than one ovuliferous unit/seed per outer integument, as in *Gnetum* and *Welwitschia* (Gnetales); (7) Although sometimes there are two seeds surrounded by fleshy tissues in *Ephedra*, the clawed tepals in *Callianthus* are distinct from the triangular bracts *Ephedra*.

Degaging does not show any trace of a third style. The smooth connection (Figs. 5.18a, 5.25, and 5.26) between the two styles and their opposite arrangement also imply that there are only two styles in *Callianthus*. This is in agreement with the two persistent styles in other infructescences.

There is a vertical mark in Fig. 5.25a, which appears narrower, much more inconspicuous, and thus different from the gap between the carpels/fruits. In addition, the dark line on the dorsal of the carpel in Fig. 5.17b may represent a dorsal vascular bundle, therefore the mark in Fig. 5.25a is interpreted as a dorsal ridge on the fruit.

5.4.3.3 Styles and Stigmas

One of the characteristic features of *Callianthus* is its conspicuous divergent styles at the top of the flower/infructescence. No similar feature has been seen in gymnosperms, with the exception of some *Ephedra*. Also, micropylar tubes in

Ephedra are glabrous rather than papillate (Yang 2007). In *Callianthus* it is hard to differentiate the style and stigma. Papillae cover the whole length of the style. Most likely the whole style functions as a stigma in this plant.

The dimensions of the papillae on the styles are very variable even in the same SEM picture (Fig. 5.18b). This is unlikely due to preservation or other artifacts. It is more plausible to interpret the papillae as being conical in form. The different dimensions of similar papillae are the result of the papillae being cut at different orientations at different levels.

5.4.3.4 Stamens

In angiospermous flowers, normal stamens take a position between the gynoecium and perianth. This is a partial basis on which the stamens are identified in *Callianthus*. The other reason includes in situ pollen grains found in the anther (Figs. 5.21, 5.22, and 5.23). The repeated occurrence of pollen grains in the anther region and their absence in other regions reduce the possibility of dispersed pollen or contamination. Typical anthers of angiosperms are borne on filaments and have four pollen sacs (Eames 1961; Friis et al. 2006). This was once taken as a character used to identify a fossil angiosperm (Friis et al. 2006), but there are exceptions to this rule. Eames (1961) has mentioned that angiospermous anthers may have two or only one pollen sac. Therefore this criterion for angiospermous anthers based on a generalization of living angiosperms should be applied with caution to early fossil angiosperms. Although *Callianthus'* anthers are not yet completely understood, their identity is self-evident considering the existence of in situ pollen grains.

Currently only two stamens are visible in the *Callianthus* specimens (Fig. 5.17a, b), but the actual total number of stamens may be more.

A unique feature of *Callianthus* stamen is bristles at the top of the anthers, a character rarely, if ever, seen in angiosperms. The anther appendages reported in some angiosperms (e.g. Melastomaceae, Eames 1961) can easily be distinguished from the bristles in *Callianthus* by morphology, number, and spatial relationship relative to the anther. Therefore the nature of these bristles and their possible counterpart in extant angiosperms require further research.

5.4.3.5 Infructescences

Infructescences are the first part of *Callianthus* recorded in the literature (Wu 1999). At that time it was hard to say much about them, but recent progress (Wang and Zheng 2009) has revealed the plant's floral organization. Comparison between the isolated infructescences and flower suggests that the "hip" of *Callianthus dilae* falls from the pedicel when mature.

The subtle differences among Figs. 5.17, 5.25, and 5.26 suggest that these infructescences are preserved in different orientations. In Figs. 5.17 and 5.25a, b the bedding plane appears parallel to the plane of the styles, therefore there is a wide space between the two divergent styles. The infructescence in Figs. 5.25c and 5.26b appears slightly rotated around its vertical axis, thus the spaces between the styles and fruits are compressed and the two styles are at different levels. The infructescence in Fig. 5.26a appears to be rotated about 90° from that in Fig. 5.17a, b since the styles are almost completely eclipsed and the figure shows a ridge in the center of the fruit that is only seen at the margin in Fig. 5.17b. The invisibility of the styles in Fig. 5.26a implies that there is a raised ring at the top of the fleshy envelope that eclipses the style and this raised ring corresponds to the raised shoulders seen in Figs. 5.17a, b, 5.25a, c, and 5.26b. The constant presence of a fleshy envelope in all flowers and infructescences preserved at various orientations (Figs. 5.17, 5.25, and 5.26) suggests that the gynoecium/infructescence is of radial symmetry and that the gynoecium is almost completely surrounded by a fleshy envelope.

5.4.3.6 In Situ Pollen Grains

In situ pollen grains are found during degaging in one detritus from the stamen of the specimen. A total of five pieces of such detritus from the region near the stamen have been observed using an SEM without any chemical processing, but only one was found with in situ pollen grains. The pollen grains in the rock matrix are in clumps and with similar sculpture. In addition, pollen grains with similar sculpture are repeatedly seen in the anther region on the replicas (Fig. 5.23a–g). All these concurrences suggest that pollen grains are unlikely to be randomly present in the matrix and that the in situ pollen grains are not an artifact attributable to contamination.

Two of the in situ pollen grains demonstrate a triangular profile (Figs. 5.21c and 5.22c), suggesting possible triaperturate pollen. If this were truly so, *Callianthus* might be more or less related to eudicots. However, caution should be taken since an SEM cannot reveal details about the aperture of the pollen and only two of the pollen grains appear to be triangular.

The possibility of a trichotomosulcate aperture in Figs. 5.21c and 5.22c cannot be dismissed. Trichotomosulate pollen grains, thought transitional between monosulcate and tricolpate, are not restricted to a certain group and have been seen in basal eudicots and monocots, as well as magnoliids (Wilson 1964; Harley 1990, 2004; Rudall et al. 1997; Sampson 2000; Furness et al. 2002).

The situation becomes more complicated when triangular pollen in basal eudicots (Wilson 1964) and at least 27 genera of monocots (Harley 2004) is taken into consideration. For example, *Agrostocrinum scabrum* (Hemerocallidaceae) has rounded triangular pollen grains with trichotomosulcate aperture (Fig. 3c–f, Harley 2004), which are similar to those of *Callianthus* (Fig. 5.22c). This complicated situation cautions us against prematurely relating *Callianthus* to eudicots.

Apparently, the in situ pollen grains of *Callianthus* alone cannot provide enough information to resolve its affinity to angiosperms.

5.4.3.7 Tepals

The term “tepal” is preferred here because no significant morphological differentiation is seen in the perianth, although the tepals look more like typical petals than

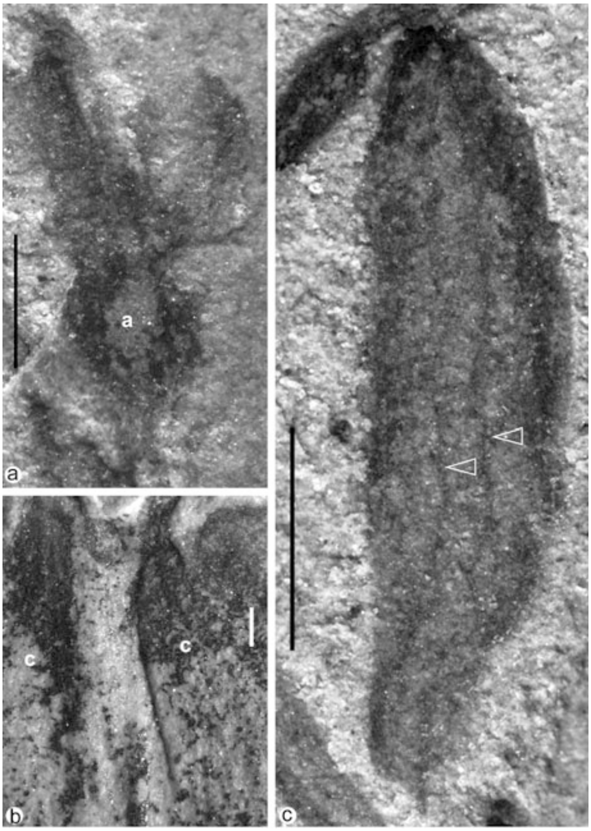


Fig. 5.19 Stamen, tepal, and gap between carpels. **A** One of the anthers enlarged from Fig. 5.17a. Note the globular anther (a), and bristles at the apex. Bar = 0.5 mm. **B** A detailed view of the gap between the carpels (c) in the flower shown in Fig. 5.17a. Bar = 0.2 mm. **C** The top portion of a tepal in Fig. 5.17a, with two parallel veins (*white arrows*). Bar = 1 mm. Courtesy of JIPB

like sepals. Currently only four tepals are visible in the specimens (Fig. 5.17a, b), but the actual number of tepals is assumed to be more.

The tepals of *Callianthus* have parallel venation (Fig. 5.19c). Usually the venation in perianth and leaf should be comparable. If missing leaves of *Callianthus* share a venation similar to that of the tepals, it may suggest that *Callianthus* appears more likely to be related to monocots rather than eudicots. However, it is also true that a similar parallel venation pattern is also seen in Gnetales (*Ephedra* and *Welwitschia*) (Biswas and Johri 1997; Yang et al. 2005) and *Chaoyangia* (see above for details) (Duan 1998). Apparently, further effort is required before a conclusion on the affinity of *Callianthus* within angiosperms can be reached.

5.4.4 Diagnosis

Callianthus Wang and Zheng
Type species: *Callianthus dilae* Wang and Zheng

Diagnosis: Flower small, bisexual, with a perianth, hypogynous, with a slender pedicel. Tepals in two cycles, spatulate, parallel veined, with a long claw and a round tip. Stamen composed of a filament and a globular anther, with numerous bristles at the apex. In situ pollen grains round-triangular. Fleshy envelope enclosing two separate carpels. Each carpel composed of a hemiglobular ovary and a papillate style. Infructescence hip-like, including two facing fruits with persistent styles. (According to Wang and Zheng 2009)

Remarks Two fossil taxa, *Spanomera* Drinnan, Crane, Friis et Pedersen (Drinnan et al. 1991) and *Lusicarpus* Pedersen, Balthazar, Crane et Friis (Pedersen et al. 2007), share similarities with *Callianthus*. However, careful comparison between *Callianthus* and these two taxa reveals that *Callianthus* is different from both of them.

Spanomera has an inflorescence of unisexual flowers related to Buxaceae found in the mid-Cretaceous of North America (Drinnan et al. 1991; Doyle and Endress 2010). Its gynoecium is bicarpellate, like *Callianthus*. However, *Spanomera* is unisexual, lacking an evident style and fleshy envelope surrounding the carpels, and without spatulate tepals. Therefore it is different from *Callianthus*.

Lusicarpus is a pistillate flower related to Buxaceae found in the Early Cretaceous of Portugal (Pedersen et al. 2007). Like *Callianthus*, its gynoecium has two carpels. However, it has a stout style, striate tricolpate pollen grains on the stigma, no fleshy envelope surrounding the carpels, no stamen, and no spatulate tepals. These differences distinguish it from *Callianthus*.

5.4.5 Description

Callianthus dilae Wang and Zheng
(Figures 5.17–5.27)

Synonyms:
Erenia stenoptera Krassilov, Wu (999, Pl. XVI, Figs. 5,5a)
Erenia stenoptera Krassilov, Wu (2003, Fig. 243)
Callianthus dilae Wang and Zheng, Wang and Zheng (2009, Figs. 1–5)
Diagnosis: (Same as that of the genus).

Description:
Holotype: The flower is small, bisexual, with perianth, hypogynous, pedicellate, 6.9 mm high, 7.3 mm wide (Fig. 5.17a, b). The pedicel is up to 1.8 mm long and 0.35 mm wide (Fig. 5.17a, b). Four tepals and two stamens are seen attached to the pedicel (Figs. 5.17a, b and 5.18c). The tepal is distinct, spatulate, with a long claw and a round tip, up to 6.5 mm long and 0.9 mm wide in the distal portion, arranged in two cycles (Figs. 5.17a, b, 5.18c, 5.19c, and 5.20a). Each tepal has two major parallel veins in the distal portion (Figs. 5.19c and 5.24d). A stoma is seen on a tepal, with stomatal aperture

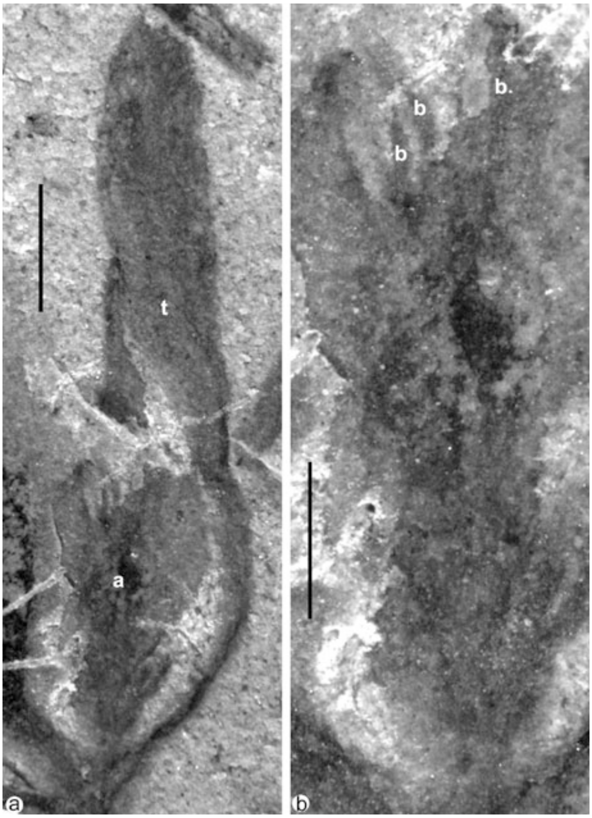


Fig. 5.20 Whole tepals and stamen. **A** Complete tepal (t) exposed after degaging. Note the spatulate shape, long claw, round tip, and its relationship to the stamen (a). Bar = 1 mm. **B** Stamen shown in Fig. 5.17b. Note its globular anther and bristles (b) at the apex. Bar = 0.5 mm. Courtesy of JIPB

1–2×7–8 µm (Fig. 5.24c). Stamens are attached just above the inner cycle of the tepals by a slender filament, which is about 1.2 mm long and 0.19 mm wide (Figs. 5.17a, b, 5.18c, 5.19a, and 5.20b). Anther is attached to the terminal of the filament, globular, about 0.5 mm wide, with numerous bristles up to 0.8 mm long and 60–65 µm wide at the apex (Figs. 5.17a, b, 5.19a, 5.20b, and 5.24a). Pollen grains in situ are compressed into various shapes, but two of them appear round-triangular, 28–32 µm in diameter (Figs. 5.21, 5.22, and 5.23). Similar pollen grains have been seen three times in the anther region on the replicas (Fig. 5.23f, g). Two stylate carpels are base-fixed in a cup-shaped fleshy envelope, which has a rough surface (Figs. 5.17a, b and 5.18a–c). The fleshy envelope is widest at the middle (about 4.2 mm wide) and about 3.75 mm wide at the top, 0.6–1.6 mm thick, with a 0.4 mm-high raised ring close to the upper margin (Figs. 5.17a, b and 5.18a). Each carpel is separated from the adjacent one almost to its base by a gap about 0.3 mm wide (Figs. 5.17a, b, 5.18a, and 5.19b). Each carpel includes an apical style and a basal ovary (Fig. 5.17a, b). The ovary is hemi-globular, about 3.1 mm high and 1.4 mm thick (Fig. 5.17a, b). The style is short, slightly curved, papillate, more than 1 mm long, and about 0.2 mm wide (Figs. 5.17a, b and 5.18a, b).

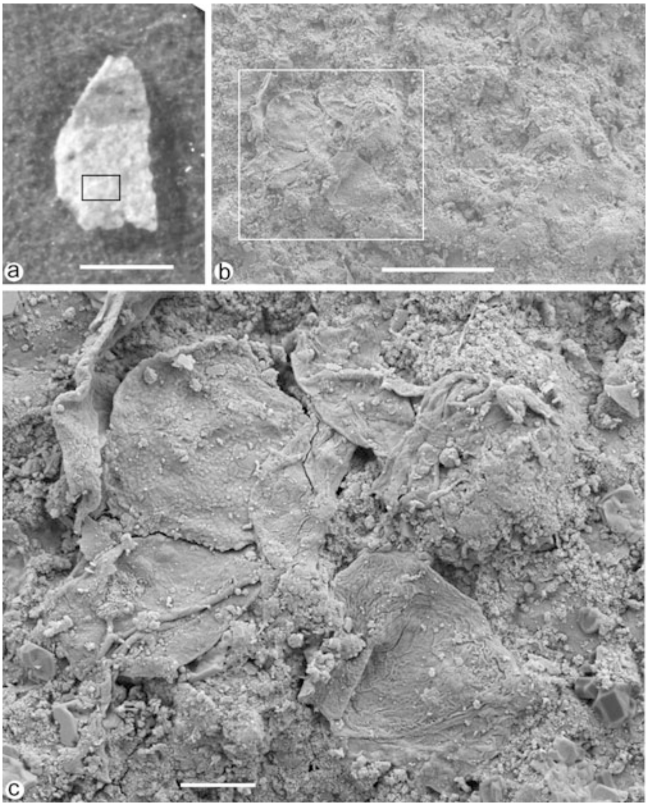


Fig. 5.21 In situ pollen grains. **A** Piece of rock removed from the anther region. The top dark mark (*top*) is left by a tepal. Bar = 0.5 mm. **B** Clusters of pollen grains visible on the surface of the rock, without chemical processing. Enlarged form the rectangle in **A**. Bar = 50 μm. **C** Pollen grains in the rectangle in **B**. Bar = 10 μm. Courtesy of JIPB

The papillae on the style are probably conical-formed, tapering distally, at least 5 μm long, covering the whole length of the style (Fig. 5.18b).

Further specimens: In morphology and dimensions, the infructescences look like the gynoecium, with a hip-like organization (Figs. 5.25 and 5.26). The "hip" includes two fruits and a fleshy envelope, about 4–5.8 mm high and 4–5.5 mm wide (Figs. 5.25 and 5.26). The fleshy envelope surrounds two facing fruits, and has a raised ring at the top (Figs. 5.25a, c and 5.26b). Each fruit is hemi-globular, with a persistent style more than 1 mm long and about 0.2 mm wide (Figs. 5.25a–c and 5.26b). Stamens and tepals are missing in the infructescences (Figs. 5.25a–c and 5.26a, b). There are traces of vascular bundles entering the fruits and envelope, respectively, in the proximal (Fig. 5.25c). Each fruit is 2.9–3.5 mm high, 1.3–1.7 mm thick, about 3.5 mm wide, separated by a gap in between, probably with a dorsal ridge (Figs. 5.25a–c and 5.26b).

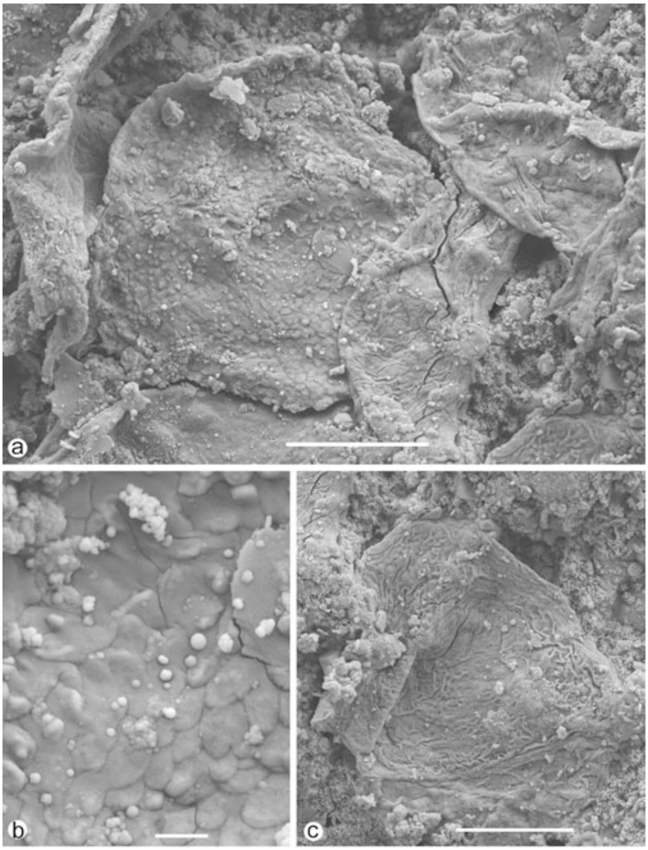


Fig. 5.22 Details of *Callianthus'* in situ pollen grains. **A** Pollen grains enlarged from Fig. 5.21c. Note the round shape of the central one. Bar = 10 μm. **B** Sculpture of the pollen grain in **A**. Bar = 1 μm. **C** Triangular pollen grain from Fig. 5.21c. Bar = 10 μm. Courtesy of JIPB

Holotype: PB21047a&b.

Further specimens: PB18320, PB21091a&b, PB21092, PB21390.

Locality: Huangbanjigou, Shangyuan, Beipiao, Liaoning, China (41°12′N, 119°22′E).

Stratigraphic horizon: the Yixian Formation (about 125 Ma), equivalent to the Barremian, Lower Cretaceous.

Depository: NIGPAS.

5.4.6 Development

The recognition of *Callianthus* is not based on a single specimen or a single type of specimens. Rather, it is based on many specimens that record different maturation

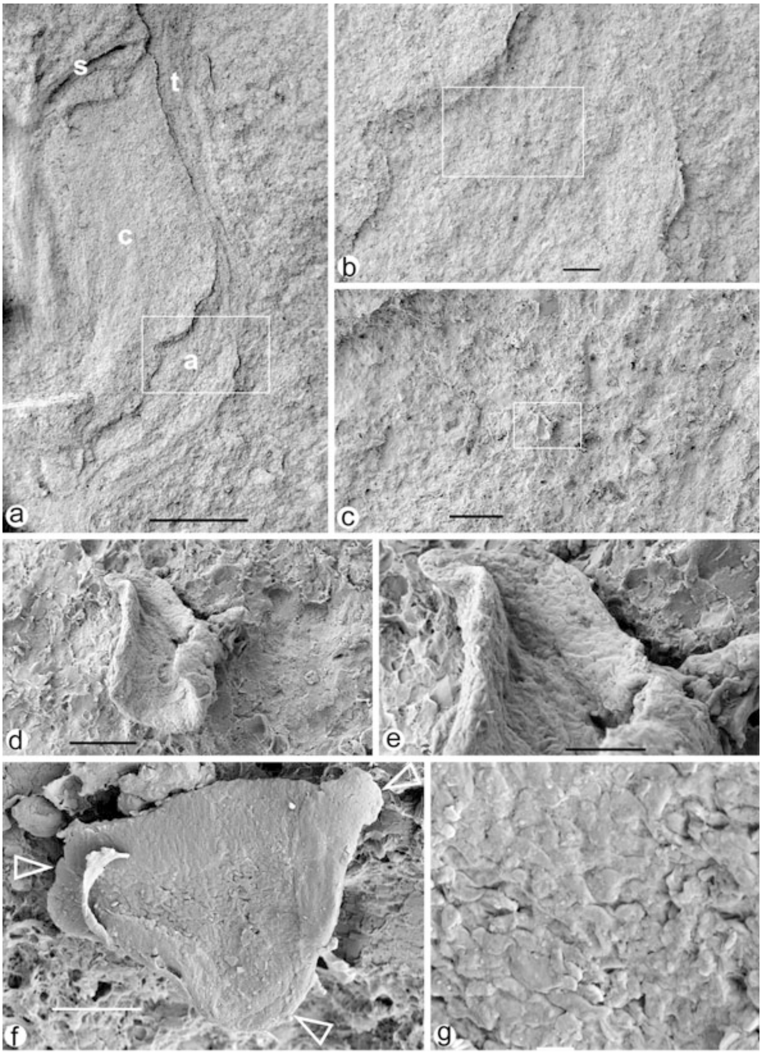


Fig. 5.23 In situ pollen grains seen on replicas. **A** Portion of the flower including anther (a), carpel (c), tepal (t), and style (s). Bar = 1 mm. **B** Details in the rectangle in **A**. Bar = 0.1 mm. **C** Details in the rectangle in **B**. Bar = 50 μm. **D** In situ pollen grain. Bar = 10 μm. **E** Sculpture on the pollen grain in **D**. Bar = 5 μm. **F** Round-triangular pollen grain in an anther. Bar = 10 μm. **G** The sculpture of the pollen grain in **F**. Bar = 1 μm. Courtesy of JIPB

stages and aspects of the same plant. This also explains why it was not correctly identified previously: a single specimen of infructescence cannot provide enough information allow anyone to confirm the real identity of a plant.

Comparison among different specimens that reflect different aspects and maturation stages of the same plant makes it possible for us to better understand the plant. The key specimens for *Callianthus* are the holotypes, which are the only specimens

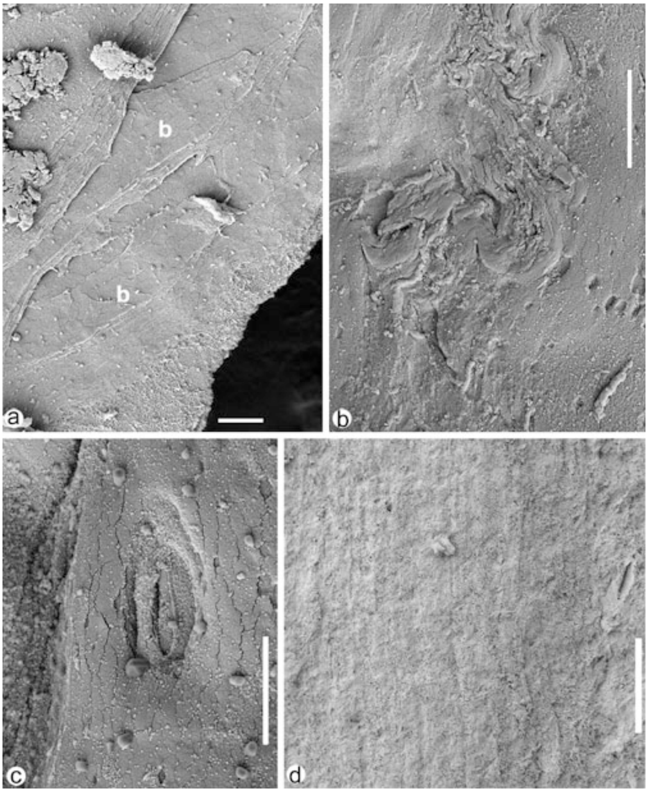


Fig. 5.24 Details of bristles, stomata, infructescence surface, and tepal veins. **A** Two bristles (b) at anther apex. Bar = 10 μm. **B** Clusters of trichomes on the surface of the fleshy envelope. The outside of the fleshy envelope is toward the left. Bar = 10 μm. **C** Stoma on a tepal. Bar = 10 μm. **D** Parallel veins in a tepal. Bar = 0.1 mm. Courtesy of JIPB

recording the flowering stage of the plant. The specimens show the various floral parts, including pedicel, tepals, stamens, and gynoecium, in physical connection. The connection among these floral parts is valuable in that it convincingly demonstrates a typical flower organization that has never before been seen in Barremian or earlier fossil plants. This may be the earliest flower with an organization typical of angiosperms. This is the key information that not only makes a correct identification possible but also makes the understanding of the development of the plant possible.

The differences among the different specimens that share certain common features and thus are identified as the same taxon make it possible for botanists and palaeobotanists to interpret the development of the plant. In the late stage of anthesis, probably after pollination, the flower of *Callianthus* still has typical floral parts and flower-like organization, as described above. It has a pedicel, tepals, stamens and gynoecium. Its ovary is enlarged probably due to its post-pollination stage and surrounded by the fleshy envelope. Its styles are divergent and have papillae on its

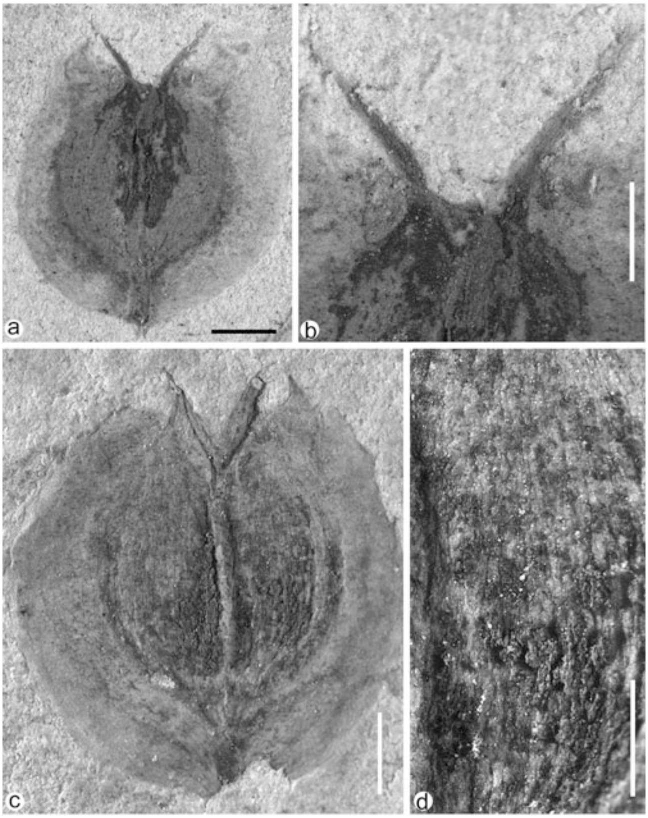


Fig. 5.25 Infructescences and their details. **A** "Hip" including two fruits with persistent styles surrounded by a fleshy envelope. PB18320, NIGPAS. Bar = 1 mm. **B** Two persistent divergent styles in **A**. Note the wide space between the styles. Bar = 0.5 mm. **C** Another "hip" including two fruits surrounded by a fleshy envelope and persistent styles. Note the space between two styles is narrower than in Figs. 5.17a, b and 5.25a, b. PB21092, NIGPAS. Bar = 1 mm. **D** Longitudinal striations on the cuticular relics of the seed in **C**. Bar = 0.5 mm. Courtesy of JIPB

surface. However, when the infructescences become mature, the tepals and stamens wither and are lost, and only the fleshy envelope and the fruits with persistent styles remain. Or to put it another way, the infructescences, including the fleshy envelope and carpel-derived tissue, fall off from the plant when mature. Future specimens will shed more light on this aspect of *Callianthus*.

5.4.7 Pollination and Dispersal

Currently, there is no evidence to indicate how *Callianthus* is pollinated. On one hand, the papillae are scattered all over the whole length of the style, suggesting that the stigma is not restricted to the terminal of the style. This feature appears more

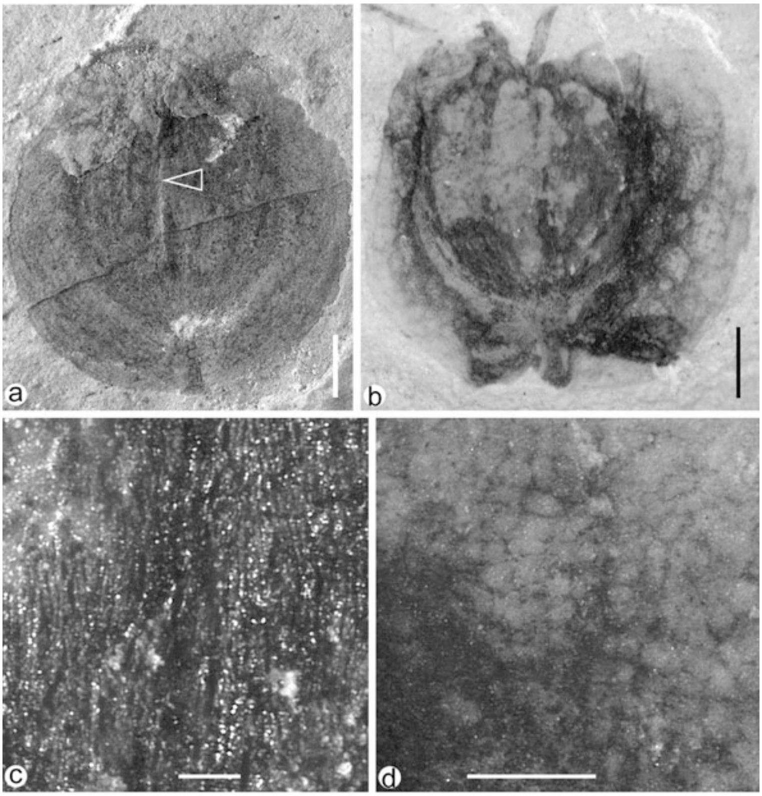
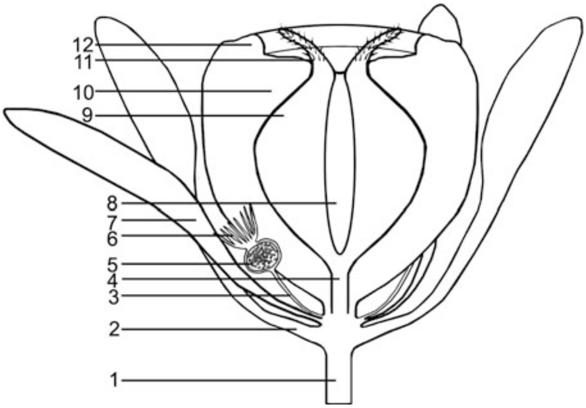


Fig. 5.26 *Callianthus* infructescences and details. **A** "Hip" with its top portion of the envelope preserved. Note the lack of apical depression, the dorsal ridge in the fruit (*arrow*), and a vascular bundle at the bottom. PB21091b, NIGPAS. Bar = 1 mm. **B** "Hip" with its styles partially preserved. PB21390, NIGPAS. Bar = 1 mm. **C** Cuticular details of the seed in **B**. Bar = 0.1 mm. **D** Reticulate pattern in the fleshy envelope in **B**. Bar = 0.5 mm. Courtesy of JIPB

Fig. 5.27 Sketch of the flower. Note the pedicel (1), outer tepal (2), inner tepal (7), filament (3), bristles (6) at the apex of the anther (5), vascular bundle (4) to the carpels, gap (8) between two carpels (9), fleshy envelope (10) around the carpels, papillate style (11), and a ring on the fleshy envelope (12). Courtesy of JIPB



like that of wind-pollinated flowers. On the other hand, the close spatial relationship between the stamens and the carpels, and bristles on the anthers imply possible animal involvement in the pollination. Otherwise the function of the bristles on the anthers would be hard to explain.

What is the function of the fleshy envelope in infructescences of *Callianthus*? This is a difficult question, but common sense and statistics on living plants can help. Most fleshy infructescences of angiosperms are dispersed with the assistance of animals. If this generalization can also be applied to *Callianthus*, at least it can be hypothesized that *Callianthus* may have obtained assistance from animals for its dispersal. This is in agreement with the conclusions based on a study of Early Cretaceous fossil angiosperms in Portugal (Eriksson et al. 2000). Formerly, people thought that animal-assisted dispersal appeared much later in the history of angiosperms. This idea now appears facing more challenge from the fossil record.

5.4.8 Affinity

In palaeobotany there is no strict consensus on the definition of a flower. The definition by Friis et al. (2006) is: "The angiosperm flower is formed by carpels (pistillate organs) and stamens (staminate organs) that are often surrounded by a perianth." Although the accuracy and completeness of this definition might be debatable, this definition does reflect the image of a typical flower in the minds of the general public. There was no well-accepted typical flower (bisexual, with a perianth) from the Yixian Formation or older strata before *Callianthus*, since *Sinocarpus* includes infructescences associated or connected with leaves (Leng and Friis 2003, 2006; Dilcher et al. 2007) and *Archaefructus* has no typical floral parts, such as a perianth (Sun et al. 1998, 2001, 2002). *Callianthus* is the first in the Yixian Formation to meet the criterion of a flower suggested by Friis et al. (2006).

Callianthus is assigned to angiosperms based on the following reasons. (1) Its bisexuality is different from all known gymnosperms, except Bennettitales and Gnetales. (2) Interseminal scales, dome-shaped receptacle, as well as fleshy pollen organs frequently seen in Bennettitales are completely missing in *Callianthus*, and its two divergent styles distinguish it from Bennettitales. (3) Two divergent papillate styles, a pedicellate solitary flower, two fruits surrounded by a fleshy envelope, and spatulate tepals in *Callianthus* are in strong contrast to Gnetales with a single ovuliferous unit/seed with glabrous micropylar tube sessile in bract axil, seed surrounded by an outer integument, and triangular bract (Biswas and Johri 1997; Yang et al. 2003; Yang 2007). (4) The flower-like arrangement of floral parts typical of angiosperms is present in *Callianthus*. (5) Seed surrounded by a fleshy envelope is also seen in Ginkgoaceae, Taxaceae and Podocarpaceae (Chamberlain 1957; Bierhorst 1971; Tomlinson et al. 1991; Tomlinson 1992; Biswas and Johri 1997; Doyle 1998; Cope 1998; Tomlinson and Takaso 2002). While their fructifications may appear similar to those of *Callianthus*, two fruits per envelope, stamens, two divergent styles, several tepals in cycles, and their arrangement in the flower distinguish *Callianthus* clearly from these gymnosperms. In short, the similarities shared with angiosperms together with the differences from known gymnosperms place *Callianthus* with angiosperms, therefore *Callianthus* is currently the oldest normal flower, bisexual and with a perianth.

5.4.8.1 Morphological Data

The stamens and carpels of *Callianthus* are different from those of *Archaefructus* from the same locality (Sun et al. 1998, 2002; Ji et al. 2004). The same can be said for *Sinocarpus* (Leng and Friis 2003, 2006). This implies that our current understanding of early angiosperms is not enough to generalize a model or pattern for them. This unexpectedly high diversity of angiosperms in the Yixian Formation (Duan 1998; Sun et al. 1998, 2001, 2002; Leng and Friis 2003, 2006; Ji et al. 2004) and early record of eudicots (Brenner 1976; Drinnan et al. 1994; Pedersen et al. 2007), which is regarded more derived than the basal clade, all point to the existence of angiosperms before the Barremian. This conclusion is in agreement not only with insect and pollen record (Ren 1998; Wang et al. 2000), but also with the recent report of a Jurassic angiosperm (Wang et al. 2007b, c; Wang 2009; Wang and Wang 2010, Zheng and Wang 2010; Wang in press) as well as molecular analyses (Soltis et al. 2004; Smith et al. 2010).

A bicarpellate gynoecium is a feature frequently seen in basal eudicots (Buxaceae, Papaveraceae, Gunneraceae, Hamamelidaceae, Menispermaceae, Ranunculaceae, Circaeasteraceae, Sabiaceae, Chenopodiaceae, and Daphniphyllaceae) (Chu et al. 1991; Drinnan et al. 1991, 1994; Takhtajan 1997; Judd et al. 1999; Zhang et al. 2004), implying a possible eudicot affinity for *Callianthus*. However, caution is necessary since a bicarpellate gynoecium is also seen in Winteraceae and core eudicots (Brassicaceae, Salicaceae, Solanales, Lamiales) (Drinnan et al. 1991; Zhang et al. 2004; Judd et al. 1999). *Suckleya* (Chenopodiaceae) demonstrates an especially high resemblance to *Callianthus* in its divergent styles (Chu et al. 1991). All these are living taxa distinguished from *Callianthus* by the assemblage of style, stamen, perianth morphology, and lack of a fleshy envelope (Chu et al. 1991; Zhang et al. 2004; Judd et al. 1999). Drinnan et al. (1994) have pointed out that the fossils on the stem lineage leading to eudicots probably have only two carpels. In addition, lack of differentiation between sepals and petals, plus the presence of a few-parted, cyclic floral architecture in *Callianthus* also appear basic to eudicots (Drinnan et al. 1991, 1994). In the fossil record, *Callianthus* is similar to *Spanomera* and *Silucarpus* from the Cretaceous in bicarpellate gynoecium. Both of the latter taxa are related to Buxales (Drinnan et al. 1991; Pedersen et al. 2007). If indeed related to *Spanomera*, *Silucarpus* or *Nelumbo*, *Callianthus* would extend the fossil record of eudicots and lend support to the position of Drinnan et al. (1991, 1994). Considering the early fossil record of tricolpate pollen in the Early Cretaceous (Brenner 1976; Hughes 1994; Drinnan et al. 1944; Harley 2004), the possible relationship of *Sinocarpus* (from the same formation) to eudicots, and the above similarities shared between *Callianthus* and eudicots, future confirmation of a relationship between *Callianthus* and eudicots would not be surprising.

The following characters of *Callianthus* fit with the imagined primitive angiosperms based on an analysis of living angiosperms: bisexuality, small size, undifferentiated perianth, superior ovary, distinct tepals, moderate or low number of floral parts, distinct stamens, and medium-sized pollen grains (Doyle and Endress 2000; Endress 2001, 2008). Doyle (2008) also believes that "the ancestral flower had a perianth, more than one stamen, and more than one carpel". It appears that the morphology of *Callianthus* favors this generalization. *Callianthus* with tepals in whorls may represent the early-derived flowers with whorled arrangement, as suggested by Soltis et al. (2000) and Doyle and Endress (2010). *Callianthus* demonstrates a certain similarity to the eudicot mesofossils from the Early Cretaceous in Portugal and North America in its small flowers, few floral parts, and undifferentiated tepals (Friis et al. 2006). However, there are several unexpected features in *Callianthus*, including its fleshy envelope, stamen with bristles, and rounded triangular pollen grains (for a discussion on the latter two, see Sects. 5.4.3.4 and 5.4.3.6).

An interesting character of *Callianthus* is its fleshy envelope. Since there is no such part in the previous Cretaceous fossil record (Dilcher 1979; Friis et al. 2006), the fleshy envelope in *Callianthus* appears unique from a fossil perspective. Similar structure and organization are rare in extant angiosperms, although there is a floral roof in some Laurales (Heywood 1979; Endress 1980) and an expanded receptacle in *Nelumbo* (Nelumbaceae) (Hayes et al. 2000). But the tepals and/or stamens are inserted on the outer surface and margin of the floral roof in the Laurales (Endress 1980), unlike the situation in *Callianthus* where the stamens and tepals are distinct and arranged below the fleshy envelope (Figs. 5.17a, b, 5.18c, 5.19a, and 5.20b). The expanded receptacle in *Nelumbo* and fleshy envelope in *Callianthus* are similar to each other in their fleshy nature and spatial relationship relative to the carpels, stamens, and perianth. Furthermore the flowers in *Nelumbo* and *Callianthus* share the following features: long pedicel, bisexual flower, evident tepals, parallel veins in tepals, distinct stamens and tepals, and surrounded carpels. However, it is also true that their differences are also obvious: *Nelumbo* has many apocarpous carpels with sessile stigmas individually surrounded by the receptacle (Hayes et al. 2000), while *Callianthus* has only two paired stylate carpels surrounded by a fleshy envelope. In addition, *Nelumbo* has tricolpate pollen, while *Callianthus* does not. The above comparison might be superficial, and the similarities shared between *Callianthus* and these living plants might be a result of convergent or parallel evolution. If this were the case, then it would mean little to phylogeny, so it is premature to relate *Callianthus* to any living taxa.

The seeds of *Callianthus* are poorly preserved and only relics of cuticle is preserved (Figs. 5.25d and 5.26c), although they can be safely interpreted as seeds. The outlines of seeds in Fig. 5.25c, d indicate that the seeds are encased within an ovary. The apical styles of *Callianthus* are distinct from the micropylar tubes of *Ephedra*, the only known taxon that may have two style-like projections. This circumstantially suggests that the seeds and the ovules of *Callianthus* are enclosed, satisfying the definition for angiosperms proposed in Chap. 3.

The above discussions favor the placement of *Callianthus* in angiosperms. If these discussions are valid, *Callianthus* is important in that it, along with

Chaoyangia (Duan 1998), *Archaefructus* (Sun et al. 1998, 2001, 2002; Ji et al. 2004), and *Sinocarpus* (Leng and Friis 2003, 2006; *Hyrcantha*, Dilcher et al. 2007), is among the earliest wide-accepted angiosperms and thus shed new light on the early radiation of angiosperms. In addition, *Callianthus* currently is the earliest flower that shows a typical angiospermous floral organization not well demonstrated in many basal angiosperms (Rudall et al. 2009).

Even if the above discussions were flawed, the botanical value of *Callianthus* would not diminish. Rather it would be the monotype of a new, isolated, perplexing class of seed plants, and thus could provide raw material for the study of seed plant evolution, diversity, and phylogeny.

Chapter 6
Flower-Related Fossils from the Jurassic

The Jurassic is an important period for the origin of angiosperms. Several reproductive organs have been excavated from the Jurassic strata in western Liaoning and Inner Mongolia, China. *Schmeissneria*, *Xingxueanthus* and *Solaranthus* are three female or bisexual organs of plants found in the Middle Jurassic in China and the Early Jurassic in Europe. All of them demonstrate the existence of enclosed ovule in their organ, satisfying the criterion for angiosperms. Among them, *Schmeissneria* is seen in both the Middle Jurassic in China and Early Jurassic in Europe, and thus sheds much more light on the origin and early evolution of angiosperms.

6.1 *Schmeissneria*

6.1.1 Previous Studies

Schmeissneria was established as a ginkgoalean genus in 1994 by Kirchner and Van Konijnenburg-Van Cittert. However, its research history is almost as long as that of palaeobotany. The first fossil plant that has certain relationship with *Schmeissneria* had been described in a book titled *Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt*, the earliest accepted palaeobotanical literature according to the International Code of Botanical Nomenclature. In the second volume of the book, Presl (1838) identified a fossil coniferous male part called *Pinites microstachys* under *Pinites* Presl. He described it on page 201 as follows:

> *4. Pinites microstachys Taf. XXXIII Fig. 12*
> *P. amentis masculis verticillatis ternis oppositis sparsisque approximatis ovato-subglobosis obtusis sessilibus semen Pisi aequantibus, squamis ovatis acutis imbricatis laevibus, rachi flexuosa angulata.*
> *P. microstachys Presl*
> *In arenaceo Keuper dicto ad Reundorf prope Bambergam.*

X. Wang, *The Dawn Angiosperms*, Lecture Notes in Earth Sciences 121,
DOI 10.1007/978-3-642-01161-0_6,

Later Schenk (1867) studied materials similar to *Pinites microstachys* from Veitlahm near Kulmbach, Germany. He thought that some of them were female parts, and put Presl's male material in *Stachyopitys preslii* Schenk, a female part he associated with a conifer called *Schizolepis*. On page 185 Schenk described it as follows:

> *Stachyopitys* Schenk
> *Flores masculi laxe spicati spica pedunculata. Stamina plurima alterna axi flexuosa inserta. Filamenta patentissima, connectivum orbiculare. Antherae 10–12 loculares, loculi rima longitudinali dehiscentes stellatim expansae. Flores foeminei racemosi, strobili in ramis sessiles verticillati ovales. Squamae apice conniventes dorso crista percursae.*
> *1) Stachyopitys preslii*
> *Tafel XLIV Figs. 9-12*
> *In den Lettenschiefern der Rhaetischen Formation: Strullendorf bei Bamberg (M.S!Kr.S!B.S!) Veitlahm bei Kulmbach, Oberwaiz bei Bayreuth (M.S!Kr.S!Br.S!W.S!), Jaegersburg bei Forchheim (Popp!)*

Heer (1876) described a similar fossil as "an axis bearing rounded bodies showing a fine striation and oval impressions. . .[It]. . . consisted of scales and represented male flowers of a conifer" (according to Wcislo-Luraniec 1992).

In 1890, Schenk described *Stachyopitys preslii* as male fructifications of *Baiera*, and interpreted it as male flowers in their early stages (Fig. 6.1). This assignment was based on association only. However, this weakly founded interpretation prevailed in palaeobotany for more than a century, being repeatedly cited in various textbooks and literature (Gothan 1914; Emberger 1944; Gothan and Weyland 1954; Zürlick 1958; Nemejc 1968) until 1992 when Wcislo-Luraniec cast doubt on its male nature and interpreted it as a female organ of unspecified group. At about the same time, Schmeißner and Hauptmann (1993) reported reproductive organs of *Schmeissneria* physically connected to *Glossophyllum*-like leaves. This discovery had the potential to correct the erroneous connection proposed by Schenk in 1890.

Kirchner and Van Konijnenburg-Van Cittert (1994) established a new genus *Schmeissneria*, based on observation of the syntype, old collections, and more completely preserved new materials, including physical connected leaves and reproductive organs. Although winged seeds had never been seen in Ginkgoales and they had convinced themselves that this kind of reproductive organ was not connected with Baiera, they did not suspect the assignment by Schenk and continued to put it in Ginkgoales. This treatment seemed natural because the internal structure of the reproductive organ, important for systematics, was still missing for schmeissneria at that time, and the vegetative parts alone did not contain enough information to justify a new systematic position.

In 1993, I started my palaeobotanical career at the Institute of Botany, Chinese Academy of Sciences in Beijing after obtaining a master's degree in botany. My first assignment was categorizing the fossil materials from a locality called "Pan's

Site". There was an interesting story about these fossils. Dr. Guang Pan (also Kuang Pan) was a coal mine engineer. During the "Cultural Revolution", he was dispatched to the remote countryside in western Liaoning, China. The local people asked Pan to help locate a coal-bearing layer. This gave Pan the chance to survey the strata in western Liaoning, and he collected many fossils from a site near Sanjiaocheng Village, a suburb of Jinxi, Liaoning, China. After much study, Pan concluded he had found many angiosperms from the Middle Jurassic, publishing a number of papers on the topics (Pan 1984, 1990, 1996, 1997). His claims attracted attention as well as criticism. Dr. Ren Xu (1987) refuted his claims, which were found most time either poorly evidenced or misidentified (Xu 1987; Zheng et al. 2003). In 1988, with support from Dr. Xu and the Laboratory of Plant Systematics, Dr. Shuying Duan (Fig. 5.1a) and her colleagues went to this now famous fossil locality, Pan's Site, and collected many additional fossil specimens. After careful examination, they did not find any fossil that could be related to angiosperms. The collection was then left until I came to work on it. In it there were many common fossil plants typical of Middle Jurassic fossil flora. Many of them were very hard to identify, including those later recognized as *Schmeissneria* (Wang et al. 2007b, c), *Xingxueanthus* (Wang and Wang 2010), and *Anomozamites* (Zheng et al. 2003). Fortunately, the internal structure was revealed in broken flowers of *Schmeissneria*. It was very perplexing to relate the fossil to any known taxon until 1 day I read the article by Kirchner and Van Konijnenburg-Van Cittert (1994).

Combining the information in the paper and my own specimens, I wrote a paper on *Schmeissneria*, in which I boldly tried to emend a just established new genus. Rejected in early 1995, the work was suspended until 2005 when I returned to China from the US after I earned my PhD, studying in Dr. David Dilcher's lab. When I learned that there had been little progress on *Schmeissneria* since 1994, so I dusted off my manuscript and borrowed specimen from the Institute of Botany, and reshot general morphology pictures, this time with a digital camera not available for me in the 1990s. Combining former results on internal structures, my colleagues and I submitted the paper to BMC Evolutionary Biology. In this paper, the reproductive organ of *Schmeissneria* was interpreted as a bilocular ovary with a closed tip, a feature previously seen only in angiosperms. Our interpretation was met with a silence in palaeobotany and only Doyle (2008) briefly commented on the paper, admitting the fact that the ovules were enclosed in *Schmeissneria*, but he hesitated to accept it as angiosperms and put it in a possible stem group of angiosperms.

In this book, new data collected since 2007 are integrated with previous work. The new information is about the syntype and nine more specimens in Bayerische Staatssammlung für Paläontologie und Geologie, München (BSPG), 26 specimens from Stefan Schmeißner personal collection (SSPC), and nine specimens in Günter Dütsch personal collection (GDPC). Thanks to their granting access to these valuable specimens, many formerly unknown or perplexing aspects of *Schmeissneria* can be revealed here. These new data basically confirm the key angiospermous feature proposed by Wang et al. (2007b, c). Furthermore, flowers in anthesis and infructescences with in situ seeds make the understanding on the plant more complete.

6.1.2 Misunderstandings and Clarifications

Schenk (1890) related the now named *Schmeissneria* to *Baiera* based on their co-occurrence in the same stratum (Fig. 6.1). By combining the two, his intention was to give readers a more complete representation of ancient fossil plants, which are usually fragmented. This type of reconstruction can be misleading because palaeobotanists may combine parts of different plants to create a single plant and, if so, instead create a chimera. A recent error of this sort was a plant reconstructed by Pedersen et al. (1989a), as pointed out by Rothwell et al. (2009) and Tekleva and Krassilov (2009). The lesson is that we can only put full faith in those reconstructions based on connected plant parts. All other reconstructions should be viewed with caution. The sign that *Schmeissneria* had been erroneously assigned to Ginkgoales started to emerge about the time the new genus was established. First, the male nature of *Schmeissneria* had been disproved, or at least suspected by Wcislo-Luraniec (1992). Second, the relationship between *Baiera* and *Schmeissneria* had been nullified by several groups (Kirchner 1992; Schmeißner and Hauptmann 1993; Kirchner and Van Konijnenburg-Van Cittert 1994), although Kirchner and Van Konijnenburg-Van Cittert (1994) could not straighten it out probably due to a lack of taxonomic significance in characters they extracted from the specimens and out of respect to Schenk. This resulted in the ensuing errors in their interpretations of seed, fruit and infructescence of *Schmeissneria*.

Winged seeds have never been seen in Ginkgoales. The presence of the so-called winged seeds in *Schmeissneria* conflicted with its assignment to Ginkgoales. In addition, the so-called wings in *Schmeissneria* lack features of a typical seed wing

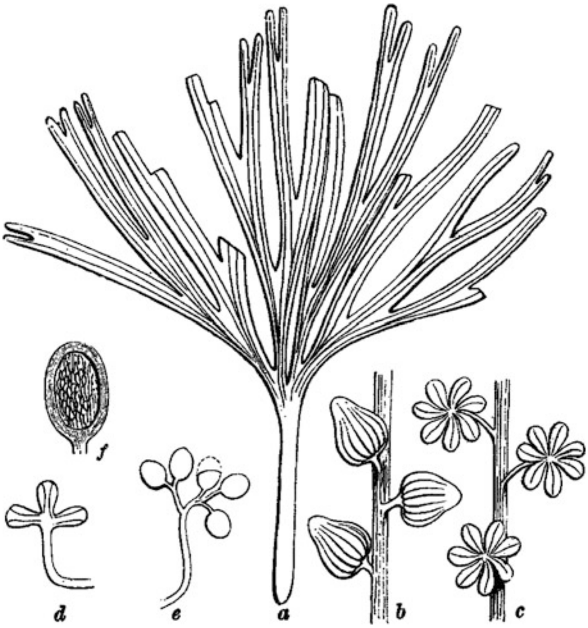


Fig. 6.1 *Schmeissneria microstachys* (**B**) was once thought to be a male organ (c) of *Baiera* (**A**) in its early development (from Schenk 1890)

Fig. 6.2 Mr. Stefan Schmeißner (**A**) and the stratum (**B**, *arrow*) yielding *Schmeissneria microstachys* at Pechgraben, Kulmbach, Bayer, Germany (50°00′20″N, 11°32′31″E)

in plants. First, as Kirchner and Van Konijnenburg-Van Cittert (1994) admitted, the so-called wings are quite variable in shape while a typical wing in plants has a relatively stable morphology (Figs. 6.3c, 6.8a–c, 6.9a–c, 6.10c, d, 6.14a–d, 6.15a–c, and 6.16d). Second, there is no vein in the so-called wings, while a seed wing usually has well-defined veins. Even if the longitudinal hairs were taken as veins, it would appear that the wing is composed solely of veins, an unusual situation in any plant (Figs. 6.8a–c, 6.9a–d, 6.14a–c, and 6.15a–c). Third, the so-called wings have no identifiable borders (Figs. 6.8a–c, 6.9a–c, 6.14a–c, 6.15a–c, and 6.16b). This is hard to conceive. Fourth, a wing, usually a two-dimensional object, is supposed to have a linear junction with a seed. The presence of hairs (according to my interpretation) over the surface of the so-called seed (Fig. 6.14b, d) conflicts with this interpretation. So the conclusion is that there is no seed wing in *Schmeissneria*, and the so-called wings are simply bundles of hairs.

Since Kirchner and Van Konijnenburg-Van Cittert (1994) interpreted *Schmeissneria* had winged seeds and a single taxon is not supposed to have drastically different seeds, the over 45 infructescences preserved on specimen BSPG 4713 became a headache for them. BSPG 4713 is a large piece of sandstone (45 cm ×1 cm) with more than 45 infructescences including more than 1,000 in situ seeds, a short shoot, and other associated fossil plants preserved on a single specimen (Fig. 6.11a–d). These infructescences with in situ seeds (see below) are hard to align with the authors' interpretation, which may explain why they chose to show only a very small portion of the specimen (Plate III, Fig. 2, Kirchner and Van Konijnenburg-Van Cittert 1994) and downplayed all other fossil materials on the same specimen. They only briefly mentioned their presence and interpreted some to be the result of desiccation.

Since establishing the genus, as more information accumulates, many changes have happened to the terms used to describe *Schmeissneria*. For the readers' convenience, the terms used at different times to describe *Schmeissneria* are summarized in Table 6.1.

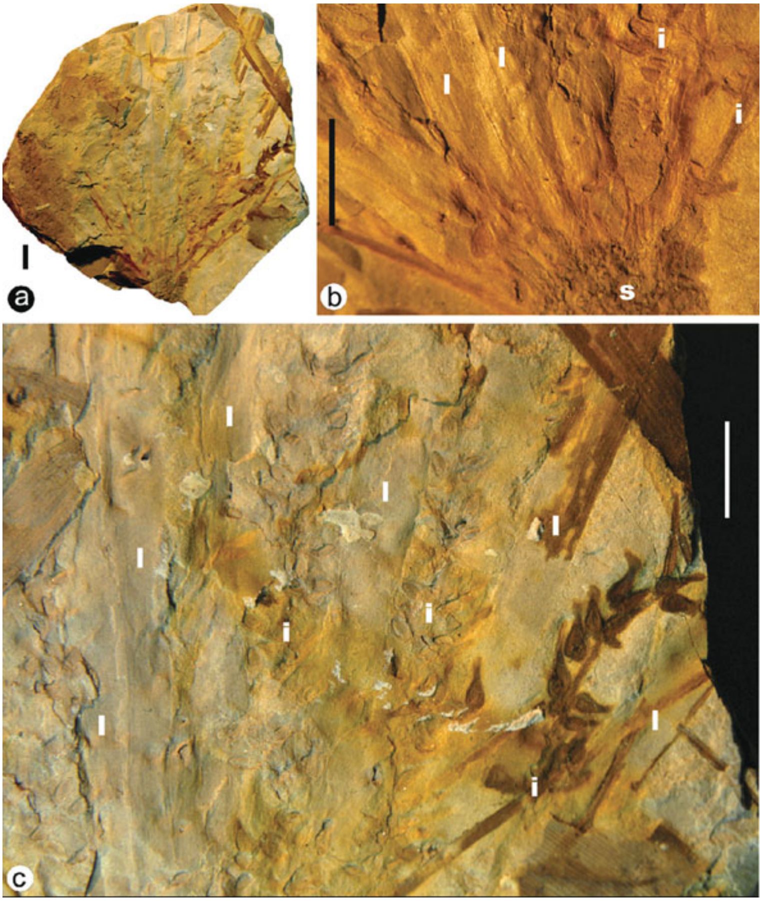


Fig. 6.3 A specimen of *S. microstachys* showing physically connected short shoot, leaves, and female inflorescences in various developmental stages. GDPC 122K04. **A** The specimen in general. Bar = 1 cm. **B** Physical connection among the short shoot (s), leaves (l), and inflorescences (i). Bar = 1 cm. **C** Leaves (l) and inflorescences (i) in various developmental stages. Bar = 1 cm

6.1.3 New Information

The specimens from China (*Schmeissneria sinensis*) and Germany (*S. microstachys*) studied here are virtually identical even though *Schmeissneria sinensis* and *S. microstachys* are from two different continents (Asia *vs* Europe) and geological epochs (the Middle Jurassic *vs* Early Jurassic). Consequently, the author will not distinguish between them in the following discussion, and they are distinguished from each other only in figure captions.

Recent studies on the German specimens deposited in BSPG, SSPC, and GDPC has yielded more information about *Schmeissneria microstachys*, including flowers

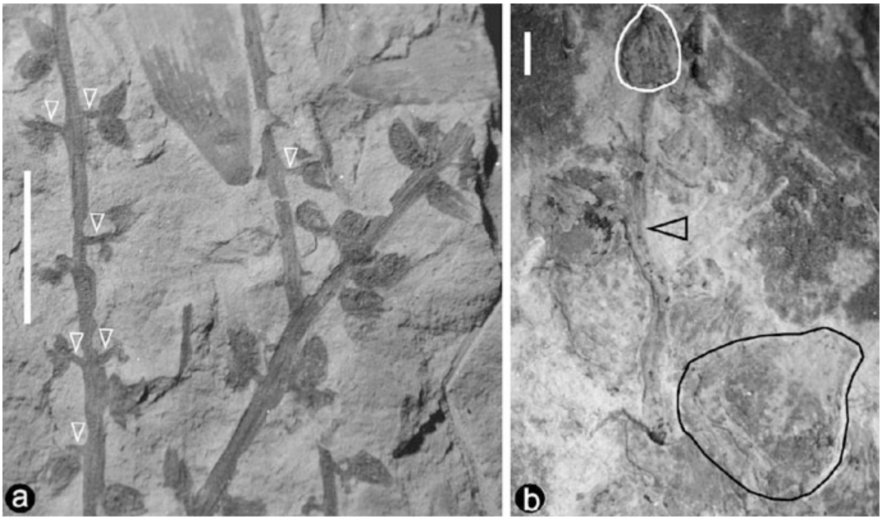


Fig. 6.4 Inflorescences. **A** three female inflorescence of *S. microstachys* preserved on the same specimen. GDPC S1K97. Note the common stalk (*arrows*) shared by two flowers. Bar = 1 cm. **B** Apical portion of a female inflorescence of *S. sinensis*. Note the inflorescence axis (*arrow*), and flower size (circled regions) decreasing distally. IBCAS 8604. Bar = 1 mm

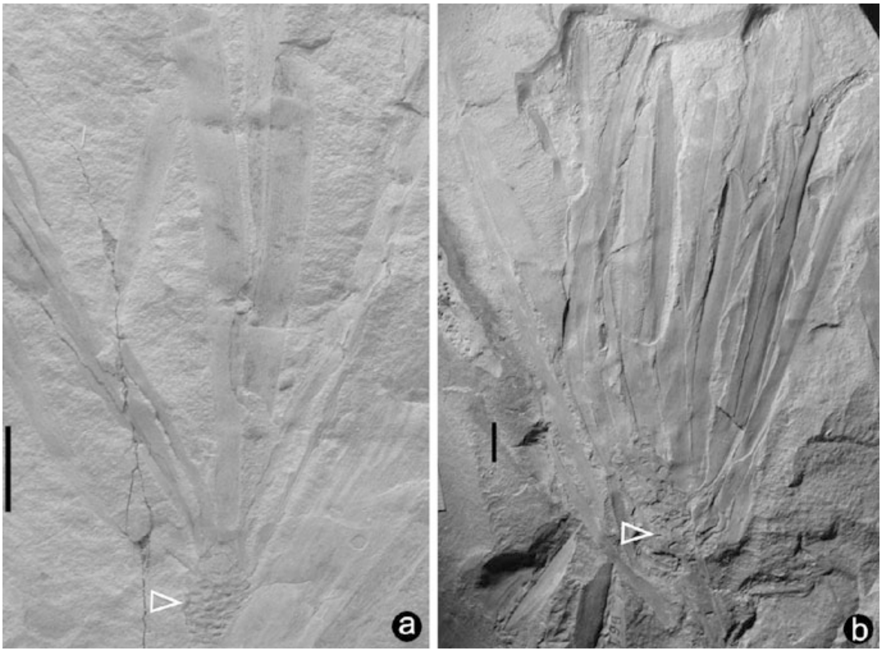


Fig. 6.5 Tufts of leaves attached to the apices of short shoots of *S. microstachys*. Note the leaf scars on the short shoot (*arrow*) and variation of the *Glossophyllum*-like leaves. SSPC G666/97, GDPC 111KI99. Bar = 1 cm

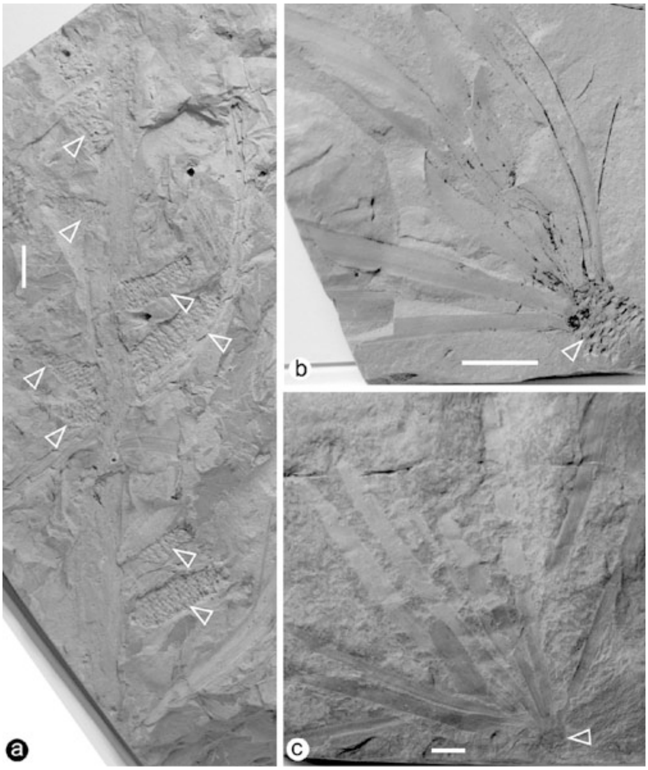


Fig. 6.6 Branches and leaves attached to short shoot of *S. microstachys*. **A** Long shoot with several short shoots (*arrows*) helically arranged. SSPC G254/90. Bar = 1 cm. **B**, **C** Tufts of leaves attached to the short shoot. Note the leaf scars on the short shoot (*arrow*) and the *Glossophyllum*-like leaves. SSPC G286/91, G475/92. Bar = 1 cm

in various developmental stages connected to the same short shoot and leaves, three tepals, hairs, in situ seeds with cellular details and micropyle. These new features will be discussed below.

6.1.3.1 Connected Vegetative and Reproductive Organs in Various Developmental Stages

As mentioned above, only physically connected parts are a reliable base for reconstruction. There appears to be no such problem for *Schmeissneria* since the genus was established based on physically connected reproductive organs and leaves on a short shoot. However, the female flowers of *Schmeissneria* were not previously well-documented and little attention was paid to variations in the flowers. Careful examination shows that the female flowers demonstrate various morphologies, for example, some of them appear to have hairs (Figs. 6.3c, 6.7b, 6.8a–c, 6.9a–c, 6.10c, d, 6.12b, 6.14a–d, and 6.15a–c) while others do not (Figs. 6.3c, 6.7a, c, 6.10a–d, 6.14a–d, 6.15a–c, and 6.16d), and some appear to have tepals (Figs. 6.15a–b and

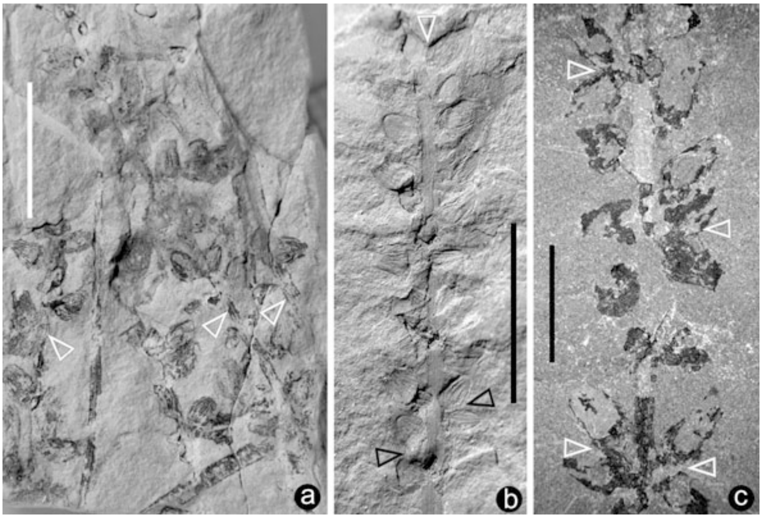


Fig. 6.7 Female inflorescences of *S. microstachys*. **A** Several coalified inflorescences (*arrow*) preserved in the same specimen. SSPC G111/90. Bar = 1 cm. **B** An inflorescence with several pairs of flowers (*arrow*). Note the longitudinal ribs on the flower surface. BSPG 2009 1 16. Bar = 1 cm. **C** A coalified inflorescence with paired flowers (*arrows*). BSPG 1972 VI 4. Bar = 5 mm. Courtesy of JSE

6.16b–d) while others do not (Fig. 6.14a–c). These differences, if found between isolated fossils, would be enough to justify new genera. Fortunately, one of the specimens in Dütsch's collection (Fig. 6.3a) has a short shoot, leaves, and female inflorescences in various developmental stages all physically connected. One of the inflorescences appears very conspicuous due to its red color, and it has numerous female flowers with bundles of hairs at their apices, while the other inflorescences in the same plant are less evident due to their dull color and they do not show any trace of hairs. This provides a unique opportunity for the author to reconstruct the development of the flowers (see below).

6.1.3.2 Young Female Flowers

The inflorescences of *Schmeissneria* are frequently preserved in whole (Figs. 6.3a–b, 6.4a, 6.7a–c, 6.8a–c, 6.9a–c, 6.10a–d, and 6.12a). The flowers in the inflorescences vary in size and dimension (Fig. 6.4b). One apparent variation in the flowers is that the apical flower is usually smaller than the proximal ones in the inflorescence (Fig. 6.4b). This variation becomes less evident in more mature inflorescences (Figs. 6.3, 6.4a, 6.7a, b, 6.8a–c, 6.9a–c, 6.10a–d, and 6.12a). It is logical to infer that the apical flowers are younger than the proximal ones.

Careful measurement of flowers in various developmental stages indicates that the diameter of the flowers ranges from 1.2 to 4 mm (Fig. 6.4b). This scope implies that the flowers in Fig. 6.13a, which has a diameter about 1.8 mm, should be close to the lower end of the size spectrum and thus immature and still early in their

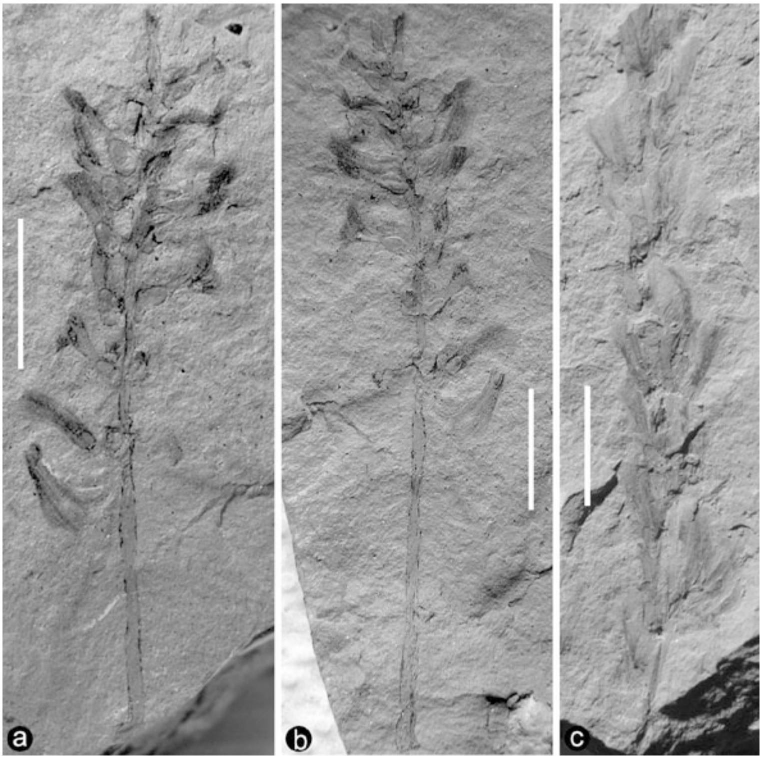


Fig. 6.8 Inflorescences of *S. microstachys* in anthesis. Note the hairs at the apices of the flowers. **A** Several flowers in the same inflorescence. SSPC G295/91. Bar = 1 cm. **B** The counterpart of the specimen in **A**. BSPG 2009 1 19. Bar = 1 cm. **C** Another flowering inflorescence. Note the vertically oriented hairs. GDPC S3K97. Bar = 1 cm. Courtesy of JSE

development. One of these young flowers appears round-triangular in shape in longitudinal profile, with less conspicuous longitudinal ribs and a narrow apical opening (Figs. 6.4b, 6.12c, and 6.13a). Tepals in these young flowers are hard to distinguish from each other. The ovary in a young flower is also round-triangular in shape (Figs. 6.12c and 6.13a). There are longitudinal ribs on the internal ovary wall in the distal portion (Fig. 6.13b), while the basal portion of the ovary appears to contain tissue that may fall off and leave a mark on the ovary wall (Fig. 6.12c). It is interesting that the ovary apex in young flowers is closed and a septum separates the ovary into two locules (Figs. 6.12c and 6.13b–c).

6.1.3.3 Apical Hairs

While Kirchner and Van Konijnenburg-Van Cittert (1994) described winged seeds in *Schmeissneria*, new study finds this interpretation hard to reconcile with observations. As Kirchner and Van Konijnenburg-Van Cittert (1994) realized that the so-called “wing” is highly variable and lacks a consistent morphology (Figs. 6.3c,

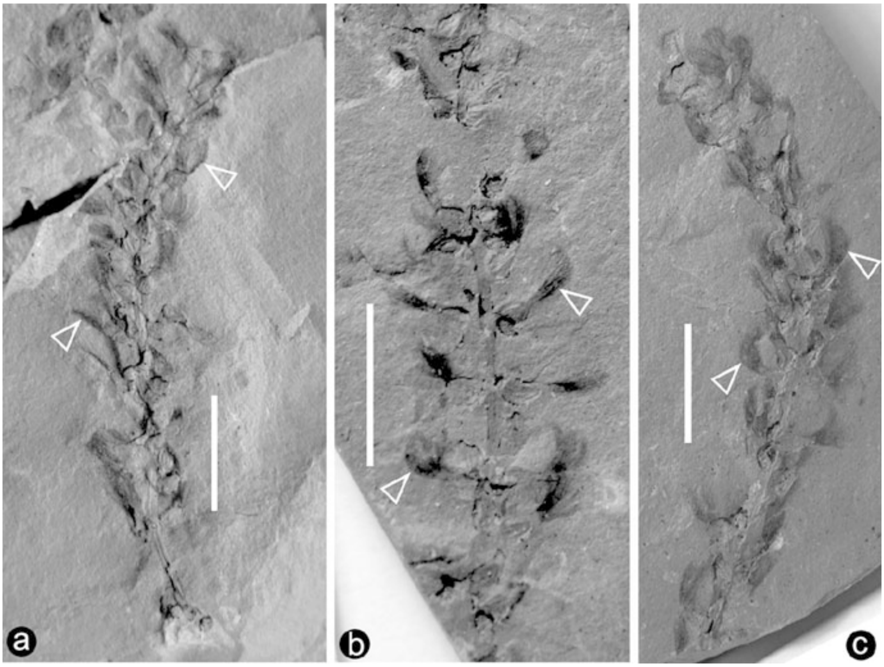


Fig. 6.9 Three more inflorescences of *S. microstachys* in anthesis. Note the variable deployment of the hairs (*arrow*) at the apices of the flowers. A SSPC G288/91. B SSPC G316/91. **C** SSPC G303/91. Bar = 1 cm

6.8a–c, 6.9a–c, 6.10c–d, 6.14a–c, 6.15a–c, and 6.16b, d). Examination of more specimens confirms that the so-called wing may appear brush-like, trifid, or in bundles (Figs. 6.8a–c, 6.9a–c, 6.14a–c, and 6.15a–c), constricted or not at the base (Figs. 6.14a–c, 6.15a–c, and 6.16b, d), and its "fibres" may be parallel (Figs. 6.8a–c, 6.14b, 6.15a–c, and 6.16b, c) or fanning out (Figs. 6.8a–c, 6.9a–c, 6.14c, and 6.16d). The "fibres" emanate from either the top (Fig. 6.14c), sides (Fig. 6.16b, c), surface (Fig. 6.14b, d), or even the base of the ovary (Fig. 6.16b). There is neither a clear border nor wing venation for the "wing". Since a seed wing usually expands only in two dimensions and it should have a linear junction on the seed surface, the distribution of hairs all over the ovary (Fig. 6.14b, d) is hard to conceive. These all contradict the previous wing-interpretation and strongly suggest that these are just bundles of hairs on the ovary.

Evidence from both German and Chinese specimens favors this new interpretation. Hair relics on the ovary have been documented for *S. sinensis*, but without an awareness of what they were and their taxonomic value (upper right of Fig. 2f, Wang et al. 2007b). One of the formerly hard-to-interpret features in *S. sinensis* (Fig. 6.12b) may well be a bundle of hairs.

All these together suggest that *Schmeissneria* has no wings but only bundles of hairs. As for the function of the hairs, since the hairs disappear as the fruits mature and appear to have no function in seed/fruit dispersal, it is possible that they helped

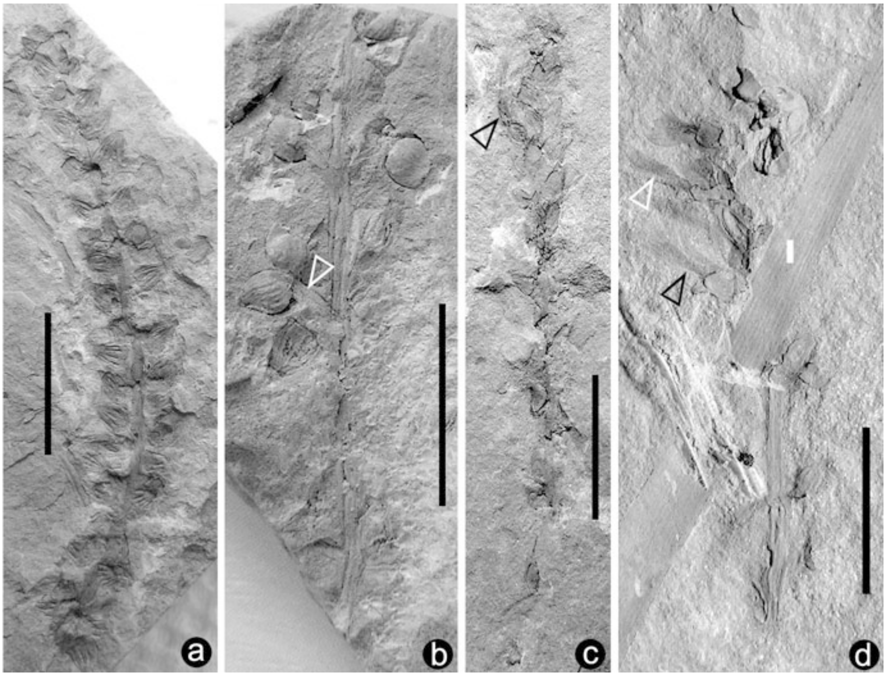


Fig. 6.10 Four female inflorescences of *S. microstachys*. Note the variable arrangement of the flowers. **A** An inflorescence with densely clustered flowers. Note the longitudinal ribs on the flower surface. BSPG. Bar = 1 cm. **B** The syntype of the genus. Note the long stalk (*arrow*) supporting the flower pair, their sparse arrangement along the inflorescence axis, and longitudinal ribs on the flowers. BSPG AS XXVI 23. Bar = 1 cm. **C** Another blooming inflorescence. Note one (*arrow*) of the flowers has hairs. BSPG 2009 1 17. Bar = 1 cm. **D** An inflorescence with blooming flowers (*arrow*) and associated leaf (l). BSPG 2009 1 18. Bar = 1 cm. Courtesy of JSE

to capture pollen grains during pollination. The occurrence of pollen grains on the distal inner surface of the tepals in *S. sinensis* (Figs. 3j–o, Wang et al. 2007b) is in line with this hypothesis. Interestingly, parallel to this, hairs are also seen on carpels of Urticaceae (Figs. 122E–F, Engler and Prantl 1889) and Ranunculaceae (Figs. 6I–K, 12D–E, Ren et al. 2010).

6.1.3.4 Infructescences

The infructescence of *Schmeissneria* was mainly overlooked until recently, although evidence has been available for over a century. The infructescence specimen studied by Schenk (Fig. 6.11a) is a large slab of sandstone from Veitlahm, about 45 cm by 32 cm. Despite more than 45 infructescences with at least 1,000 in situ seeds on this single specimen, they were ignored or downplayed by Schenk, probably because he

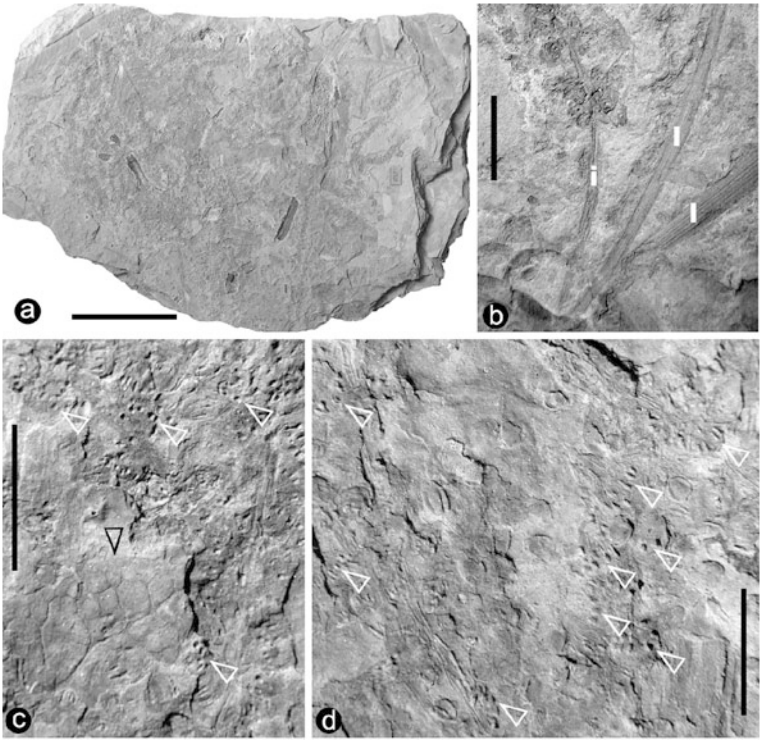


Fig. 6.11 Infructescences, fruits and in situ seeds of *S. microstachys.* BSPG 4713. **A** Sandstone slab with more than 45 infructescences on it. Bar = 10 cm. **B** Detailed view of the upper-right corner of the specimen in **A**, showing almost connected leaves (l) and infructescence (i). Bar = 1 cm. **C** A few of infructescences. Note the oval depressions left by groups of seeds (*white arrow*), and an associated leaf with reticulate venation (*black arrow*). Bar = 1 cm. **D** A few of infructescences with groups of in situ seeds (*arrow*, oval depressions). Bar = 1 cm. Courtesy of JSE

thought *Schmeissneria* stachyopitys was a male part. Recently, when Kirchner and Van Konijnenburg-Van Cittert (1994) examined and documented the same specimen, they also ignored almost all these infructescences and only showed an isolated short shoot in their publication (Plate III, Fig. 2), so the potential information on fruits of Schmeissneria again was not explored.

Reexamination of the specimen revealed that among the 45 inflorescences, one was almost physically connected to leaves (Fig. 6.11b). An infructescence usually has a slender axis (Fig. 6.11c–d) that is longitudinally striated as an inflorescence axis. Along the axis are clusters of fruits. The number of fruits per infructescence is usually more than ten. The dimension of these fruits is comparable to that of mature flowers in inflorescences (Figs. 6.10a–d, 6.11b–d, and 6.12a). Each fruit has an elongate round triangular profile with seeds in its basal portion. The number of seeds per fruit is usually more than four (Figs. 6.11a–d and 6.17a–d).

Table 6.1 Comparison of terms used to describe *Schmeissneria* in previous papers and this book

Kirchner and Van Konijnenburg-Van Cittert (1994)	Wang et al. (2007b)	This book
Cupule-ovule complex	Female organ	Flower
Female inflorescence	Female structure	Inflorescence
Cupule	Sheathing envelope	Tepals
Hole	–	Seed
Wing/fibres	Wing	Hairs
Ovule/seed	Central unit	Ovary
–	Septum	Septum
–	–	Fruit
Fructification	–	Infructescence
–	–	Wrinkles
–	Locule	Locule

6.1.3.5 Enclosed Seeds

Seeds of *Schmeissneria* could be alternatively interpreted as resin bodies. Since resin bodies are well known in Ginkgoales, this interpretation may appear reasonable and attractive considering the formerly assumed ginkgoalean affiliation of *Schmeissneria*. However, resin bodies lack cellular structure, especially internal cellular structure and it is clear that seeds of *Schmeissneria* have internal cellular structures (Fig. 6.18f–g). The co-existence of a rough, sometimes cellular, surface and a smooth surface in the same seed (Fig. 6.17e) would not be expected for resin bodies, but is conceivable for a seed. Seed coat-like layer (Fig. 6.18f) is not expected for resin bodies, either. In addition, the presence of a micropyle at one end of the seeds (Fig. 6.18a–c) further strengthens the case that the oval bodies in the fruits are seeds, since resin bodies do not have such or similar structures. Another alternative is that the seeds may be insect fecal pellets. This possibility can be easily eliminated due to the layered structure of the seeds (Fig. 6.18f) and presence of micropyles on the seeds (Figs. 6.18a–c) In short, the oval bodies within the fruits are fossil seeds of *Schmeissneria*. This is the first time that in situ seeds of *Schmeissneria* have been identified.

Seeds of *Schmeissneria* are situated in fruits (Fig. 6.17a–d). Although it may be safely inferred that the seeds are enclosed, a typological feature of angiosperms, caution should be taken when doing so. An enclosed seed does not always mean that its ovule is enclosed. A good example for this is *Caytonia*, whose seeds are enclosed in a cupule, but this enclosure is achieved only after pollination and its ovules are exposed to the exterior by channels (Harris 1940, 1964; Reymanowna 1973), consequently, *Caytonia* is now accepted as a gymnosperm rather than an angiosperm (Doyle 1978, 2006, 2008; Taylor et al. 2006b; Taylor and Taylor 2009). Therefore, to make a convincing case for *Schmeissneria*'s angiospermous affinity, enclosed seed alone is good but not enough.

Fortunately, the multitude of specimens available for study makes obtaining more convincing evidence possible. In all gymnosperms, the ovule is open to the exterior through an opening, no matter how narrow it is, at the time of pollination (Chamberlain 1957; Sporne 1971; Bierhorst 1971). The opening has to be large enough to allow pollen grains to pass through. There are many examples of preserved inflorescences of *Schmeissneria*, some of which with young flowers. As discussed above, two young flowers in *S. sinensis* (Fig. 6.13a) are in their early development. In one of the flowers (Fig. 6.13b, c), any opening larger than 20 μm (normal size of an average pollen grain), if present, should be visible. Careful examination failed to reveal any trace of such an opening at the ovary apex in *Schmeissneria*. Therefore the ovary apex of *S. sinensis* was physically closed, at least to pollen grains, probably before the pollination. This distinguishes *Schmeissneria* from *Caytonia* (Harris 1940, 1964; Reymanowna 1973) or other similar taxa, including seed ferns.

In one of the flowers of *Schmeissneria sinensis*, the rough internal surface (Fig. 6.12c) and the longitudinal ribs (Fig. 6.13b–d) in the upper portion of the ovary wall demonstrate a strong contrast to the smooth surface in the lower portion of the internal ovary wall (Fig. 6.12c), suggesting that the upper portion of the ovary is empty, while its lower portion is occupied by another inherent substructure (probably an ovule). This interpretation is further strengthened by seeds found in situ in the basal portion of the fruits of *S. microstachys* (Fig. 6.17a–d). Internal empty space is never seen in ovules or seeds, therefore making Kirchner and Van Konijnenburg-Van Cittert's (1994) winged seed interpretation implausible.

The distinction between these small flowers and the so-called winged large seeds (Kirchner and Van Konijnenburg-Van Cittert 1994), which are actually flowers in anthesis, implies the immaturity of the small apical flowers of *S. sinensis*. Considering all (Wcislo-Luraniec 1992; Kirchner and Van Konijnenburg-Van Cittert 1994; Wang et al. 2007b, c; Wang in press), it is safe to say that the immature ovaries of *Schmeissneria* have two locules and a closed apex, which becomes closed probably before closed pollination. This is a feature only seen in angiosperms and is also a feature defining angiosperms (Tomlinson and Takaso 2002; Wang et al. 2007b, c; Wang 2009; Wang in press).

Lack of a pollen entrance at the ovary apex in *Schmeissneria* may be interpreted in two ways: there never had been such an entrance or the entrance had been destroyed post-fertilization before fossilization. The latter situation is seen in *Gnetum* (Berridge 1911; Sporne 1971), *Ephedra, Pinus, Cedrus, Cephalotaxus* (Singh 1978), and possibly *Caytonia* (Harris 1940, 1964; Reymanowna 1973). The pollen canals in these plants are plugged or destroyed by tissue outgrowth or cell proliferation post-pollination, which is accompanied with morphological changes (Berridge 1911; Singh 1978). In *Schmeissneria*, however, there was no trace of abnormal tissue outgrowth or evident morphological changes at the apices of the flowers or fruits. Considering the smaller size and earlier developmental stage of these young flowers (Fig. 6.13a), it is most likely that they are still in a pre-pollination stage. This feature is what convinced the author that the ovules and seeds in *Schmeissneria* were enclosed, and that the flowers of *Schmeissneria* are angiospermous flowers.

It is interesting to note that the seeds in *Schmeissneria* are smaller (0.11–0.46 mm long) (Figs. 6.17a–g and 6.18a–g) and their seed coat is thinner (Fig. 6.18f) than most seeds seen in living plants. However, the size of *Schmeissneria* seeds falls well within the size range for angiosperm seeds. For example, orchid seeds may be as small as 0.05 mm long (Arditti and Ghani 2000). Moreover, studies indicate that small, thin-walled seeds were widespread in early angiosperms (Friis and Crepet 1987; Eriksson et al. 2000, 2008). Interestingly, their small size also reveals some information about their habit and ecology (see below).

6.1.3.6 Septum in the Fruits

Existence of a septum dividing an ovary into two locules was first recognized in young flowers of *Schmeissneria sinensis* by Wang et al. (2007b, c). Because such a division is not supposed to be seen in a gymnosperm seed or ovule, but frequently seen in ovaries of angiosperms, its presence was used as one of the key features to distinguish *Schmeissneria* from gymnosperms (Wang et al. 2007b, c; Wang in press). If *S. sinensis* and *S. microstachys* really are congeneric, it would be logical to see a similar divider in *S. microstachys*, in either an ovary or fruit. Therefore finding such a structure or its equivalent in *S. microstachys* could become a touchstone to test the validity of the conclusions reached by Wang et al. (2007b, c).

A new investigation of German specimens of *Schmeissneria microstachys* showed a septum extending from the base to the apex of the fruits (Fig. 6.17a–d, f, g). The septum is a very thin sheet with longitudinal wrinkles (Fig. 6.17b–d). The spatial relationship between the septum and seeds may be revealed by the relationship between the wrinkles and seeds. When a wrinkle on the septum runs above a seed, it can be inferred that the septum is positioned in the foreground (Fig. 6.17f). When such a wrinkle runs beneath a seed, it can be inferred that the seed is positioned in the foreground (Fig. 6.17g). When both above cases occur in a single fruit, as in Fig. 6.17d, f, g, it is safe to claim that a septum divides the seeds within a fruit into two groups. In addition, such an interpretation is in agreement with the presence of additional space behind the septum (Fig. 6.17b, c). The septum divides the fruit into two locules in *S. microstachys* (Fig. 6.17a–d, f, g), as it divides the ovary into two locules in young flowers of *S. sinensis* (Fig. 6.13a–d). This corroborates that the septum is a stable characteristic feature of *Schmeissneria*, rather than an artifact or misinterpretation of Chinese material. Furthermore, one advantage of the German specimens is that they contain such features of *Schmeissneria* in a different developmental stage: fruit.

6.1.4 Emended Diagnosis

Schmeissneria Kirchner and Van Konijnenburg-Van Cittert, emend. Wang

Type species: *Schmeissneria microstachys* Kirchner and Van Konijnenburg-Van Cittert, emend. Wang

Further species: Schmeissneria sinensis Wang

Diagnosis: Plants with long- and short-shoots. Leaves helically arranged on short shoots. Short shoots covered with leaf cushions. Leaves slender, slightly cuneiform, apex obtuse. Veins parallel, branching in the lower third of the

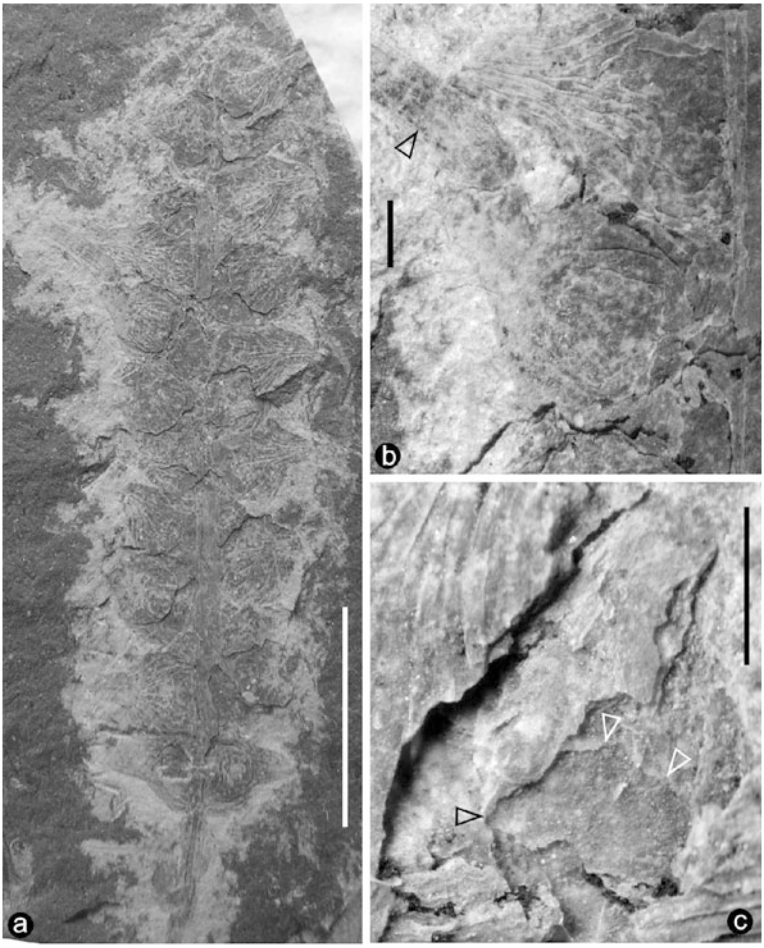


Fig. 6.12 Inflorescences of *S. sinensis*, and their details. IBCAS 8604. **A** Inflorescence with densely clustered flowers. Bar = 1 cm. **B** Detailed view of two flowers with evident longitudinal ribs from the *upper left* in **A**. Note the possible hair bundle (*arrow*). Bar = 1 mm. **C** Broken flower showing internal septum (*black arrow*), from the *middle left* in **A**. Note the shadow cast by the raised septum to its *right*. The internal wall of the ovary base is smooth due to mark (*white arrow*) *left* by fallen tissues. Bar = 1 mm. Courtesy of BMCEB

lamina. Female inflorescence spicate, with a slender axis. Axis of the inflorescence with longitudinal striations. Flower pairs borne on stalks helically arranged along the inflorescence axis. Flower with an ovary surrounded by three tepals. Ovary bilocular, subdivided by a vertical septum, with a closed apex, sometimes bearing hairs at its top. Hairs long, narrow, straight, scattered on the ovary. Fruit with two locules, subdivided by a septum, enclosing several seeds. Seeds very small, elongate or oval in shape, round in cross section, with a smooth thin seed coat, enclosed in the fruit.

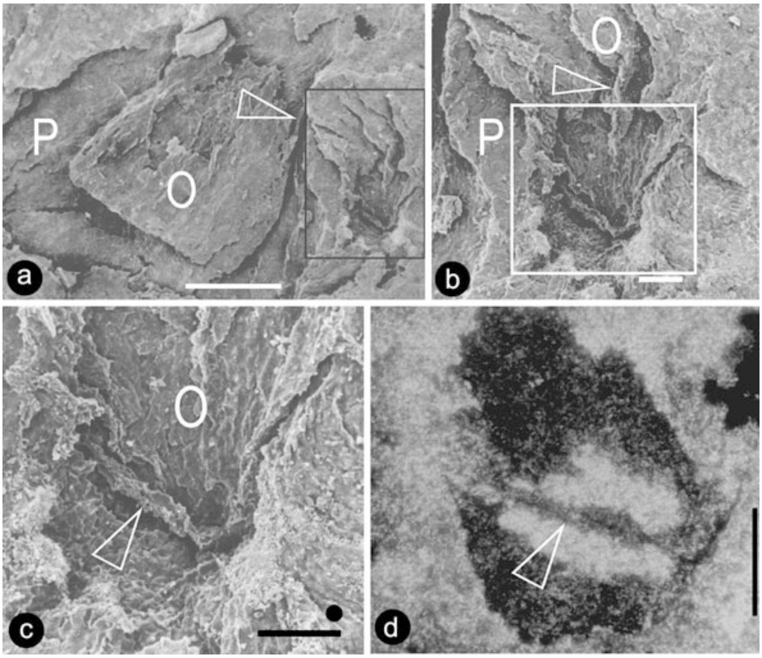


Fig. 6.13 Young flowers of *S. sinensis* showing closed ovary tip. IBCAS 8604. **A** Two young flowers, one in vertical view and the other (*in rectangle*) in cross view. Note the ovary (O) surrounded by the perianth (P and *arrow*). Bar = 0.5 mm. **B** Detailed view of the flower in *rectangle* in **A**. Note the perianth (P), and internal wall of ovary (O) with longitudinal ridges (*arrow*). Bar = 0.1 mm. **C** Detailed view of the *rectangle* in **B**. Note the ovary (O) with a closed tip and the stub of a broken septum (*arrow*) across the ovary tip. The *black dot* is 20 μm in diameter. Bar = 0.1 mm. **D** Thin section of the ovary tip shown in **C**. Note the septum (*arrow*) across the ovary tip. Bar = 0.1 mm. Courtesy of BMCEB

Remarks Several fossil taxa, including *Ktalenia*, *Schizolepis*, *Caytonia*, *Leptostrobus*, and *Karkenia*, are more or less similar to *Schmeissneria* in certain aspects. However, *Schizolepis* has spirally arranged bilobate two-seed-bearing scales in bract axils (Wang et al. 1997); *Ktalenia* has oppositely arranged globose seed-bearing cupules with micropyle pointing downward (Taylor and Archangelsky 1985); Caytoniales has globose multiple-seed-bearing cupules with micropyles pointing to the axis (Thomas 1925; Harris 1940, 1964; Reymanowna 1973; Nixon et al. 1994; Barbacka and Boka 2000b; Wang 2010); *Leptostrobus* has spirally arranged bivalvate multiple-seed-bearing cupules with slit-like openings (Krassilov 1972; Harris and Millington 1974; Liu et al., 2006b); and *Karkenia* has an oval-elongate fructification of irregularly disposed atropous, pedunculate ovules/seeds with micropyles pointing to the axis, a genus distinctly different from *Schmeissneria* (Kirchner and Van Konijnenburg-Van Cittert 1994; Schweitzer and Kirchner 1995). The above differences distinguish these genera from *Schmeissneria*, which has paired female flowers on a stalk that is spirally arranged along the inflorescence axis.

6.1.5 Description

Schmeissneria microstachys Kirchner
and Van Konijnenburg-Van Cittert, emend. Wang
(Figures 6.3a–c, 6.4a, 6.5a–b, 6.6a–c, 6.7a–c, 6.8a–c, 6.9a–c, 6.10a–d,
6.11a–d, 6.14a–d, 6.15a–c, 6.16a–d, 6.17a–g, 6.18a–g, and 6.19)

Diagnosis: Plants including physically connected long shoots, short shoots, leaves and female inflorescences. Leaves *Glossophyllum*-like. Inflorescence with densely or sparsely clustered flowers. Flowers borne on a stalk in pairs. The stalk short or long. Flowers with longitudinal striations, with three tepals distinct or not, with bundles of hairs or not. Infructescence of numerous fruits. Fruit round triangular in shape, with two locules containing several seeds. Seed elongate to oval in shape.

Description: Plants have long- and short-shoots (Fig. 6.6a–c). Long shoot at least 17.3 cm long and 6.2 mm wide (Fig. 6.6a–c). Short shoot up to 8.8 mm in diameter and 2.65 cm long (Figs. 6.6a–c). Leaves are inserted on the apex of a short-shoot, which is covered with leaf-cushions (Figs. 6.3a–c, 6.5a–b, 6.6b, c, and 6.19). Leaves are slightly cuneiform, up to 7.7 mm wide and 13.6 cm long, with obtuse apex and up to 12 parallel veins (Figs. 6.3a–c, 6.5a–b, 6.6b–c, 6.11b, and 6.19)

Female inflorescence is attached to the apex of a short shoot, up to 7.9 cm long and 1.29 cm wide, with flower pairs in dense or loose helical arrangement along the axis (Figs. 6.3a–c, 6.4a, 6.7a–b, 6.8a–c, 6.9a–c, and 6.10a–d). Each inflorescence has dozens of flowers (Figs. 6.3c, 6.4a, 6.7a–c, 6.8a–c, 6.9a–c, and 6.10a–d). The inflorescence axis is longitudinally striated, free of flowers proximally, up to 1.8 mm in diameter at the base, tapering distally (Figs. 6.3c, 6.4a, 6.7a–c, 6.8a–c, 6.9b, and 6.10b). Flower stalk is about 0.56 mm in diameter, variable in length up to 2.5 mm long, and bears a pair of flowers (Figs. 6.4a and 6.7a–c). The flower is round triangular to oval in shape, 3.1 mm (9.7 mm when including hairs) long and 2.3 mm in diameter, and consists of an ovary surrounded by three tepals (Figs. 6.3c, 6.4a, 6.7a–c, 6.8a, 6.9a–c, 6.10a–d, 6.14a–c, 6.15a–c, and6.16b–d). The tepals are round triangular in shape, up to 3.5 mm long and 3.5 mm wide, and longitudinally striated (Figs. 6.15a, and 6.16b–d). Some tepals are missing when hairs are present on the ovary (Figs. 6.8a–c, 6.9a–c, 6.10c–d, 6.14a–d, 6.15a–b, and 6.16b–d). The ovary is round triangular in shape when young but oval at maturity, up to 1.4 mm in diameter and 2 mm long, hair-free when young but covered with hairs (probably at anthesis) (Figs. 6.4a, 6.7a–c, 6.8a–b, 6.9a–d, 6.14a–d, and 6.16b–d). Hairs are scattered over the ovary, brush-like or in bundles, straight, very fine to 0.2 mm wide, up to 7.8 mm long (Figs. 6.8a–c, 6.9a–c, 6.10c, d, 6.14a–d, 6.15a–c, and 6.16b–d).

Infructescences are up to 9 cm long, about 6–8 mm wide, with an axis 0.9–1.5 mm wide (Figs. 6.3a–c, 6.4a, 6.7a–c, 6.8a–c, 6.9a–c, and 6.10a–d). Fruits are arranged along the infructescence axis, 2.1–3.7 mm long, 1.7–3.0 mm in diameter, and usually enclose more than four seeds in two locules that are separated by a vertical septum (Figs. 6.11a–d and 6.17a–d). Seeds are elongate to oval in shape, 0.11–0.46 mm long, 0.09–0.3 mm in diameter, with a smooth surface when intact but rough when abraded, with a thin seed coat and internal cellular details (Figs. 6.17e–g and 6.18a–g). Some of the seeds demonstrate the existence of micropyles that are about 23 × 35 μm (Fig. 6.18a–c).

Syntype: BSPG AS XXVI 23.

Further specimens: BSPG 1994I, 4707, 4709, 4711, 4713, 1972 VI 4, 2009 1 16, 2009 1 17, 2009 1 18, 2009 1 19; SSPC G288/91, G348/91, G349/91, G286/91, G117/90, G254/90, G476/92, G475/92, G479/92, G120/90, G275/91, G316/91, G315/91, G351/91, G303/91, G297/91, G298/91, G257/90, G317/91, G111/90, G313/91, G312/91, G295/91, G632/97, G666/97, G759/02; GDPC 122K04, S1K97, S3K97, S2K97, 111KI99, S14K97, S13K97, 121K04, 110KI99+.

Holotype locality: Reundorf near Bamberg, Germany.

Further locality: Oberwaiz, Unternschreez (Lautner) and Schnabelwaid (Creußen) near Bayreuth, Veitlahm, Pechgraben near Kulmbach, Großbellhofen, Rollhofen (Wolfshöhe) northeast of Nuremberg (all in Germany); Odrowaz, Holy Cross Mounts, Poland.

Stratigraphic horizon: the Liassic, the Lower Jurassic (Germany and Poland).

Depository: BSPG, SSPC, GDPC.

Schmeissneria sinensis Wang
(Figures 6.4b, 6.12a–c, and 6.13a–d)

Diagnosis: Female inflorescences associated with *Glossophyllum*-like leaf, attached to the apex of a short shoot. Inflorescence of numerous female flowers clustered in pairs along inflorescence axis, maturing acropetally. Flowers varying in size, becoming smaller distally. Flowers with a short stalk. Tepals indistinct, forming an envelope, with longitudinal striations. Ovary in center of flower, with a closed apex and a vertical septum, and relics of hairs on its surface.

Description: A *Glossophyllum*-like leaf is closely associated with two female inflorescences. The leaf is incomplete, over 19 mm long and up to 1.8 mm wide. It is slender and cuneiform, but its apex is missing. The venation appears parallel. The apex of a short shoot is connected to a female inflorescence. The short shoot is about 2.4 mm long and 2.3 mm wide, with leaf cushions. Leaf cushion is about 0.56 mm high and 1.8 mm wide.

The female inflorescences are spicate, up to 9.4 mm wide, up to more than 6 cm long, and generally tapering distally (Figs. 6.4b and 6.12a). The

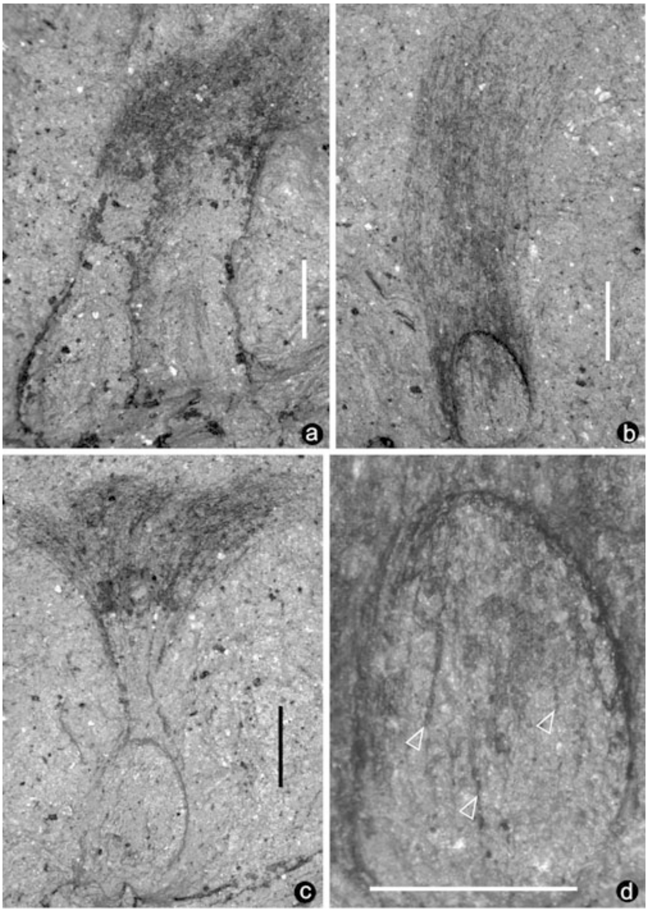


Fig. 6.14 Blooming flowers in a *S. microstachys* inflorescence, shown in Fig. 6.8b, and their hairs. BSPG 2009 1 19. **A** Two adjacent flowers with brush-like hairs. Bar = 1 mm. **B** Detached ovary with parallel hairs. Bar = 1 mm. **C** Ovary with diverging hairs. Bar = 1 mm. **D** Detailed view of the ovary in B. Note the hairs are emanating from not only the ovary margin, but also the ovary surface. Bar = 0.5 mm. Courtesy of JSE

axes of the female inflorescences are up to 1.3 mm across basally and only 0.2 mm across apically (Fig. 6.12a). The inflorescences may be straight or sinuous, longitudinally striated, but free of flowers for about 1.8 cm at the base (Fig. 6.12a). One of the inflorescences is connected to the apex of a short shoot. One inflorescence has more than 21 flowers attached (Fig. 6.12a). Generally, the flowers at the basal part are larger and more mature than those toward the distal of the inflorescence (Figs. 6.4b and 6.12a). Some flowers are connated basally. The stalk of the flower pair, rarely seen, is about 0.5 mm long.

Flowers are about 1.6–4.6 mm long, about 1.2–4 mm in diameter, widest at the base and constricted at the apex (Figs. 6.4b, 6.12a–c, and 6.13a). They

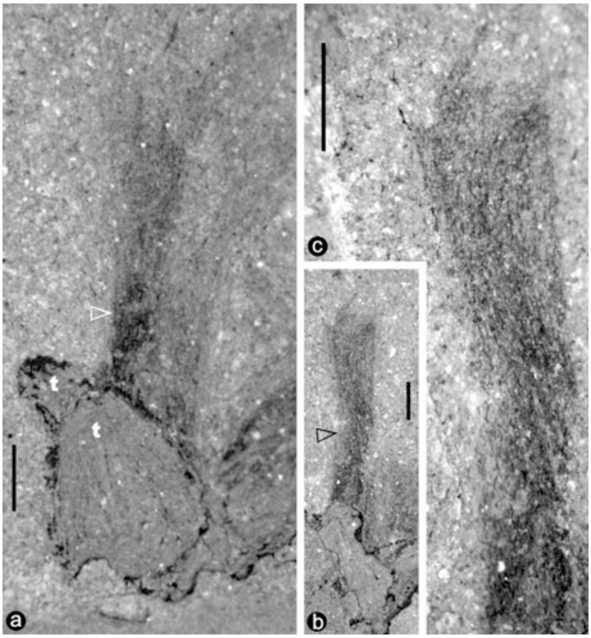


Fig. 6.15 Blooming flowers of *S. microstachys* and their hairs. BSPG 2009 1 18. **A** The flower marked by *black arrow* in Fig. 6.10d, with two tepals (t) and apical hair bundles (*arrow*). Bar = 1 mm. **B** Flower marked by *white arrow* in Fig. 6.10d, with parallel hairs (*arrow*). Bar = 1 mm. **C** Detailed view of the hairs in B. Note that there is neither a border nor a vein. Courtesy of JSE

have an onion-like appearance, including an ovary and a sheathing envelope (Figs. 6.4b, 6.12a–c, and 6.13a). The envelope (composed of tepals) is longitudinally striated internally and externally (Fig. 6.12b). The apices of the flowers point away from the axis of the inflorescence (Figs. 6.4b and 6.12a, b). The envelope apex of a large flower is more extended than that of a small one (Figs. 6.4b and 6.12a). The envelope in mature flowers is inflated in shape (Fig. 6.12a, b). The surface of the envelope is smooth locally with elongated epidermal cells. The cells in the envelope are elongated: 18–33 μm long and 6–12 μm wide. Rugulate pollen grains on the internal surface of the tepal apex are about 26 μm in diameter. The ovaries are about 1.5–3.3 mm long and 1–3.2 mm in diameter, widest basally and constricted apically (Figs. 6.4b, 6.12a–c, and 6.13a). The ovary is attached to a receptacle by a wide base about 1.6 mm in diameter. The distal part of the ovary wall is longitudinally ribbed internally and externally (Fig. 6.13a–c). The ovary is bilocular, completely separated by a vertical septum 9–19 μm thick (Fig. 6.13a–d). The internal ovary walls are smooth and flat at the base and rough in the upper part (Fig. 6.12c). The septum is complete, extending from the base (Fig. 6.12c), through the middle part, to the apex of the ovary (Fig. 6.13b–d). The septum may be papillate.

Holotype: IBCAS 8604.
Holotype locality: Sanjiaocheng Village, Jinxi, Liaoning, China.
Stratigraphic horizon: the Jiulongshan Formation (former Haifanggou Formation), the Middle Jurassic.
Depository: IBCAS.

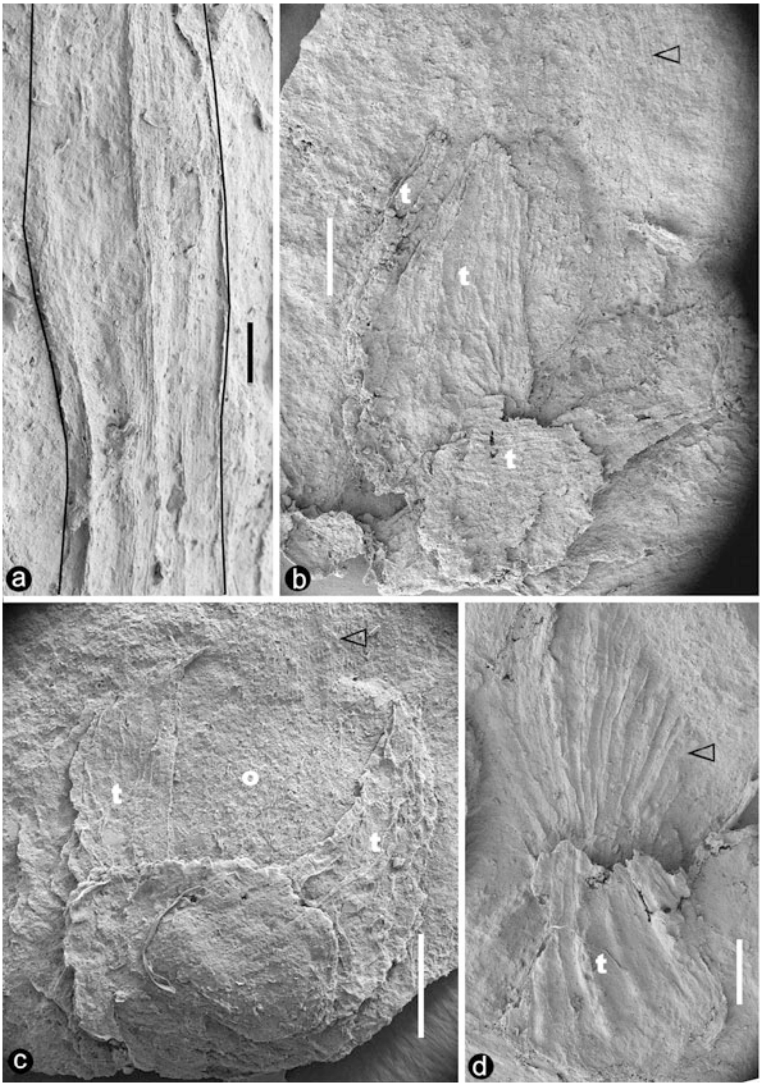


Fig. 6.16 Infructescence axis and tepals in the flowers of *S. microstachys.* **A** Infructescence axis (outlined by *black lines*) with longitudinal striations. BSPG 4713. Bar = 0.1 mm. **B** Flower with tepals (t) and parallel hairs (*arrow*). Note toward to the base there is a tepal (t) of an adjacent flower. BSPG 2009 1 17. Bar = 0.5 mm. **C** Two tepals (t) bracketing an ovary (o) with apical parallel hairs (*arrow*). Bar = 0.5 mm. **D** Longitudinally-ribbed tepal (t) covering an ovary with apical hairs (*arrow*). Bar = 0.5 mm. Courtesy of JSE

Remarks There is little difference between *Schmeissneria sinensis* and *S. microstachys*. The scope of variation in *S. microstachys* is much wide and overlaps with that of *S. sinensis*. The current basis for validity of *S. sinensis* is restricted to its probably fused tepals with no evident longitudinal ribs, its distribution in the Middle Jurassic in China (*vs* the Early Jurassic in Europe), and the fact that the number of tepals is hard to ascertain

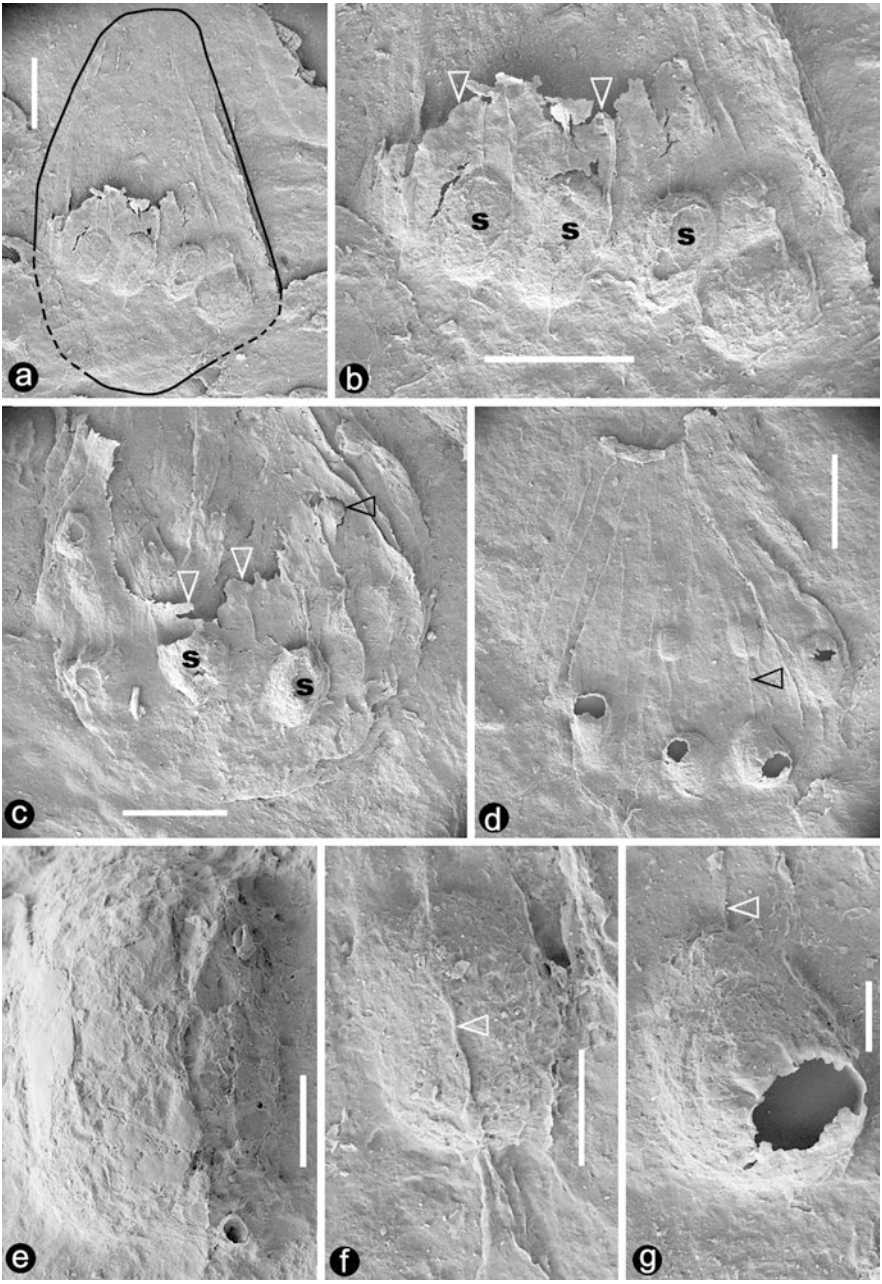


Fig. 6.17 Fruits and in situ seeds of *S. microstachys.* BSPG 4713. **A** Fruit (*outlined by the line*) with in situ seeds. Bar = 0.5 mm. **B** Detailed view of the seeds (s) and septum (*white arrow*) in the fruit shown in **A**. Note that there still is additional space behind the septum. Bar = 0.5 mm. **C** Another broken fruit showing in situ seeds (s) and septum (*white arrow*). Note that there is still another seed (*black arrow*) and additional space behind the septum. Bar = 0.5 mm. **D** Another fruit

6.1.6 Development

Both *Schmeissneria sinensis* and *S. microstachys* have inflorescences or flowers preserved in various stages of development. *S. sinensis* has flowers of various ontogenetic stages, ranging from small premature ones at the top to large mature ones at the base of the inflorescences (Figs. 6.4b and 6.12a). Considering the differences in morphology and dimension between the topmost (most immature) and basalmost (most mature) flowers, it is reasonable to assume that the small flowers are premature and not yet pollinated. This is further circumstantially confirmed by fruits of *S. microstachys*, recognized only recently, enclosing seeds of a size similar to that of mature flowers. It is also in line with the absence of seeds in all *S. sinensis* specimens. Flowers in anthesis are connected to leaves and are larger in size and different in shape from the young female flowers reported here, also implying the immaturity of the apical small flowers of *S. sinensis*. Considering all this (Wcislo-Luraniec 1992; Kirchner and Van Konijnenburg-Van Cittert 1994; Wang et al. 2007b, c; Wang in press), it is safe to say that the immature ovaries of *Schmeissneria* have two locules and a closed apex, probably closed before pollination. This is a feature only seen in angiosperms and is also a feature defining angiosperms (Tomlinson and Takaso 2002; Wang et al. 2007b, c; Wang 2009, in press).

Observation of specimens in various ontological stages provides a unique opportunity to reconstruct the floral development in *Schmeissneria*. Initially, the flowers are very small, with a round base and an apex barely extended, of round-triangular shape (Fig. 6.4b). Their ovaries are subdivided by a septum into two locules (Fig. 6.13a–d). The tepals are hard to distinguish from each other, and they form an envelope-like structure surrounding the ovary (Figs. 6.4b, 6.12b, and 6.13a). There are weak longitudinal ribs on the surface of the flowers (Fig. 6.12b). The flowers are organized in pairs in an inflorescence, as in more mature stages and infructescences (Figs. 6.4a and 6.7b, c). As the flowers develop, their size increases. They become inflated in shape, with a more extended apex (Fig. 6.12a). The upper portion of each locule in the ovary is empty and with a rough striated wall, while its basal portion is occupied by a mass of tissue (presumably ovules) (Fig. 6.12c). The mass may fall off and leave a mark on the ovary wall (Fig. 6.12c). Hairs start appearing on the ovary surface. Three of the tepals are hard to distinguish from each other, and are covered with longitudinal striations, giving the flowers an onion-like appearance (Figs. 6.4b, 6.12a, b, and 6.13a). Next the flowers come into anthesis, and reach their maximal size. This stage is featured by the presence

Fig. 6.17 (continued) with in situ seeds of variable sizes. Note that there are longitudinal wrinkles (*arrow*) on the septum. Bar = 0.5 mm. **E** Another in situ seed. Note that the seed surface is smooth to the *left*, but becomes rough to the *right*, probably due to abrasion. Bar = 50 µm. **F** Seed above the arrow in **D**. Note that the septum wrinkle (*arrow*) runs over the seed. Bar = 0.1 mm. **G** Seed below the *arrow* in **D**. Note that the same septum wrinkle (*arrow*) now runs beneath the seed. Bar = 0.1 mm. Courtesy of JSE

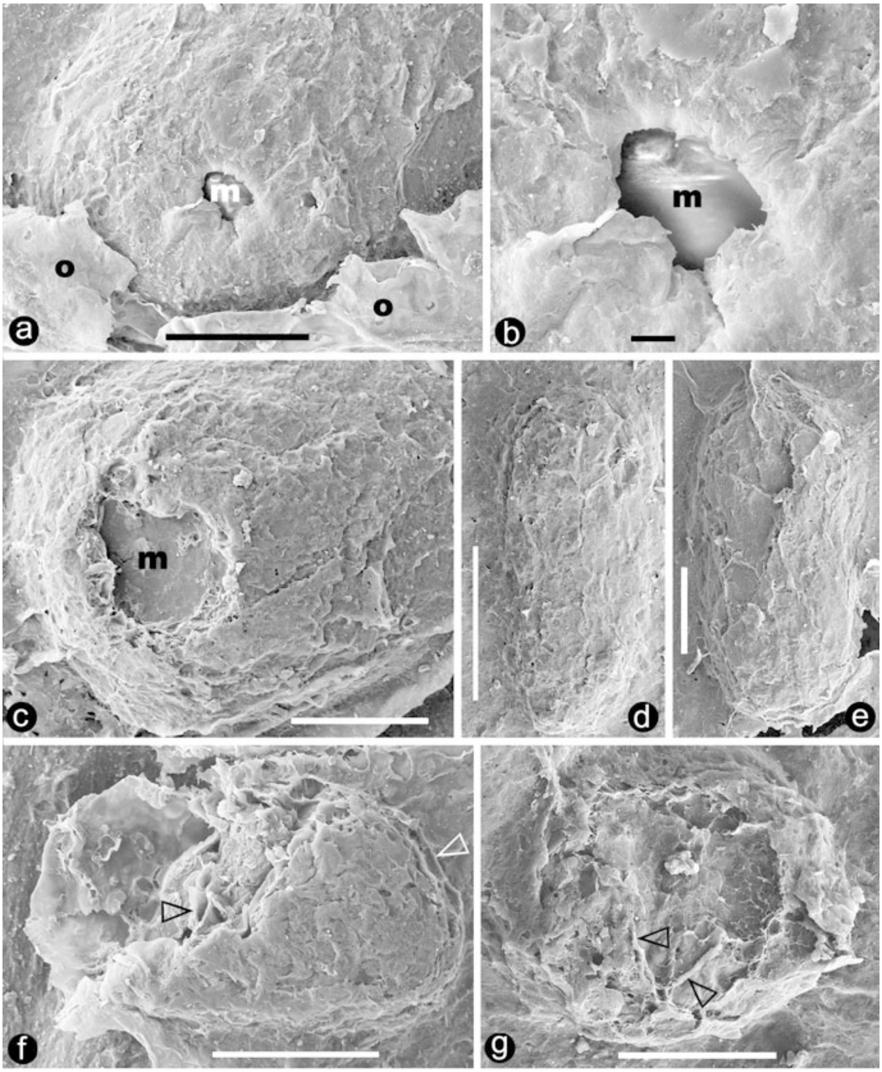


Fig. 6.18 Details of in situ seeds within fruits of *S. microstachys.* BSPG 4713. **A** Seed with a micropyle (m) within the ovary (O). Bar = 0.1 mm. **B** Detailed view of the micropyle (m) region of the seed in **A**. Bar = 10 μm. **C** Another seed with a micropyle (m). Bar = 0.1 mm. **D**, **E** Two elongate-oval shaped in situ seeds. Bar = 0.1 mm. **F** Seed with cellular details (*black arrow*) and seed coat (*white arrow*). Bar = 0.1 mm. **G** Another seed with cellular details (*arrow*). Bar = 50 μm. Courtesy of JSE

of bundles of hairs extended well above the former flower apices (Figs. 6.3c, 6.7b, 6.8a–c, 6.9a–c, 6.10c–d, 6.14a–d, 6.15a–c, and 6.16b–d). The flowers look more elongate in shape, with bundles of hairs attached to the ovary (Figs. 6.14a–c and 6.15a–c). The organization of the hairs is not constant and varies from one flower

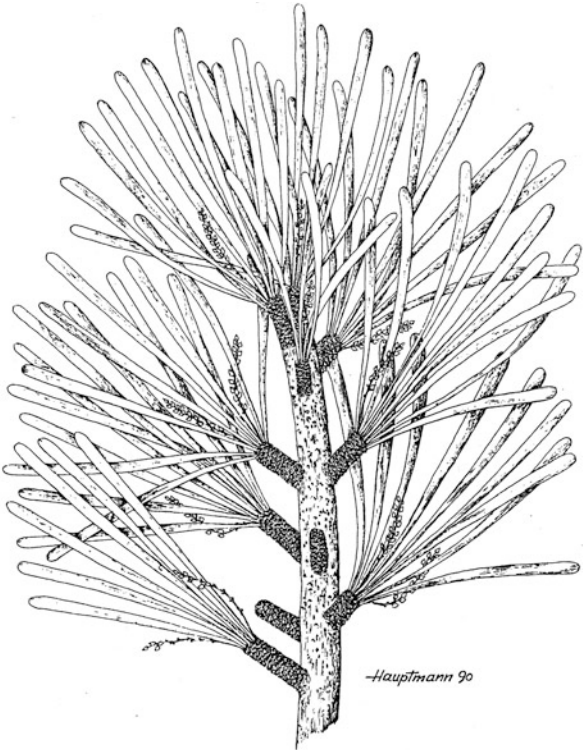


Fig. 6.19 Reconstruction of *Schmeissneria microstachys.* Note the long shoot, short shoots, and attached leaves and inflorescences (reproduced from Dr. Schmeißner and Hauptmann 1993; with permission from Dr. Schmeißner and Hauptmann and from Naturwissenschaftliche Gesellschaft Bayreuth)

to another (Figs. 6.14a–c and 6.15a–c). Three tepals become distinct and surround the hairy ovaries (Figs. 6.15a and 6.16b–d). Like in relatively younger flowers, the tepals remain longitudinally striated (Fig. 6.16b–d). The apex of the tepals may reflex slightly outward (Fig. 6.16a). The final stage for the flowers is fructification. Normally, the fructifications do not fall from the former inflorescence (now infructescence) axis (Fig. 6.11a–d). The fruits show little difference in dimension from the mature flowers (Fig. 6.11b–d). The major difference in appearance is loss of the hairs and, frequently, tepals. The essential difference, however, is the formation of seeds inside the fruits (Fig. 6.17a–d). As expected, seeds in the fruits are separated into two groups by a septum (Fig. 6.17a–d). The seeds are very small, oval to elongate elliptic in shape (Figs. 6.17e–g and 6.18a–g). Sometimes the micropyle can be seen (Fig. 6.18a–c). The seed coat appears very thin, but most likely is quite firm, as judged from their three-dimensional form (Figs. 6.17a–g and 6.18a–g). The fruits are probably dry and non-fleshy, and appear to have been slightly shrunken during fossilization, as suggested by the longitudinal wrinkles on the fruit surface and septum (Fig. 6.18a–d). This developmental series is sketched in Fig. 6.20a–i.

It is interesting to note that although the flowers mature acropetally in the inflorescences of *Schmeissneria sinensis*, the flowers in inflorescences of *Schmeissneria microstachys* appear blooming synchronously (Figs. 6.8a–c and 6.9a–c). This

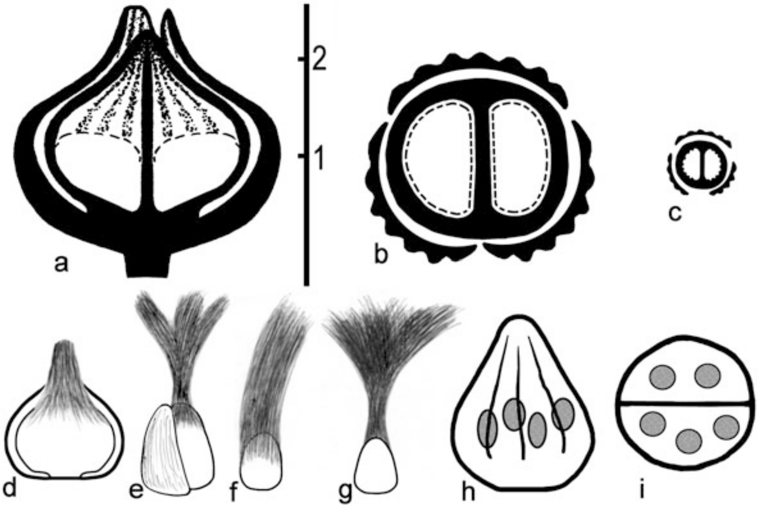


Fig. 6.20 Sketches of the flowers in various stages and perspectives. **A** Longitudinal profile of a flower. Note the tepals surrounding a bilocular ovary, which has a closed apex, is separated by a vertical septum into two locules and contains possible ovules at its base. **B** Cross section of the flower in **A** at level 1. Note the three tepals surrounding the bilocular ovary. **C** Cross section of the flower in **A** at level 2. Note the three tepals surrounding the bilocular ovary. **D** Section of a flower, showing tepals bracketing the hair bundles on ovary apex. **E** Flower with one tepal remaining and a trifid hair bundle. Refer to (Fig. 6.16b). **F** Flower with a parallel hair bundle. Refer to (Fig. 6.14b). **G** Flower with a fanning out hair bundle. Refer to (Fig. 6.14c). **H** Fruit in longitudinal view with seeds inside and longitudinal wrinkles on its surface. **I** Cross view of a fruit showing seeds in two locules. Courtesy of JSE

suggests either that these two species have different developmental patterns, or that *Schmeissneria* has a prolonged anthesis. The latter is more likely and explains the multitude of specimens showing blooming flowers.

6.1.7 Pollination

There is little convincing information on the male part of *Schmeissneria*, although associated fossil male parts and isolated pollen grains have been reported (Kirchner and Van Konijnenburg-Van Cittert 1994). *Stachyopitys preslii* was related to *Schmeissneria* based on association (Kirchner and Van Konijnenburg-Van Cittert 1994; Van Konijnenburg-Van Cittert in press). Wang et al. (2007b) reported a few pollen grains perching on the inner surface of a tepal apex. It is tempting to assume that these pollen grains are probably of *Schmeissneria*, and they may have been captured by the hairs on the ovary. However, this is at most a speculation. If *Schmeissneria* were really dioecious, as suggested by currently available data, it could be possible that the relationship between the female and male parts may never be confirmed for *Schmeissneria*. Van Konijnenburg-Van Cittert and Schmeißner

(1999) have reported that eggs, probably of dragonfly, were laid in leaves of *Schmeissneria*, suggesting that the plant lives somewhere close to water, but whether or not dragonfly plays any role in the pollination of *Schmeissneria* cannot be determined. Its woody habit (Figs. 6.6a and 6.19) makes *Schmeissneria* a shrub or tree, which is ideal for pollen dispersal by wind. The hairs (Figs. 6.14a–c and 6.15a–c) on ovary are reminiscent of the pollen capturing hairs in living anemophilous angiosperms. If this comparison is valid, then it is possible that *Schmeissneria* is wind-pollinated. Unfortunately, SEM examination of ovary hairs failed to reveal any trace of pollen. Therefore this hypothesis is at most an educated guess.

6.1.8 Fruit Dispersal

There is little positive information directly related to the dispersal of *Schmeissneria* fruits. As judged by the dry, non-fleshy fruits, the dispersal of *Schmeissneria* appears unlikely to have been assisted by animals since non-fleshy fruits and very small seeds appear not attractive to most animals. The size of the seeds suggests that the plant may have lived in an open habitat, probably close to a water body. This induction is favored circumstantially by the observation of many infructescences preserved on a single specimen (BSPG 4713) and further strengthened by study of insect eggs (probably of dragonfly) laid in leaves of *Schmeissneria*, which suggests that the plant lives close to water (Van Konijnenburg-Van Cittert and Schmeißner 1999), and an ecological study on the correlation between small seed size and open habitat (Crane 1987). The fruits in this kind of habitat appear to be easily dispersed by wind: The high profile of the trees makes the fruits well exposed to air flow which may be conducive to fruit dispersal.

6.1.9 Affinity

In palaeobotanical history, fossils of or similar to *Schmeissneria* had been put in Conifers (Presl 1838; Schenk 1867; Heer 1876), Ginkgoales (Schenk 1890; Gothan 1914; Emberger 1944; Gothan and Weyland 1954; Nemejc 1968; Kirchner and Van Konijnenburg-Van Cittert 1994), and unspecified group (Wcislo-Luraniec 1992). Kirchner and Van Konijnenburg-Van Cittert (1994) did not justify their assignment except by comparing the paired "ovules" of *Schmeissneria* with paired ovules of *Ginkgo* in two sentences (p. 207). However, the so-called winged seeds of *Schmeissneria* had never been seen in any Ginkgoales, and the connection between *Schmeissneria microstachys* and Weber's *Glossophyllum*? sp. A (Weber 1968) alienated *Schmeissneria microstachys* from *Baiera münsteriana*.

The background for the above treatment is that all information available before 1994 was restricted to the general morphology of the plant and no detailed information of the internal structure of the reproductive organ was available. Wang et al. (2007b) first revealed the internal structure of *Schmeissneria*'s female flower. Their success can partially be attributed to the fact that their sample was nothing but reproductive organs. This forced them to extract as much information as possible from their limited materials. Through careful work, ovaries with two locules and closed apices were revealed in *Schmeissneria*. These features placed *Schmeissneria* in angiosperms, because the only consistent difference between angiosperms and gymnosperms is that the ovules at pollination are exposed in gymnosperms, but enclosed in angiosperms (Tomlinson and Takaso 2002; Wang et al. 2007; Wang 2009, in press).

In palaeobotany, such a claim by Wang et al. (2007b, c) was met with a deafening silence, although this silence could alternatively be interpreted as that no one could provide strong evidence against such a claim. Doyle (2008) was the first palaeobotanist to discuss *Schmeissneria* after Wang et al. (2007b, c) published it. Doyle put the plant as a possible stem relative of angiosperms because the material was a "difficult" compression, the interpretation was "uncertain", and there was no morphological analysis, although he admitted "the fact the ovules [of *Schmeissneria*] are enclosed". If ovules of a plant are enclosed, then it is an angiosperm. This conclusion is independent of whether there is a morphological analysis or not.

According to Hoffmann (2003), a theory is accepted not only because it explains, but because it predicts. If the claim by Wang et al. (2007b, c) is neutrally taken as a simple prediction, its validity can easily be tested by further study. If the prediction proves true, then it is valid. Otherwise, it is false. Wang et al. (2007b, c) made two key claims, (1) there is a septum in the ovary, and (2) the apex of the ovary is closed. The second cannot be validly proven in a fruit because a fruit is already mature and its closure does not necessarily stand for a closed apex at or before pollination, as in some conifers (Tomlinson and Takaso 2002). However, the first hypothesis or prediction can be tested with the German specimens, which include many infructescences. According to Wang et al. (2007b, c), there is a septum in the ovary of *Schmeissneria*, so it is a reasonable deduction that there should be such a septum or its counterpart in the fruit. As clearly seen in Fig. 6.17a–d, there is a septum in each fruit and this septum divides the ovary into two locules, in each of which there are more than one seeds. In this point, the hypothesis proposed by Wang et al. (2007b, c) is proven true.

Considering all above, a septum and closed ovary apex are facts in *Schmeissneria*. According to the current knowledge of seed plants, *Schmeissneria* should be put in angiosperms without reservation.

The latest progress potentially related to *Schmeissneria* is a work on *Stachyopitys preslii* and its *in situ* pollen by Van Konijnenburg-Van Cittert (in press), in which moncolpate pollen grains are the major character used to "confirm" the ginkgoalean affinity of *Stachyopitys*, a possible male organ of *Schmeissneria*. However, this implication should be discounted because 1) solid evidence of relationship between *Schmeissneria* and *Stachyopitys* is still missing despite frequent association, 2) the argument in the paper is fundamentally flawed. In this paper, monocolpate pollen grains are presumed to be restricted to cycadophytes and Ginkgoales and their presence in angiosperms is completely ignored and not mentioned at all. This misleading presumption and incomplete consideration make the conclusion in the paper very spurious.

Although the position of *Schmeissneria* in seed plants can be resolved with confidence, its position within angiosperms is hard to determine. It is true that *Schmeissneria* does not look like or can be related to any known angiosperms. This is conceivable since the early angiospermous taxa may be much more diversified and may have gone extinct (Friis et al. 2005, 2010) and we know little of these taxa. Without knowledge of its contemporary relatives, extreme caution should be exercised when poorly understood Jurassic angiosperms are compared with extant ones.

6.1.10 Ecology and Environment

There is extremely limited information on the interaction between *Schmeissneria* and contemporary animals. Van Konijnenburg-Van Cittert and Schmeißner (1999) documented dragonfly eggs laid in leaves of *Schmeissneria*, and interpreted that this relationship implied that the plant lived in a habitat close to water body. This conclusion does not contradict any inference based on seed size analysis or taphonomy. According to Crane (1987), Upchurch and Wolfe (1987), and Wing and Tiffney (1987), small seeds tend to live in an open and light rich habitat. The seeds of *Schmeissneria* are submillimetric in dimension, implying such a habitat for the plant. Its close-to-water habitat can be circumstantially proven by multitude of infructescences in a single specimen (BSPG 4713). There are more than 45 inflorescences on the 31 cm × 45 cm sandstone slab. Although there are a few fossils of other plants, the dominating taxon is *Schmeissneria*. This suggests that the plant is very close to the depositional site. Otherwise the infructescences should have been dispersed and mixed with many other fossil plants as a minor element in the taphno flora. Furthermore, the unattractive appearance of *Schmeissneria* fruits reduces the possibility that some animal might have stored the plant parts in a specific site. The growth habit of *Schmeissneria* apparently is woody tree or shrub according to currently available fossil evidence and the reconstruction by Schmeißner and Hauptmann (1993) (Fig. 6.19). Considering all this, it appears most likely that *Schmeissneria* is a woody plant living in an open, light-rich habitat close to water.

6.1.11 Comparison with Other Relatives

If the new theory in Chap. 8 is correct, namely, Cordaitales-related plants in the Paleozoic gave to rise to angiosperms, then the similarity between *Schmeissneria* and Cordaitales is noteworthy. They appear to share similar leaf form and venation, similar woody growth habit, and close to water habitat. Short shoot organization is not obvious in Cordaitales, however, it very well-developed in Coniferales, a descendent group of Cordaitales.

6.1.12 Summary

The only controversy, if any, about the age of *Schmeissneria* is whether it is the Late Triassic or Early Jurassic in age. Thus there is no problem calling *Schmeissneria* an Early Jurassic angiosperm. Although this may appear unexpected to many palaeobotanists, it is in agreement with results from some molecular clock studies (Martin et al. 1989a, b; Soltis and Soltis 2004b; Anderson et al. 2005; Bell et al. 2005; Moore et al. 2007; Smith et al. 2010) and provides an important support for these conclusions based on molecular data. New data on seeds in fruits confirm the claim by Wang et al. (2007b, c) that *Schmeissneria* is a Jurassic angiosperm, thus mark a new step in the research concerning the origin of angiosperms. This result, if accepted, will fundamentally extend the history of angiosperms and certainly add to the on-going debate about the origin and early evolution of angiosperms. However, it should be kept in mind that the early angiosperms may well have been sporadic in the vegetation dominated by gymnosperms, and that the occurrence of *Schmeissneria* in the Jurassic is far different from the subsequent ecological radiation and diversification of angiosperms.

6.2 *Xingxueanthus*

6.2.1 Background

Xingxueanthus is a genus established recently by Wang and Wang (2010), although the study on this fossil plant can be traced back to early 1990s. As mentioned in Sect. 6.1.1, when I started working on the Middle Jurassic fossil plants from Pan's Site in 1993, there were quite a few plants that were hard to identify. Among them are *Schmeissneria* and *Xingxueanthus*. The work on *Xingxueanthus* was restarted when new technology allowed us to observe this fossil in depth and recognize its identity (Wang and Wang 2010).

6.2.2 Features of the Plant

The specimen of *Xingxueanthus* is preserved as coalified material with good contrast to the light colored sediment matrix and thus making its morphology obvious under LM (Figs. 6.21, 6.22, 6.23, 24, and 6.27a) and SEM, even without gold coating (Figs. 6.21–6.26, 6.27b–f, 6.27, 6.28, and 6.29). Some cellular details are faithfully preserved in the coalified material (Fig. 6.28a, b). The sediment adjacent to the fossil material is very fine grained, which allows a faithful replica of the surface features of the fossil (Figs. 6.25a, b, 6.26a–c, 6.27c, f, and 6.29b–d). It is therefore logical to infer that morphological and anatomical details are faithfully preserved in this fossil plant. At least in one case, the inference drawn this way has been

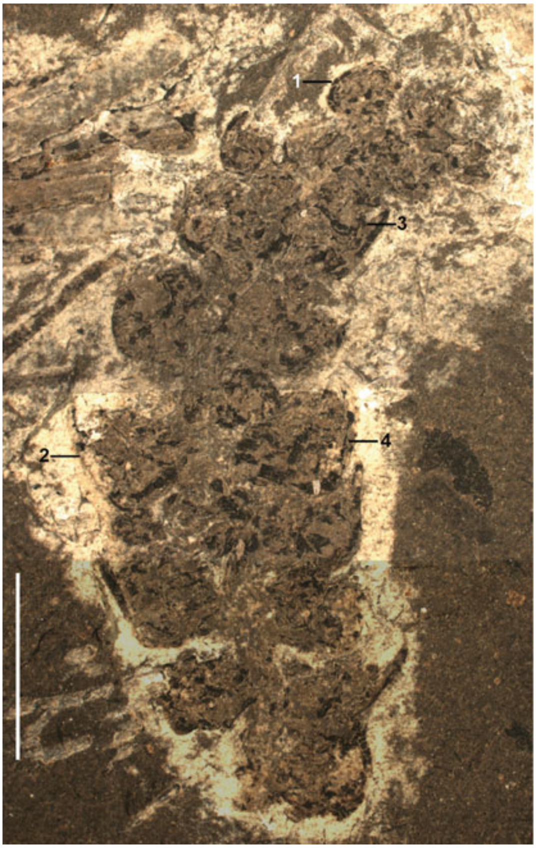


Fig. 6.21 The inflorescence of *Xingxueanthus sinensis*. Note the curved inflorescence tapering distally, and more than 20 flowers attached spirally. Pieced from two original photographs. Holotype. IBCAS 8703a. Bar = 5 mm. Courtesy of AGS

proven true. Figure 6.25a, b show a similar region of the same flower, before and after removing certain sediments. In Fig. 6.25a, the context of the central column suggests that there is a funiculus to the left, as marked by the white arrow, which, however, is eclipsed by sediments and not visible. When the sediments are carefully removed, the funiculus becomes visible (Fig. 6.25b, white arrow). This testability of the inferences on the morphology of *Xingxueanthus* constitutes a solid foundation for the following interpretation.

Judging by its general morphology, it is apparent that *Xingxueanthus* is a vascular plant. The organization of the fossil appears distinct from a vegetative part of any known plant. The possibility of male or pollen organs can be ruled out because careful SEM examination on the whole specimen (total 7 times, 19 h, 226 pictures) has failed to reveal any trace of pollen grains, pollen sacs, or sori. In addition, no pollen organ like *Xingxueanthus* has been recognized in extant or fossil plants. Considering all this, the only viable alternative is that it is a female organ of a seed plant.

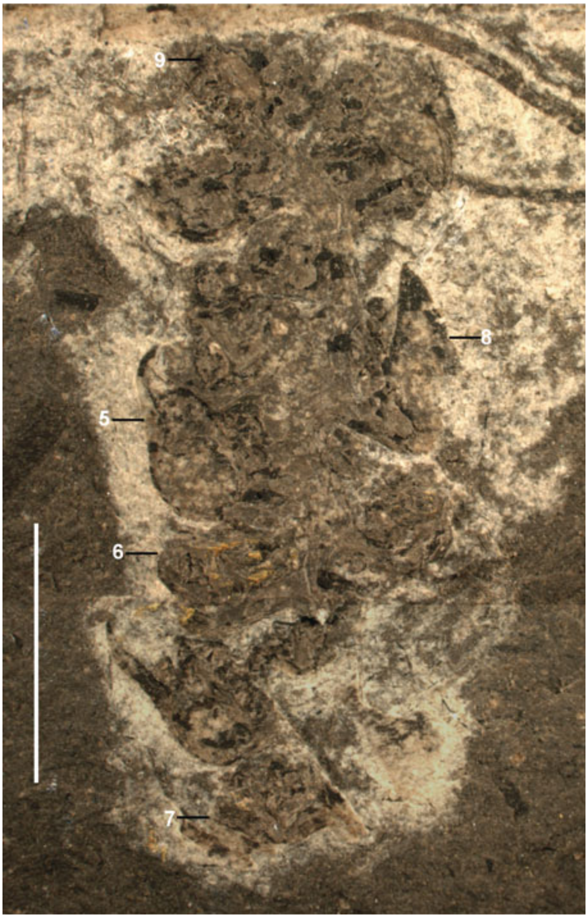


Fig. 6.22 The inflorescence of *Xingxueanthus sinensis*. The counterpart of the lower portion of the specimen shown in Fig. 6.21. IBCAS 8703b. Bar = 5 mm. Courtesy of AGS

Several features of the fossil plant, including the structure of female flowers, apical style, and free central placentation, are revealed through SEM observation. These features are unique, never before seen in any Jurassic or earlier fossil plants, and they are the key features pinning down the phylogenetic position of the plant in angiosperms.

6.2.2.1 Female Flowers

The specimen of *Xingxueanthus* is a coalified compression of an inflorescence (Figs. 6.21 and 22). The inflorescence includes more than twenty female flowers. The flowers are small in size, only 2–3 mm in dimension (Figs. 6.23a, c, 6.24a, 6.26a, c, 6.29a). They are big in the proximal and small in the distal portion of

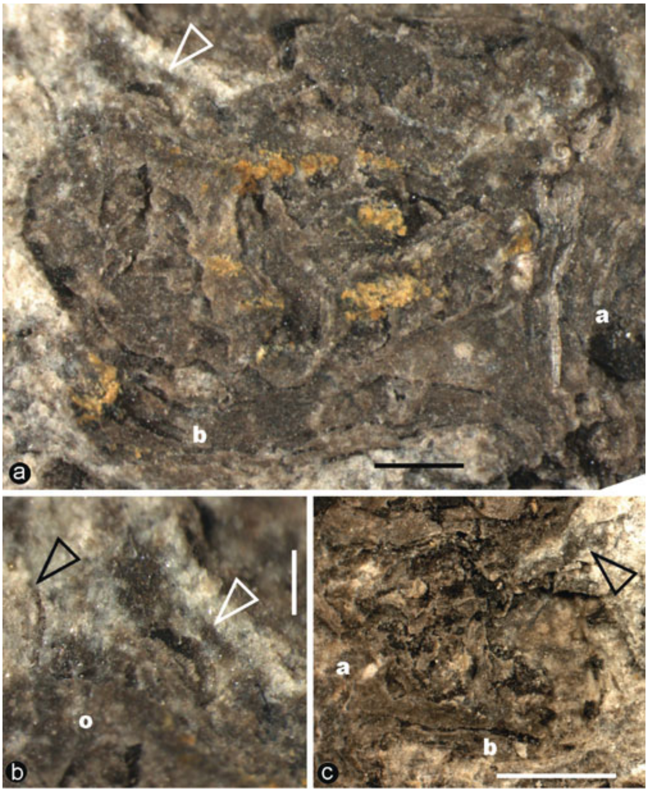


Fig. 6.23 A flower in axil of a bract and its details. **A** Flower 6 in Fig. 6.22. Note the style (*arrow*) on the top of the ovary, subtending bract (b), and inflorescence axis (a). Bar = 0.2 mm. **B** Detailed view of the style (*white arrow*) and trichome (*black arrow*) on the ovary. Note the organic connection between the ovary (o) and style. Bar = 0.1 mm. **C** The counterpart of the flower shown in **A**. Note the style (*arrow*), inflorescence axis (a), and the subtending bract (b). Bar = 1 mm. Courtesy of AGS

the inflorescence (Figs. 6.21 and 6.22). They are spirally arranged along an inflorescence axis, which twists to accommodate the flowers. From the inflorescence axis bracts diverge at angle of about 90° (Fig. 6.23a, c). Each bract has two lateral pointed apices (Figs. 6.22 and 6.27a, b). Each bract subtends a flower in its axil and the terminal of the bract barely extends beyond the base of the ovary (Fig. 6.23a, c). Each flower includes a sub-globose ovary and an apical style (Figs. 6.23 and 6.24). The ovary is completely separated from the bract (Figs. 6.23a, c and 6.27d). In each ovary, there is a vertical central column (Figs. 6.25, 6.26, and 6.29a–d). This central column connects the base and apex of the ovary (Figs. 6.23a, 6.26a, c, and 6.29a–d). Along this central column are spirally arranged funiculi. There are longitudinal striations on the surface of the central column and funiculi. It is the orientations of these striations that reveal the arrangement of the funiculi and ovules in the

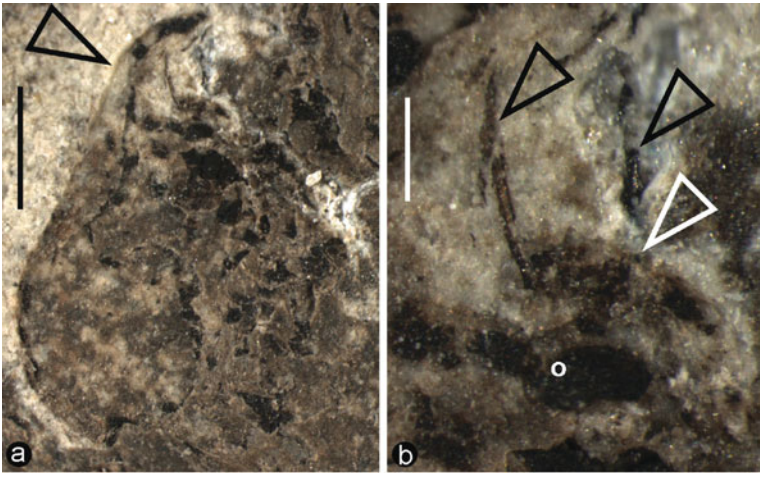


Fig. 6.24 A flower covered by a bract and its details. **A** Flower 5 in Fig. 6.22. Note the bract (*arrow*) covering the ovary. Bar = 1 mm. **B** Detailed view of the style (*white arrow*) and trichome (*black arrow*) on the ovary. Note the organic connection between the ovary (o) and style. Bar = 0.2 mm. Courtesy of AGS

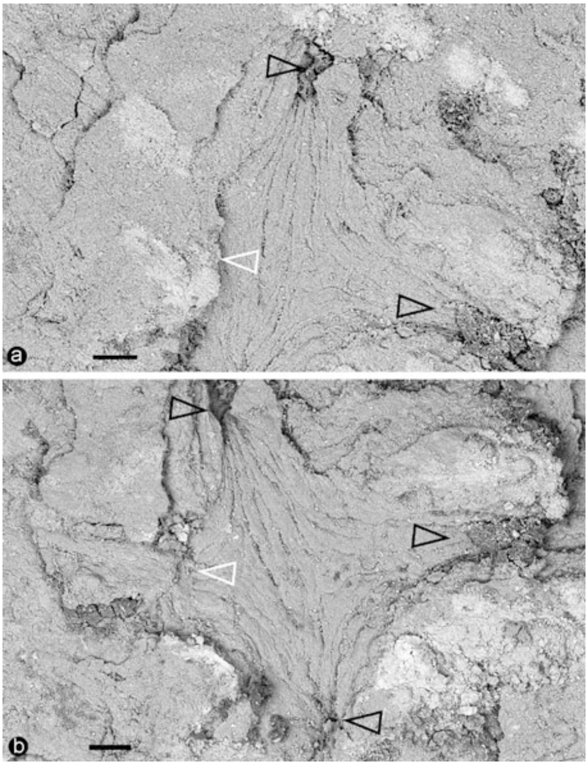


Fig. 6.25 SEM of the placenta in flower 5 in Fig. 6.22. The funiculi (*arrow*) with organic relics spirally arranged along the central column. **A** and **B** are of almost the same area. One of the funiculi (*white arrow*) in **A** is not visible, but is suggested by striations on the central column. This funiculus becomes visible after the covering sediment is removed in **B** (*white arrow*). Bar = 0.1 mm. Courtesy of AGS

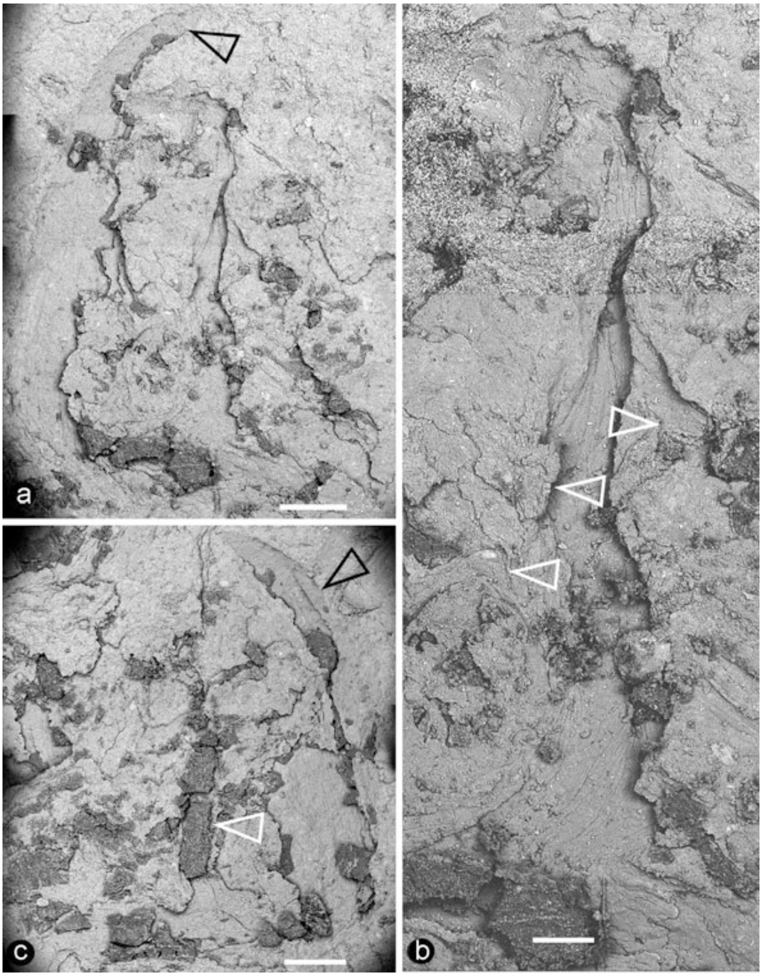


Fig. 6.26 SEM of placenta in flowers. **A** Flower 2 in Fig. 6.21. Note the bract (*arrow*) covering the ovary and the groove *left* by the central column that connects the apex and base of the ovary. Bar = 0.5 mm. **B** A detailed view of the placenta of flower in **A**. Note the funiculi (*arrows*) attached to the central column, as suggested by the striation on the column surface. Bar = 0.2 mm. **C** Flower 4 in Fig. 6.21. Note the bract (*black arrow*) covering the ovary, and the central column of organic material (*white arrow*). Bar = 0.5 mm. Courtesy of AGS

ovary (Figs. 6.25, 6.26, and 6.29a–d). On the apices of these funiculi are ovules (Fig. 6.29a, b). Sometimes there is a depression or cavity in the tissue of the ovule (Fig. 6.28a, b). On the ovary surface are trichomes, probably unicellular. The trichomes are about 0.3 mm long and 40–50 µm wide (Figs. 6.23b, c, 6.24b, and 6.27f). On the top of the ovary is a style about 0.9 mm long and 0.1–0.2 mm wide (Figs. 6.23 and 6.24).

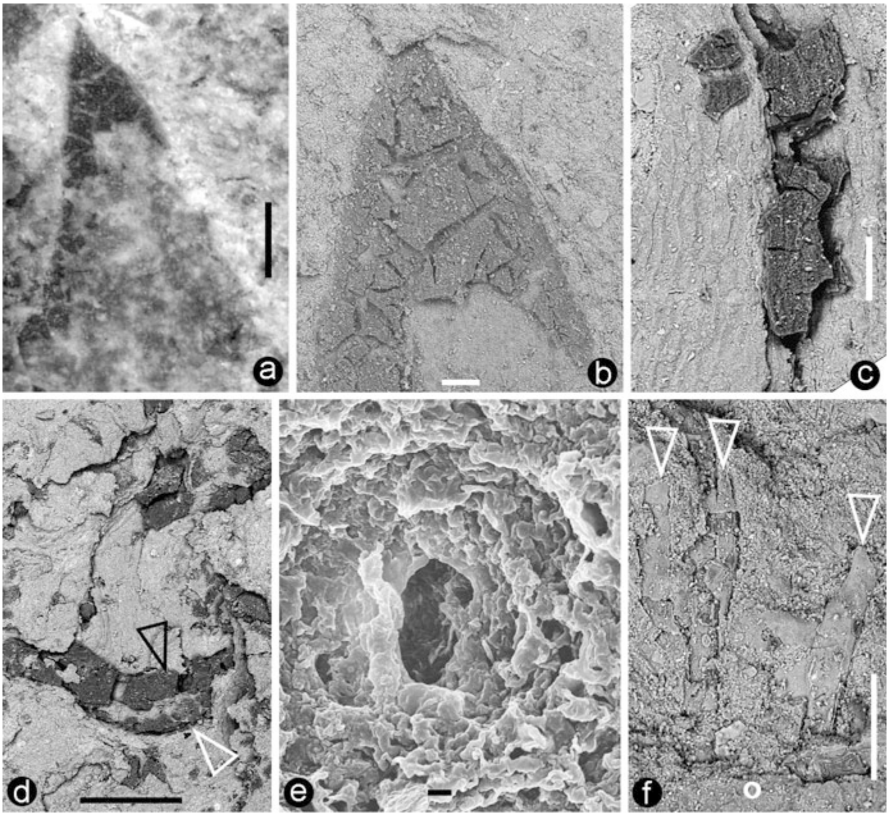


Fig. 6.27 Some details of flowers. **A** One of the bract tips of flower 8 in Fig. 6.22. Note the organic material. Bar = 0.5 mm. **B** Detailed view of the apical portion of the bract in **A** under SEM. Note its organic material. Bar = 0.1 mm. **C** Details of bract near flower 3 in Fig. 6.21. Note the bract of organic material and longitudinal impressions the bract *left* on the sediment. Bar = 0.1 mm. **D** Flower 3 in Fig. 6.21. Note the organic materials of the bract (*white arrow*) and ovary base (*black arrow*) and the separation between them. Bar = 0.5 mm. **E** Stoma on the surface of a flower. Bar = 1 µm. F Trichomes (*arrow*) on the ovary (o) of flower 6 in Fig. 6.22. Bar = 0.1 mm. Courtesy of AGS

6.2.2.2 Apical Style

In *Xingxueanthus* trichome and style are distinct, because the sizes of the two are different (0.3 mm *vs* 0.9 mm long) and (40–50 µm *vs* 130–190 µm wide, respectively) (Figs. 6.23b, 6.24b, and 6.27f). In addition, for each ovary there is only one style, inserted at the top of the ovary (Figs. 6.23b and 6.24b), but there may be many trichomes scattered on ovary surface (Figs. 6.23b, 6.24b, and 6.27f). The style does not look like a piece of fossil material that accidently overlaps the ovary because the same style has been seen in two facing counterparts of the same flower (Figs. 6.23a, c), and the style is physically connected to the ovary (Figs. 6.23b and 6.24b).

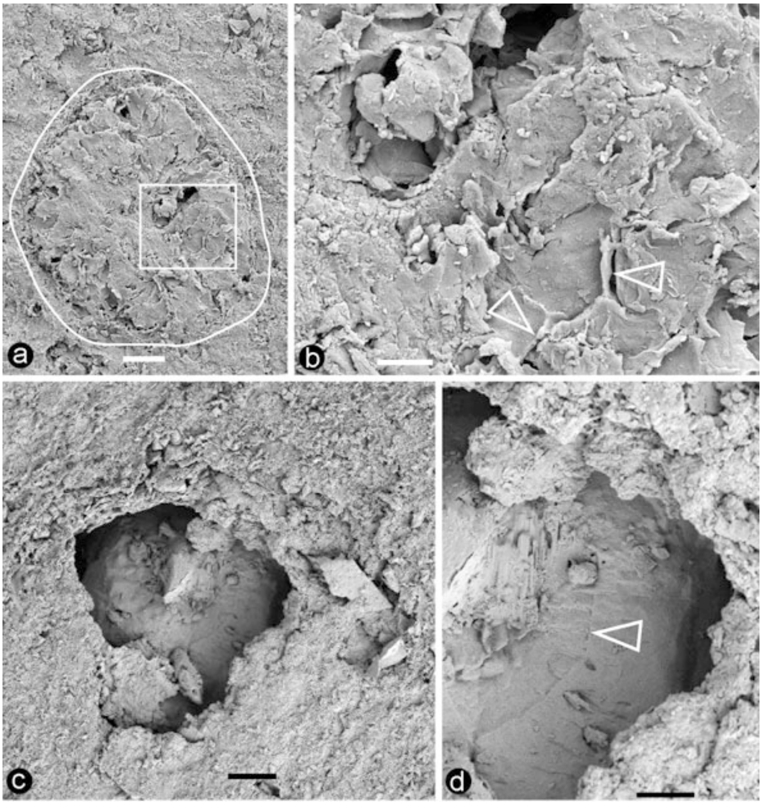


Fig. 6.28 Some details of ovules in flowers from specimen 8703b. **A** Oblique section across an ovule, outlined by the *circle*. Note the cavity to the middle right of the ovule. Bar = 10 μm. **B** Detailed view of the rectangular region in **A**. Note the cavity on top, cellular details and cell wall (*arrows*) between cells. Bar = 5 μm. **C** Ovule still embedded in the sediment. Bar = 20 μm. **D** Detailed view of the ovule tip in **C**. Note the radial cellular deployment reminiscent of a micropyle (*arrow*). Bar = 10 μm. Courtesy of AGS

Besides angiospermous style, the style of *Xingxueanthus* may be alternatively interpreted as a micropylar tube, which is seen in Gnetales, Erdtmanithecales, and Bennettitales (Chamberlain 1957; Bierhorst 1971; Biswas and Johri 1997; Friis et al. 2009; Rothwell et al. 2009). Although these three groups may have been abundant in the Mesozoic flora, these alternatives can be easily eliminated if other fossil features are included in consideration. Erdtmanithecales have isolated seeds with conspicuous longitudinal ribs and the internal structures in its seed (Friis et al. 2009) are distinct from the free central placentation inside the ovary of *Xingxueanthus*. Bennettitalean seeds also are distinct in their internal structures (Rothwell et al. 2009). In addition, the seeds and interseminal scales in Bennettitales have no counterparts in *Xingxueanthus* (Rothwell et al. 2009). Similarly, the oviliferous units and their characteristic decussate arrangement in Gnetales alienate

Xingxueanthus from Gnetales (Martens 1971; Biswas and Johri 1997; Wang and Zheng 2010). After elimination of all these alternatives, the only viable remaining alternative is an angiospermous style.

The presence of a style in the flower makes *Xingxueanthus* unique among Jurassic fossil plants. Considering the female nature of the flower, it is logical to assume that it may function like those in angiosperms. This is in line with the inference that the ovules inside the ovary are enclosed.

6.2.2.3 Enclosed Ovules and Free Central Placentation

As seen clearly in Figs. 6.23a, 6.25, 6.26, 6.27, 6.28 and 6.29, there is a central column in each ovary connecting the ovary base and apex and there are several funiculi spirally arranged along the central column. On the distal end of each

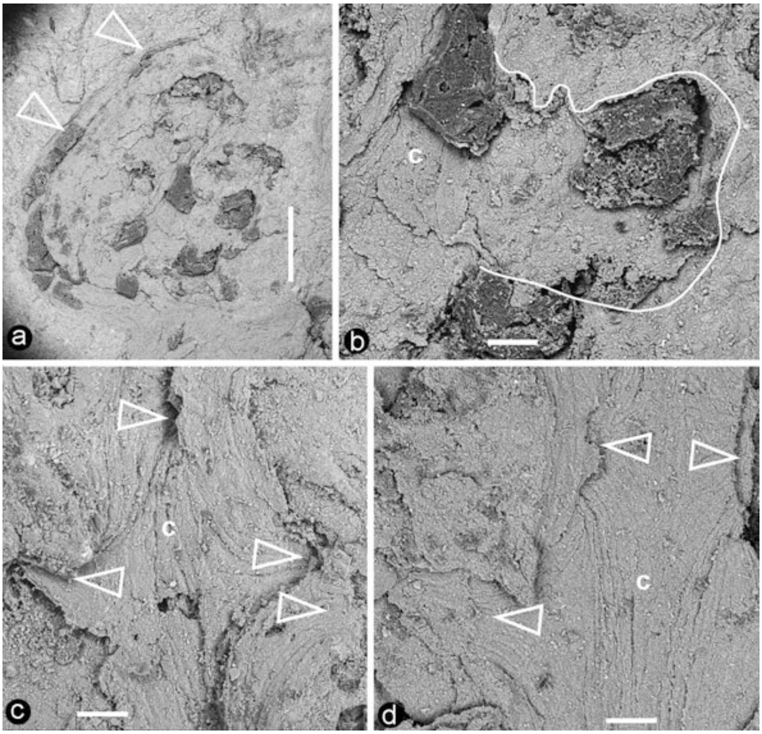


Fig. 6.29 Some details of flower placenta. **A** Flower 1 in Fig. 6.21. Note the bract (*arrow*) covering the ovary. Bar = 0.5 mm. **B** Detailed view of the ovule in **A**. Note the ovule (*outlined by white line*) and its relationship to the central column. Bar = 0.1 mm. **C** Placenta of flower 7 in Fig. 6.22. Note the spiral arrangement of funiculi (*arrow*) along the central column (c), as suggested by the striations. Bar = 0.1 mm. **D** Placenta of flower 9 in Fig. 6.22. Note the spiral arrangement of funiculi (*arrow*) along the central column (c), as suggested by the striations. Bar = 0.1 mm. Courtesy of AGS

funiculus is an enlarged tissue, which is interpreted as an ovule (Fig. 6.29a–b). SEM observation reveals the existence of cellular details and a cavity in the ovule (Fig. 6.28a–b). Since the cavity in the tissue (Fig. 6.28a–b) is much deeper than any stomata or gland-like structure in *Xingxueanthus*, and no canal or cavity other than a micropyle is expected in any other part of an ovule, the cavity probably is a micropyle formed by an integument. Furthermore the radial deployment of cells at the end of the ovule (Fig. 6.28c–d) is reminiscent of the ovule micropyle in some angiosperms (Endress and Igersheim 2000a; Igersheim et al. 2001). All these collectively point to the existence of ovules and free central placentation in *Xingxueanthus*. Free central placentation in a Jurassic angiosperm is surprising. First, this is not a structure expected for any gymnosperms or ferns. To the contrary, it is restricted to angiosperms. Second, if the current evolutionary theories are correct, its occurrence appears too early for angiosperms. The traditional doctrine on angiosperm evolution states that the most primitive angiosperms had conduplicate carpel and marginal placentation, and the free central placentation is always derived (Puri 1952; Tahktajan 1980; Cronquist 1988). Recently proposed theories based on molecular data and morphological analyses suggest that the most primitive angiosperms had ascidiate carpels with one or two ovules (Endress and Igersheim 2000a, b). The evidence from *Xingxueanthus* contradicts both doctrines. There are two ways to resolve these contradictions. One is that *Xingxueanthus* is a "wrong" fossil, the other is that these theories are wrong and need further modification. The possibility of the former appears nil, while the possibility of the latter is within expectations, as the history of science has repeatedly proven (Kuhn 1962).

6.2.3 Description

Xingxueanthus Wang et Wang

Type species: *Xingxueanthus sinensis* Wang et Wang

Diagnosis: Numerous flowers spirally arranged along an axis, forming an inflorescence. Each flower in the axil of a bract, composed of an ovary and a style at the top. Ovules arranged spirally along a vertical column within the ovary.

Etymology: *Xingxue-*, dedicated to Dr. Xingxue Li, a leading Chinese palaeobotanist, for his contributions to palaeobotany; *-anthus* for flower in Latin.

Xingxueanthus sinensis Wang et Wang

(Figures 6.21, 6.22, 6.23a–c, 6.24a, b, 6.25a–b, 6.26a–c, 6.27a–f, 6.28a–d, 6.29a–d, 6.30a–d)

Diagnosis: The inflorescence is slightly curved, over 23 mm long and 7.5 mm wide at base, tapering distally, with over 21 flowers attached. Flower is composed of an ovary and a style at the top. The ovaries are up to 3 mm from the adaxial to abaxial side, up to 2 mm from side to side, up to 2.6 mm high. The central column connects the base and top of the ovary, 1.1–2.5 mm long, about 0.5 mm wide at base and tapering to about 50 μm wide at top. More than three ovules are spirally arranged along the central column at an angle about 90°. Styles are 130–190 μm wide and up to 0.9 mm long, inserted on the top of the ovary.

Description: The inflorescence is spicate, slightly curved, over 23 mm long and 7.5 mm wide at the base, tapering distally, with over 21 flowers attached, maturing acropetally (Figs. 6.21 and 6.22). Inflorescence axis is about 1 mm wide at base, tapering distally, slightly twisted to accommodate flowers, with longitudinal striations (Figs. 6.21, 6.22, and 6.23a, c).

Flowers and their subtending bracts are spirally arranged along the inflorescence axis (Figs. 6.21 and 22).

Bracts are about 3.5–5 mm long, diverging from the inflorescence axis at an angle slightly greater than 90°, upturning at both lateral sides of the flowers, each with two inward-curving tips of about 35°, completely separated from the flowers in their axils, with their terminals not extended beyond the base of the flowers (Figs. 6.23a, c, 6.24a, 6.26a, c, 6.27a, b, d, and 6.29a).

The ovaries are in the axils of the corresponding bracts, up to 3 mm from the adaxial to abaxial side, 2 mm from side to side, and 2.6 mm high (Figs. 6.23a, c, 6.24a, 6.26a, c, and 6.29a). A flower is composed of an ovary and a style at the top (Figs. 6.23a–c, 6.24 a, b, and 6.30 a–d). The ovary has a slightly depressed top and a vertical central column within (Figs. 6.23a–c, 6.24a, b, 6.26a, c, 6.29a, and 6.30a–d). The central column connects the base and the top of the ovary, almost parallel to the adjacent inflorescence axis, 1.1–2.5 mm long, about 0.5 mm wide at the base, tapering to about 50 μm wide near the top (Figs. 6.23a, 6.26a, c, and 6.30a–d). When the organic material is preserved, the central column and its attached ovules are visible as dark material (Figs. 6.26c and 6.29a, b); when the organic material falls off, the presence of a central column and its attached ovules is suggested by their imprints left on the sediment (Figs. 6.25a, b, 6.26a–c, and 6.29b–d). Striations on the central column converge where funiculi are attached (Figs. 6.25a–b, 6.26b, and 6.29c–d). Three or more ovules are spirally arranged along the central column at an angle of about 90° (Figs. 6.25a–b, 6.26b, 6.29b–d, and 6.30a–d). Funiculi range from 100 to 320 μm in diameter (Figs. 6.25a–b, 6.26b, and 6.29b–d). Ovules attached to the distal ends of funiculi are 100–380 μm in diameter (Fig. 6.29a, b). A cavity and cellular details (including cell content relics) in the ovule are seen in some ovule (Fig. 6.28a, b). Some of the epidermal cells on ovule are arranged radially (Fig. 6.28c, d). A style 130–190 μm wide and up to 0.9 mm long is inserted on the top of the ovary (Figs. 6.23a–c and 6.24a, b). The epidermal cells are elongate subrectangular (Fig. 6.27c). There are trichomes on the surface of the ovary (Figs. 6.23b, 6.24b, and 6.27f). Trichomes are about 1–2 cells (40–50 μm) wide, up to 328 μm long, single or in fascicles (Figs. 6.23b, 6.24b, and 6.27f). Stomatal aperture is about 6–7 μm long and 2–3 μm wide, slightly sunken (Fig. 6.27e).

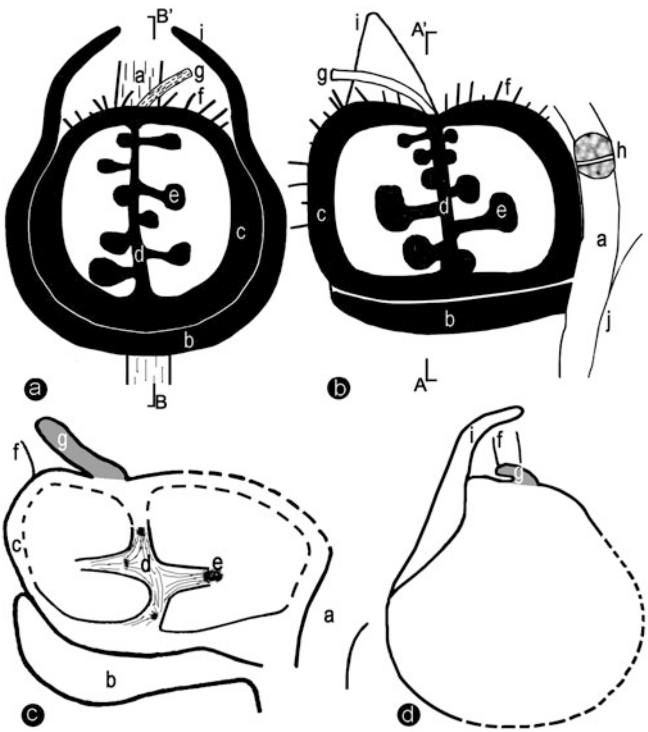


Fig. 6.30 Reconstructions and sketches of the flowers. Labels: inflorescence axis = a, bract = b, ovary wall = c, central column = d, ovule = e, trichomes = f, style = g, scars of the bract and flower = h, bract tip = i, and a portion of another flower = j. **A** Longitudinal section from side to side of the flower. Note the inflorescence axis, bract, ovary wall, central column, ovule, trichomes, style, and bract tip. BB'marks the position of the section that is shown in **B**. **B** Longitudinal section from the inflorescence axis to the distal of the flower. Note the slightly twisted inflorescence axis, bract, ovary wall, central column, ovule, trichomes, style, scars of the bract and adjacent flower, bract tip, and a portion of another flower. AA' marks the position of the section that is shown in **A**. **C** Sketch of the flower in Fig. 6.23a. **D** Sketch of the flower in Fig. 6.24a. Courtesy of AGS

Holotype: 8703a.

Paratype: 8703b.

Etymology: *sin-* for *sino*, referring to China, where the specimens were found; *-ensis*, Latin suffix.

Type locality: Sanjiaocheng Village, Jinxi, Liaoning, China (120°21′E, 40°58′N).

Stratigraphic horizon: the Jiulongshan Formation (=Haifanggou Formation), Middle Jurassic (>160 Ma).

Depository: IBCAS.

Remarks Figure 6.28a–d show details of ovules in flowers in specimen 8703b, which were originally embedded in the sediment. They were exposed by grinding away the covering sediment, so they cannot be correlated with the flowers numbered in Fig. 6.22. Photo in Fig. 6.27e is taken on the cleaned macerate of the dégaged detritus, therefore the exact source cannot be specified.

6.2.4 Affinity

Among the known Mesozoic and extant seed plants, an ovulate part in the axil of a bract compares well with those in conifers (Chamberlain 1957; Bierhorst 1971; Biswas and Johri 1997). But the ovules are situated on the adaxial surface of the scale in conifers (except Taxaceae and Podocarpaceae, out of the question here) (Chamberlain 1957; Bierhorst 1971; Biswas and Johri 1997), while the ovules are spirally arranged around a central column inside an ovary in *Xingxueanthus*. Some early Coniferales and Cordaitales may have megasporophylls spirally arranged, but they are different from *Xingxueanthus* in their lack of an ovule-enclosing structure and a style (Taylor 1981). As for potential relationship with these two groups, please refer to Chap. 8. Bennettitales have ovules spirally arranged on a dome-shaped receptacle, but their numerous and unique interseminal scales (Taylor 1981; Delevoryas 1982, 1991; Crane 1986) are totally absent in *Xingxueanthus* and their ovulate organs are borne on a conical receptacle in the center of the "flower" (Taylor 1981; Delevoryas 1982, 1991; Crane 1986), not in the axils of bracts as in *Xingxueanthus*. The relationship between the ovules and their subtending bracts and the arrangement of the ovules around a central column in *Xingxueanthus* exclude the possibility for its placement in Ginkgoales (Taylor 1981; Zhou 2003; Zhou and Zheng 2003). Similarly, the spiral arrangement of ovules around a central column in an ovary excludes the possibility of Cycadales, Caytoniales, Glossopteridales, Czekanowskiales, Pentoxylales and Gnetales (Berridge 1911; Thoday and Berridge 1912; Chamberlain 1919, 1920, 1957; Thomas 1925; Harris 1940, 1941, 1961, 1964, 1969; Harris and Miller 1974; Harris and Millington 1974; Retallack and Dilcher 1981b ; Taylor 1981; Delevoryas 1982, 1991, 1993; Yang 2001, 2004; Yang et al. 2005). Furthermore, the ovary wall and the style at the top distinguish *Xingxueanthus* from all the above taxa. Therefore, the only remaining possibility in seed plants for *Xingxueanthus* is an angiosperm.

When compared to angiosperms, the fossil demonstrates certain similar features. The general morphology of this inflorescence compares well with that of catkins (Heywood 1979). Ovules attached to a central column in their container compare with those of a free central placentation in an ovary (Puri 1952; Heywood 1979), the latter only found in angiosperms to date. A style at the top of an ovary is a character seen only in angiosperms, Gnetales, Bennettitales and Erdtmanithecales (Friis et al. 2009; Rothwell et al. 2009), if it is assumed that there is no difference between style and micropylar tube. The latter three groups are distinct from *Xingxueanthus* in general organization. Gynoecium alone in the axil of a bract appears strange in angiosperms, but the pistillate inflorescences of *Cercidiphyllum* display such an arrangement (Eames 1961).

Angio-ovuly is the only consistent difference between angiosperms and gymnosperms (Tomlinson and Takaso 2002), and ovule enclosure at fertilization is a character sufficient to identify an angiosperm (Wang et al. 2007b, c; Wang 2009). It is apparent that the ovule is enclosed in the ovary in *Xingxueanthus*, satisfying the criterion set up for angiosperms in Chap. 3. If accepted as a Jurassic angiosperm, *Xingxueanthus*, together with *Schmeissneria* (from the same locality), would lend strong support to the hypotheses of the pre-Cretaceous origin of angiosperms, and enrich the diversity of angiosperms in the Jurassic. This will help to resolve the discrepancy between the molecular clock (Chase 2004; Sanderson et al. 2004; De Bodt et al. 2005; Mathews 2009; Smith et al. 2010) and the fossil record (Friis et al. 1987, 2000, 2005, 2006, 2010; Cronquist 1988; Hughes 1994). The occurrence of angiosperms in the Jurassic is in agreement with the paradoxically high diversity of angiosperms in the Yixian Formation (Early Cretaceous), including *Chaoyangia*, *Archaefructus*, *Sinocarpus* (*Hyrcantha*) and *Callianthus* from the Yixian Formation in western Liaoning (Duan 1998; Sun et al. 1998, 2002; Leng and Friis 2003, 2006; Ji et al. 2004; Dilcher et al. 2007; Wang 2009; Wang and Zheng 2009), if the Barremian is taken as the earliest epoch for angiosperms. Characters such as free central placentation and evident style were thought to be derived based on data of extant plants (Puri 1952; Eames 1961; Tahktajan 1980; Cronquist 1988). The presence of such assumed derived characters in a Jurassic angiosperm undermines the foundation of these theories that are mostly based on analyses of molecular and morphological data of living plants. These theories may be correct in certain contexts but certainly not so if fossil data are included. Currently angiosperms are taken as monophyletic. If this is true and also applicable to fossil angiosperms, then the so-called evolutionary trend and the assumed character polarity in these theories may be flawed. If this monophyly is incorrect or inapplicable to fossil angiosperms, then the well-accepted monophyly of angiosperms will face challenges. Either the monophyly of angiosperms, the current evolutionary model, or both need revision.

Alternatively, if *Xingxueanthus* were recognized as a new class in seed plants, it would imply that angiospermy is not unique to angiosperms any more but shared with other seed plants. Some seed plants other than angiosperms might have achieved such advanced protection for their ovules far before the angiosperms did. If this were the case, then much effort would be required to draw a line between angiosperms and gymnosperms. It is conceivable that many arbitrary proposals will be advanced for such a line. While it is easy to make a proposal, it is not easy to convince most botanists of the validity of such a new definition for angiosperms.

6.2.5 Evolutionary Implications

According to the currently dominant evolutionary doctrines, free central placentation is thought derived (Puri 1952; Eames 1961; Tahktajan 1980; Cronquist 1988). There seem to be no opponents to this hypothesis, at least not recently.

Therefore, according to this hypothesis, the discovery of *Xingxueanthus* was not anticipated and placing it in angiosperms requires a fundamental change in thinking about angiosperm evolution. However, this superficial contradiction weakens if we adopt some of the now-abandoned hypotheses or a new hypothesis (see details in Chap. 8).

According to Puri (1952), at one time there were quite a few scientists who proposed that free central placentation was an axial structure and was the most primitive in angiosperms; these scientists included, but not limited to, J. B. Payer (1857), O. Hagerup (according to Puri 1952), and F. Fagerlind (1946). According to them, the placenta is an axial structure bearing ovules that is enclosed by a foliar structure. Although this hypothesis had been redeemed by recent progress in developmental genetics (Skinner et al. 2004), it appears that this school of thought has lost its voice in the past decades. Nonetheless, it should be kept in mind that the free central placentation in some Primulaceae, Juglandaceae, and Loranthaceae cannot be satisfactorily interpreted if placenta is interpreted as a carpellary structure (Puri 1952). The author believes that all these arguments are based only on living plants, which embody limited information about time and history. No matter how convincing it appears, this kind of debate pales when confronted with fossil evidence. Interestingly, conclusions drawn in this way can be self-contradicting. For example, as to whether primitive stigma being wet or dry, there are two papers on this subject published in the same issue of *American Journal of Botany*. In one, Endress and Doyle (2009) argued that the most primitive angiosperms should have carpels sealed by secretions. In the other, Sage et al. (2009) argued that the most primitive angiosperms should have dry stigmas. This author does not question their diligence, intelligence, honesty, or reasoning of these botanists. The contradiction may be derived from the simple fact that the information cited by both sides lacks information about time and history. Thus, the key point is the lack of fossil information supporting either of argument, so only limited trust can be invested in this kind of conclusions. Similarly, Eames (1961), an exponent of carpellary structure for placenta, dominated the argument about the nature of carpels based on his study of many living angiosperms. He challenged the proponents of axial theory by stating "If a carpel be considered an axis, it would be a hollow structure containing other axes, the placenta and its branches, the ovules". *Xingxueanthus*, in addition to examples in Amaranthaceae (Joshi 1938), demonstrates exactly what Eames demanded from his opponents, strongly supporting the axial placenta hypothesis. The support from *Xingxueanthus* for the axial theory is not a simple nullification of a statement. It requires a rethinking in botany since botany has been taught in such a way that the other side of the story is rarely heard. This rethinking is directly related to the origin of the carpel and of angiosperms (see Chap. 8) and may be expanded to related fields.

6.2.6 Problem Unsolved

Unlike the situation for *Schmeissneria,* there is limited fossil evidence on *Xingxueanthus*. Only one inflorescence, though with many flowers, is available for study. Many aspects of this plant remain obscure. There is little information on the root, shoot, leaf, male flower, seed, or fruit. The reconstruction of the plant and its ecological habitat is beyond current capability. It is believed that future study on Mesozoic fossil plants may help amass more information on this important pioneering angiosperm.

6.2.7 Summary

Xingxueanthus and *Schmeissneria* demonstrate certain resemblance to the angiosperms in one key aspect: angiospermy. Their angiospermy suggests that this feature may well be a common convergence point for many seed plants during the Jurassic. It is very possible that some of them had successfully reached such an advanced protection of their ovules. Their failure to dominate the vegetation may be due to other factors. The context in which angiospermy occurred may be a key factor determining the fate of these plants. It is the interaction with the surrounding organisms and environment that determines the fate of a plant or a feature.

If monophyly of angiosperms is assumed and angiospermy is restricted to angiosperms, it appears that the common ancestor of angiosperms must be much older than the Cretaceous, probably occurring in the Triassic or even earlier.

6.3 *Solaranthus*

6.3.1 Possibly Related Previous Studies

Although *Solaranthus* is a recently established genus (Zheng and Wang 2010), studies of similar or potentially related fossil plants have a much longer history. Despite the fact that the relationship between *Solaranthus* and these fossil plants cannot yet be ascertained, it is necessary to briefly mention them.

Heer (1876) described many fossil plants from the Jurassic in eastern Siberia and Amurland. Among them, he recognized three new species in the genus *Kaidacarpum*, namely, *Kaidacarpum sibiricum, K. stellatum* and *K. parvulum*. These fossils are characterized by their hexagonal configuration, size, and aggregation of "flowers". He put them in Pandaneae (Monocotyledon). However, Heer did not give details about *Kaidacarpum*, so a comparison cannot be done with *Solaranthus*.

Prynada (1962) described *Equisetostachys sibiricus*, which is very similar to the above mentioned *Kaidacarpum sibiricum, Loricanthus resinifer, Aegianthus sibiricum* (to be discussed below), and *Solaranthus*. With these taxa, *Solaranthus* shares arrangement of the whole organ and hexagonal configuration of the "flower", but details of these taxa are not available for comparison.

Kvacek and Pacltov (2001) recognized *Bayeritheca hughesii* from the Cenomanian of Bohemia. This is a coalified compression of a complete cone. From this fossil they extracted in situ *Eucommiidites* pollen grains. The cone is characterized by the spiral arrangement of its angular heads. The synangia in the fossil are assumed attached to the adaxial side of a peltate structure. It is noteworthy that *Bayeritheca* looks very similar to *Kaidacarpum parvulum* in general configuration. In addition, the exact position of the pollen sacs in the fossil was not specified. Currently available information does not allow exclusion or confirmation of the correlation between "synangia" in *Bayeritheca* and carpel-like structures in *Solaranthus,* although the "tepals" in *Solaranthus* are not seen in *Bayeritheca*.

There are two interesting plants, *Loricanthus resinifer* (Krassilov and Bugdaeva 1999; Tekleva and Krassilov 2009) and *Aegianthus sibiricum* (Krassilov and Bugdaeva 1988) from the Hauterivian-Barremian (Lower Cretaceous) in Transbaikalia, Russia. These two fossil taxa, though sometimes studied by the same authors, might be congeneric. Both genera share similar hexagonal peltate head, monocolpate pollen grain, and papillate surface (Krassilov and Bugdaeva 1988, 1999; Tekleva and Krassilov 2009) with *Solaranthus* described here. Study on in situ pollen grains of *Loricanthus resinifer* indicates that they have columella-like elements perpendicular to the foot layer, just like those seen in the pollen grains of *Solaranthus* (Krassilov and Bugdaeva 1999; Tekleva and Krassilov 2009; Figs. 6.39j–k). However, they differ in details on pollen grains, sporangia shape, and density of papillae. The so-called "resin body" in *Loricanthus* (Krassilov and Bugdaeva 1999) is an isolated part and has no contextual information for further comparison. It might well be an isolated and/or broken part of a carpel-like structure in *Solaranthus*. The "empty shrivelled sporangia" in *Loricanthus* (Krassilov and Bugdaeva 1999) and "tepal" in *Solaranthus* may well be the same thing.

It is interesting to note that *Kaidacarpum sibiricum*, *K. stellatum*, *K. parvulum* (Heer 1876), *Equisetostachys sibiricus* (Prynada 1962), *Loricanthus resinifer* (Krassilov and Bugdaeva 1999; Tekleva and Krassilov 2009), *Aegianthus sibiricum* (Krassilov and Bugdaeva 1988), *Bayeritheca hughesii* (Kvacek and Pacltov 2001), and *Solaranthus* may well all be different preservations of the same taxon. *Kaidacarpum parvulum*, very similar to *Bayeritheca hughesii* in general morphology, may be the early developmental stage of *K. sibiricum,* while *K. stellatum* may be isolated parts of *K. sibiricum*. There is little difference among *Equisetostachys sibiricus*, *Loricanthus resinifer*, and *Aegianthus sibiricum*. There is no information about the female parts of the taxa other than *Solaranthus*. If future study indicates that all of them have both male and female parts, it would not be surprising that they would all be grouped into a single taxon. However, doing so requires further information from the corresponding fossil materials.

6.3.2 New Information and Implications

Due to new techniques applied in this research, *Solaranthus* is demonstrated to have several unique features never seen in the previously studied, potentially related fossil materials. These features include the presence of closed female parts, namely carpel-like structures, and filamentous and sessile stamens with in situ pollen grains.

6.3.2.1 Carpels

Since the male parts, namely stamens, which are self-evident with their in situ pollen grains, have been identified in *Solaranthus* (see below), carpel-like structures in *Solaranthus* cannot be male parts. Before going further, it is necessary to eliminate other alternatives and ascertain the identity of carpel-like structures first. The carpel-like structures in *Solaranthus* may be alternatively interpreted as fruits, seeds, ovules, insect eggs, fecal pellets, or resin bodies. However, careful examination finds all these possibilities remote. As for fruits and seeds, specimens should include seeds, which would be more likely to fossilize. There are no apparent seeds in *Solaranthus*, but there are subunits that can be interpreted as being ovule-like structures. That seeds do not have internal space between their content and their seed coat is contradicted by the information in Fig. 6.41a–d. Ovules also should have no internal space, but Fig. 6.41a–d clearly demonstrates the existence of space surrounding a substructure within the carpel-like structure. The coherent relationship of the substructure to the carpel-like structure (Fig. 6.41a–d) eliminates the possibility of insect eggs or fecal pellets. Resin bodies have no infrastructure and they do not contain internal space, especially when they are inside plants. Again, Fig. 6.41a–d contradicts this. Therefore, after eliminating all other alternatives, the structures in Figs. 6.40a–f and 6.41a–d have only one counterpart in living plants: carpels or their equivalent, and the subunit within each can be reasonably interpreted as an ovule or ovule-like structure.

Volcanic ash is ubiquitous in *Solaranthus*, even inside the tiny cavity under the cuticle (Fig. 6.40g–h). In strong contrast to its apparent ubiquity, the absence of

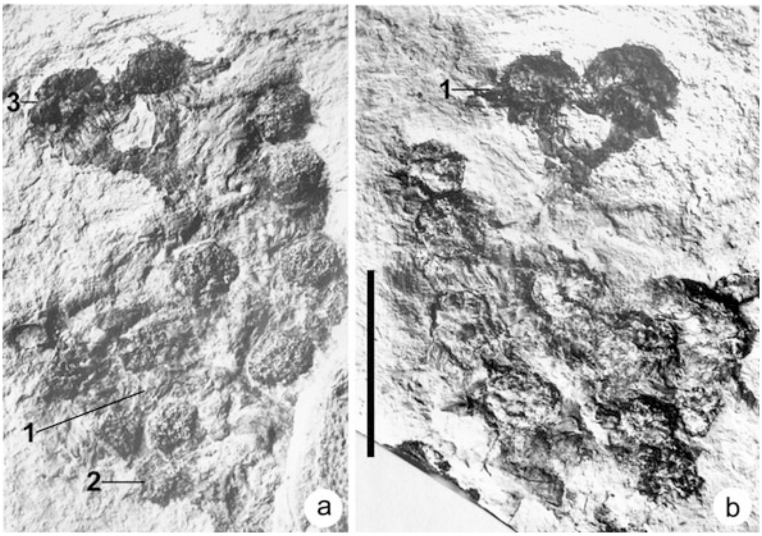


Fig. 6.31 Two facing parts of the same "inflorescence" with more than 13 "flowers". PB21046a, PB21046b. Bar = 1 cm. Courtesy of AGS

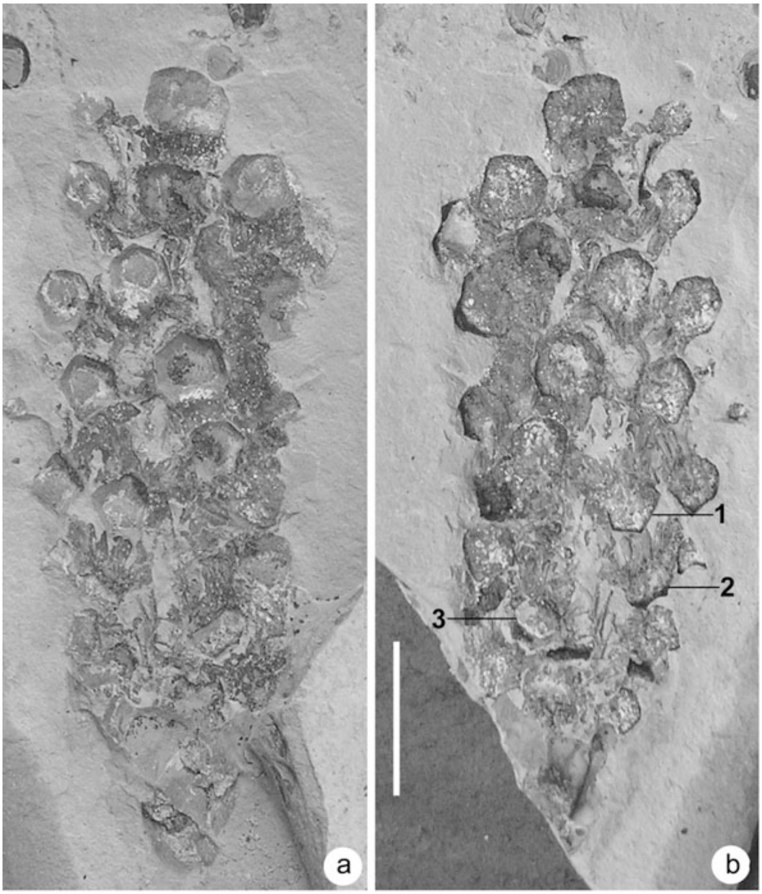


Fig. 6.32 Two facing parts of the same “inflorescence” with up to 27 “flowers”. Note the hexagonal or pentagonal angular profiles of the “flowers”. B0201a, B0201b. Bar = 1 cm. Courtesy of AGS

volcanic ash inside the carpel-like structure (Fig. 6.40f) becomes especially noteworthy. This situation suggests strongly that the carpel-like structure is completely closed in *Solaranthus*. This feature alone is sufficient to place *Solaranthus* in angiosperms, considering the ovule-like structure inside. Further examination of ovule-like structures enclosed in carpel-like structures (Fig. 6.41a–d) lends more support to the angiospermous affinity of *Solaranthus*. The ovule-like structures in the carpel-like structures have smooth, regular and natural outlines, refuting any possibility of artifact. In addition, there is space between the ovule-like structure and “ovary” wall (Fig. 6.41a–d). This is distinct from the situation in any gymnosperm, in which ovules are always immediately surrounded by an integument. All these features collectively pin down the angiospermous identity of *Solaranthus*, according to the definition for fossil angiosperms in Chap. 3.

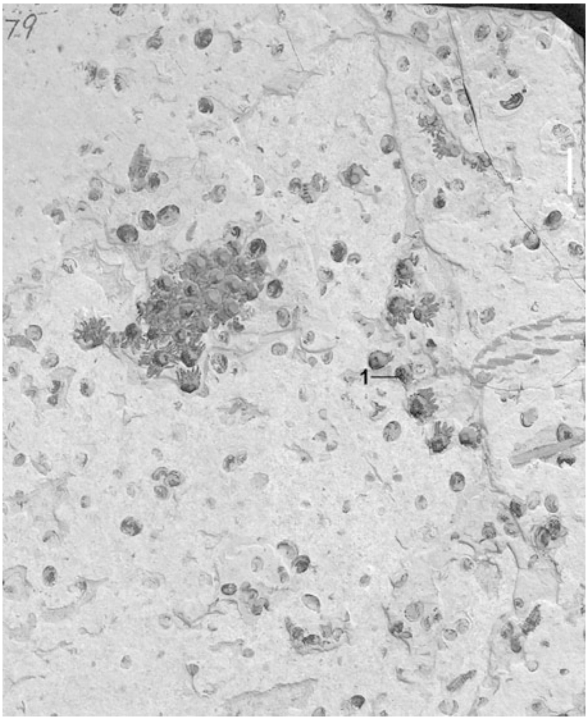


Fig. 6.33 A general view of two to three "inflorescence" (white arrows) on the same slab. Note the varying arrangement of the "flowers", numerous associated conchostracans (*Euestheria*) and an insect wing (*middle right*). B0179. Bar = 1 cm. Courtesy of AGS

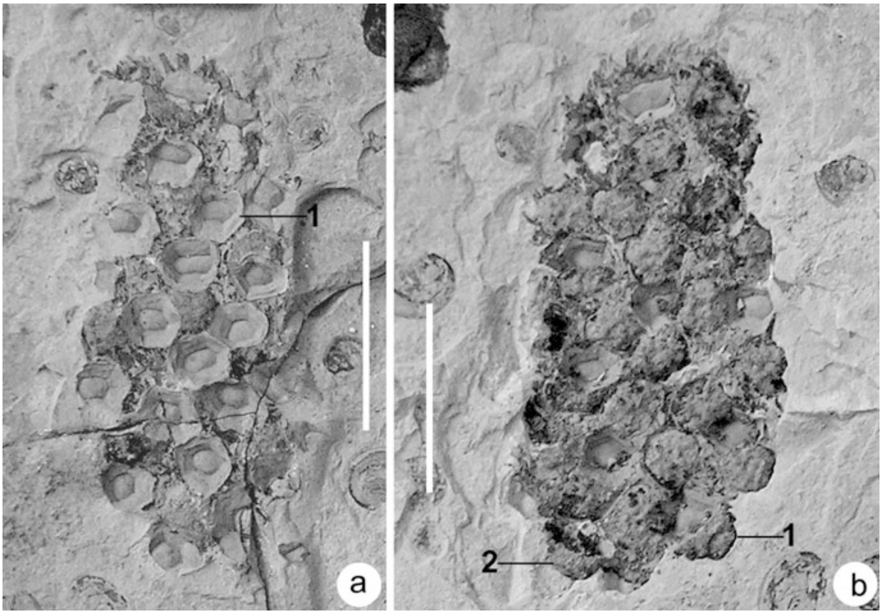


Fig. 6.34 Two facing parts of another "inflorescence". PB21107b&a. Bar = 1 cm. Courtesy of AGS

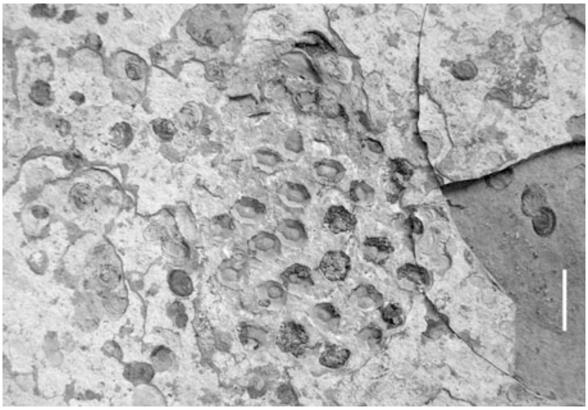


Fig. 6.35 Another "inflorescence" with clustered hexagonal/pentagonal "flowers". GBM3, SFLBG. Bar = 1 cm

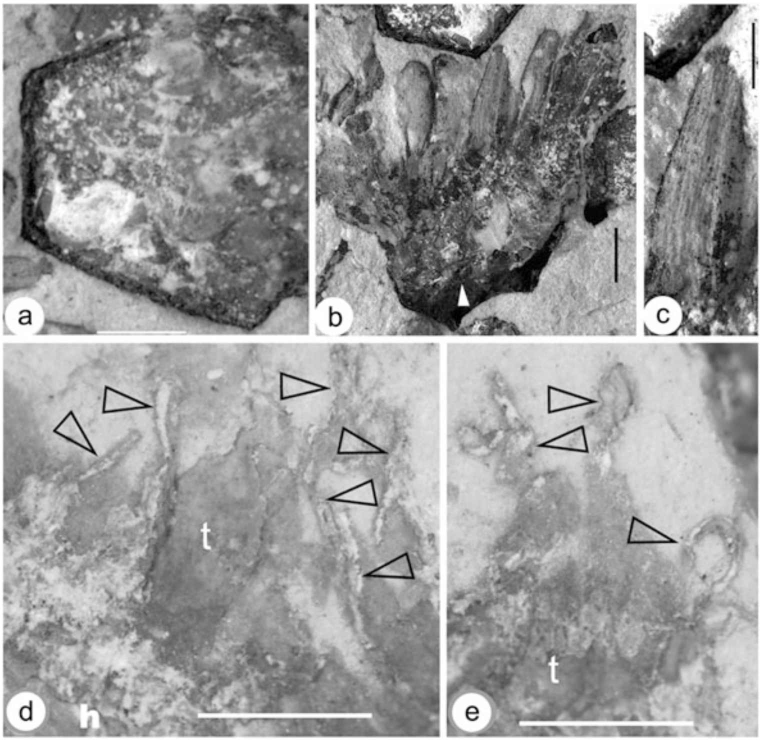


Fig. 6.36 Details of the "flowers". **A** Transverse view of hexagonal "flower" (No. 1 in Fig. 6.32b). Bar = 1 mm. **B** Longitudinal view of the "flowers" (No. 2 in Fig. 6.32b). Note the bottom outline of the "flowers" and attached "tepals". At least one fruit (*white triangle*) is embedded in the sediment. Bar = 1 mm. **C** Detailed view of a "tepal" in **B**. Note the longitudinal files of epidermal cells. Bar = 0.5 mm. **D** Several slender filaments of the stamens, from "flower" No. 1 in Fig. 6.31a. Note the rim of the peltate head (h), filaments (*arrows*) and "tepals" (t) eclipsing the filaments. Bar = 1 mm. **E** Stamens (*arrows*) extended above the "tepals" (t), from "flower" No. 2 in Fig. 6.31a. Bar = 1 mm. Courtesy of AGS

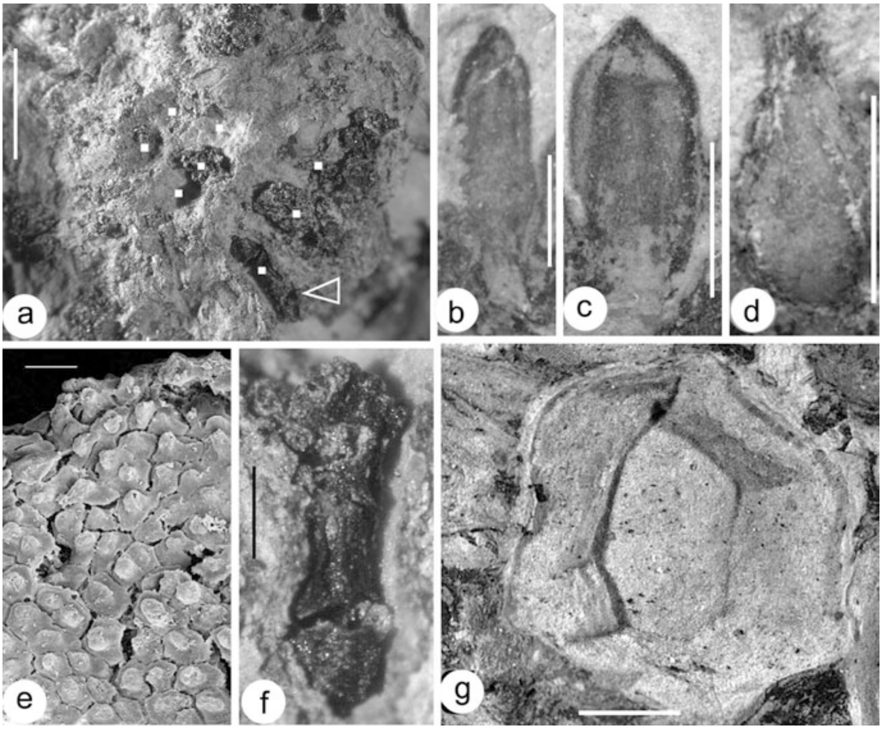


Fig. 6.37 Details of the "flowers". **A** Bottom view of the "flower" No. 2 in Fig. 6.34b, lit from *upper left*. Carpel-like structures left depressions on the sediments and are marked with squares. Bar = 1 mm. **B**–**D** Three types of "tepals" inserted on the rim of the peltate head. Note their variations in shape, length, width. Bar = 1 mm. **E** Detailed view of the papillate sculpture on the peltate head surface of a "flower" No. 1 in Fig. 6.34b. Note the polygonal outline of the epidermal cells. Bar = 20 µm. **F** Carpel-like structure, arrowed in **A**, embedded in the volcanic ash. Bar = 0.2 mm. **G** Cast of a hexagonal peltate head of the "flower" No. 1 in Fig. 6.34a. Bar = 1 mm. Courtesy of AGS

6.3.2.2 Stamens, Anthers, and In Situ Pollen Grains

As mentioned above in Sect. 6.3.1, many of those fossil plants potentially related to *Solaranthus* have yielded pollen grains though no detailed information about the exact sources within the fossils is provided. Pollen wall structure and general organization of some fossils are available for comparison. Therefore it is not surprising that *Solaranthus*, whether related to those fossils or not, has male parts or pollen organs. The existence of male part in *Solaranthus* is confirmed since the in situ pollen grains are self-evident (Figs. 6.38h and 6.39b, e, h–k). What is surprising about *Solaranthus* is the morphologies of the stamens, the pollen wall structure, and their co-occurrence with female parts in the same organ.

The stamens of *Solaranthus* are heterandrous. Some of them are filamentous, namely, borne on the apices of slender filaments (Figs. 6.36d, e, and 6.38c–g), while others may be sessile (Fig. 6.39a–b). However, the in situ pollen grains in these

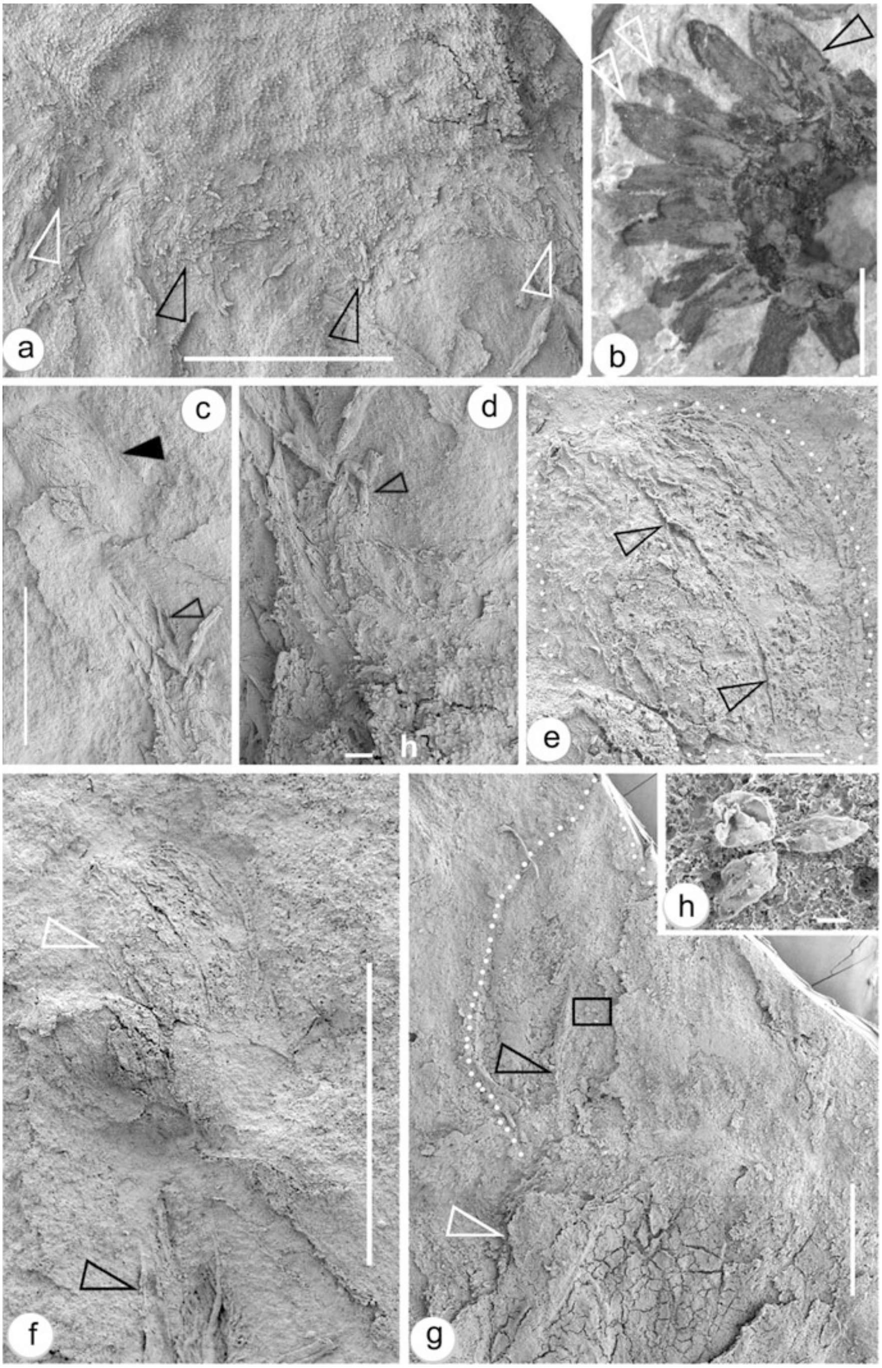


Fig. 6.38 Details of the "tepals" and "stamens". **A** Four fascicles of filaments (*arrows*) along the hexagon side of the peltate head, from "flower" No. 1 in Fig. 6.31b. Bar = 1 mm. **B** "Flower" with more than one cycle of "tepals" of various shapes (*arrows*) inserted along the adaxial rim of the

stamens appear virtually identical (Figs. 6.38h and 6.39b, e, h–i). The congruence in pollen morphology supports the heterandry in *Solaranthus*.

The pollen wall structure of *Solaranthus* is different from known gymnosperms, especially in the rodlet layer. This feature does not appear to be due to artifacts or other factors, but is a real feature of the original pollen grains because a similar pollen wall structure has recently been seen in *Loricanthus resinifer* (Tekleva and Krassilov 2009), which, as mentioned above, is potentially congeneric with *Solaranthus*. The pollen wall in *Loricanthus* appears to have a better preserved topmost layer compared to *Solaranthus*. Whether the rodlet layers in these two taxa are homologous with the columellae in angiospermous pollen is an interesting question deserving further enquiry. If future study confirms this homology, it will help to relate these two taxa to angiosperms.

The co-occurrence of male and female parts in the same "flower" of *Solaranthus* is a unique feature. This is rarely seen in gymnosperms except in some Bennettitales and Gnetales (Chamberlain 1957; Bierhorst 1971; Biswas and Johri 1997), which, however, are apparently out of the question here. But this hermaphrodism is frequently seen in angiosperms. To be honest, the arrangement of the floral parts ("tepals" sandwiched between stamens and carpel-like structures) and that of the "flowers" in the "inflorescences" (Fig. 6.42) do not look typical of angiosperms. This makes the position of *Solaranthus* in angiosperms equivocal. If both "tepals" and carpel-like structures were derived from microsporangia (Frohlich and Parker 2000) through diverted development (Crane and Kenrick 1997), then this unusual arrangement would be possible, and the mixing of pollen sacs and "tepals" in *Loricanthus* (Krassilov and Bugdaeva 1999), if congeneric with *Solaranthus*, would not be surprising.

6.3.3 Diagnosis and Description

Solaranthus Zheng et Wang

Type species: *Solaranthus daohugouensis* Zheng et Wang

Diagnosis: "Inflorescence" with numerous peltate "flowers" helically arranged along an axis. Each "flower" including a stalk, a peltate head, carpel-like structures, "tepals", and stamen. The peltate head hexagonal or pentagonal in abaxial view. Stamen heterandrous, in fascicles, inserted on the periphery

Fig. 6.38 (continued) peltate head. Bar = 2 mm. **C** "Stamen" (*triangle*) and its possible filament at the bottom (*arrow*), to the right of the "flower" in **A**. Bar = 1 mm. **D** Details of the filaments in fascicles (*arrows*) attached to the adaxial rim of the peltate head (h). Note there is no trace of "tepals" between the papillate peltate head and the filaments. Bar = 0.1 mm. **E** Anther (*dotted line*) of the "stamen" shown in **C**, with a separation (*black arrows*) between the two portions. Bar = 0.1 mm. **F** Top portion of the "stamen" in **C**. Bar = 1 mm. **G** Anther with in situ pollen grains extended above the "tepals". Note the possible separation between the two lobes. The TEMs in Fig. 6.39j, k are from this anther. Bar = 0.5 mm. **H** In situ pollen grains from the anther in **G**. Bar = 10 μm. Courtesy of AGS

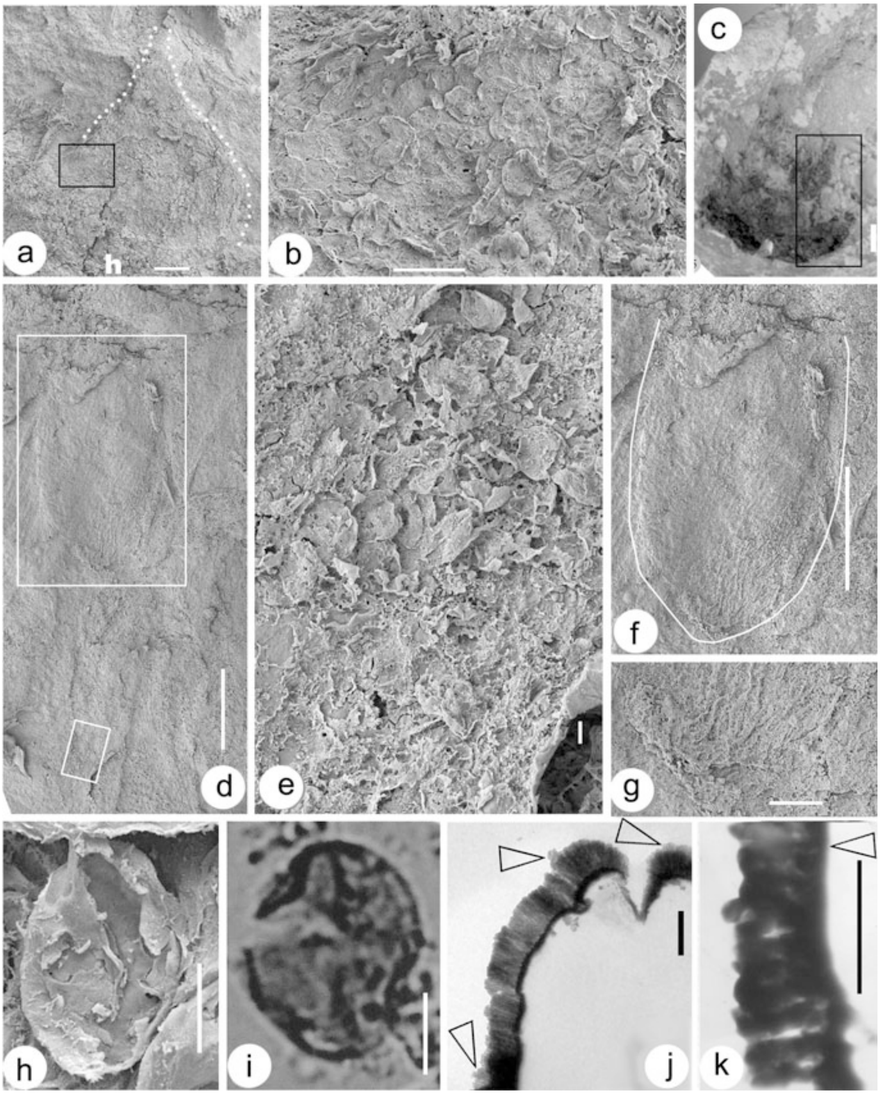


Fig. 6.39 Details of the "tepals" and "stamens". **A** Triangular-shaped sessile "stamen" (*dotted line*) attached to the rim of the peltate head (h). Bar = 0.2 mm. **B** Ellipsoid in situ pollen grains, enlarged from the rectangle in **A**. Bar = 50 µm. **C–G** Physically connected "stamens" and carpel-like structures. **C** Replica made from "flower" No. 3 in Fig. 6.31a Bar = 1 mm. **D** The same "flower" shown in **C**, showing "stamen" and carpel-like structure in the flower. Two rectangular regions are detailed in **E** and **F**. Bar = 0.5 mm. **E** In situ pollen grains in the "anther", enlarged from the *smaller rectangle* in **D**. Bar = 10 µm. **F** Carpel-like structure (*white outline*) in the "flower", enlarged from the *larger rectangle* in **D**. Bar = 0. 5 mm. **G** Details of the tip of the carpel-like structure in **F**. Note additional material on the carpel-like structure surface. Bar = 0.1 mm. **H** Monocolpate in situ pollen grain. Bar = 10 µm. **I** Monocolpate in situ pollen grain. LM. Bar = 10 µm. **J** Portion of the pollen wall. Note the thin foot layer, rodlet layer, and possible residue of top layer (*arrows*). Bar = 100 nm. **K** Portion of pollen wall showing the foot layer (*arrow*) and perpendicular rodlets. Bar = 100 nm. Courtesy of AGS

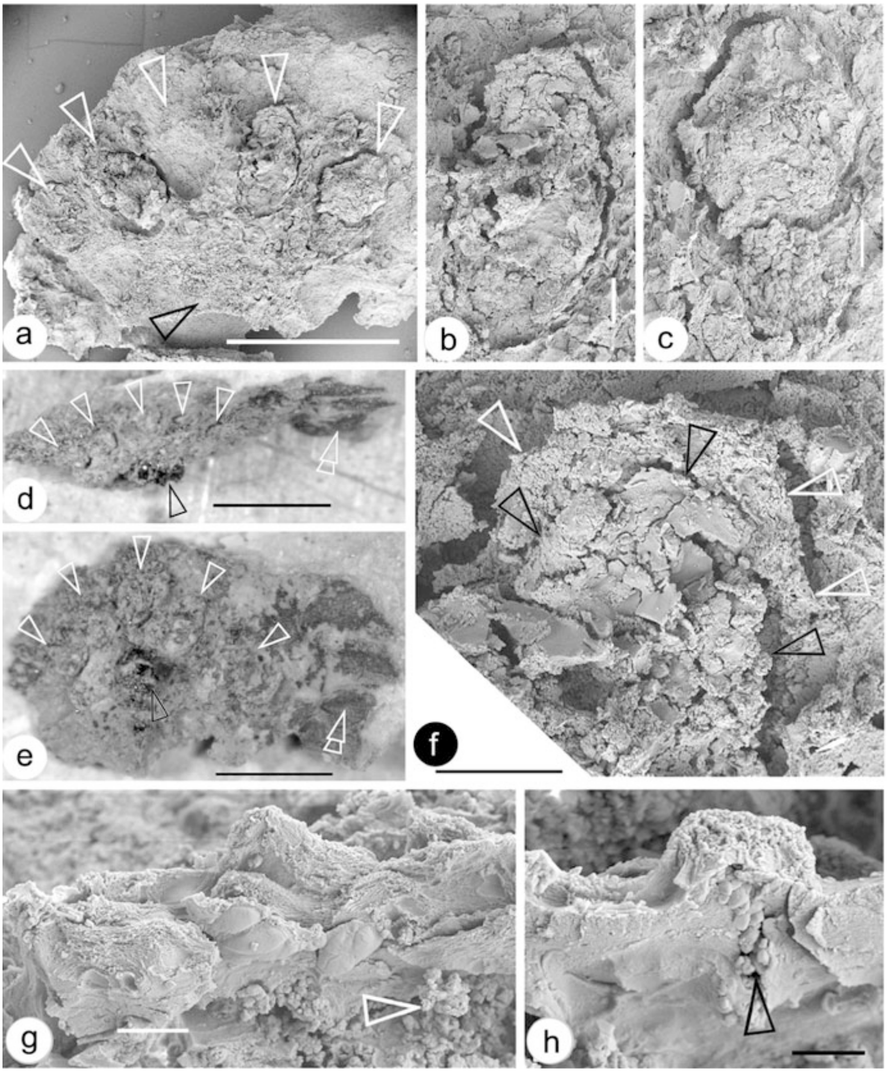


Fig. 6.40 Details of the "gynoecium". **A**, **D**, **E** Different views (*bottom*, *side* and *bottom*, respectively) of the same gynoecium of "flower" No. 1 in Fig. 33. Note the center of the gynoecium (*black arrow*), embedded carpel-like structures (*white arrows*), and impression (*central white arrow*) left by a carpel-like structure, and "tepals" (*double white arrows*). Bar = 1 mm. **B**, **C** Details of two carpel-like structures shown in **A**. Bar = 0.1 mm. **F** Detailed view of the carpel in **B**, not cleaned. Note volcanic ash outside the carpel-like structure (*white arrows*), and their lack on the possible ovule-like structure (*black arrows*) in the carpel-like structure. Bar = 0.1 mm. **G** Epidermis of the gynoecium in **A**. Note the papillae on the surface and volcanic ash within the tissue (*arrow*). Bar = 10 μm. **H** Details of a papilla on the surface of the same gynoecium as in **G**. Note the tiny granules on its surface and volcanic ash inside (*arrow*). Bar = 5 μm. Courtesy of AGS

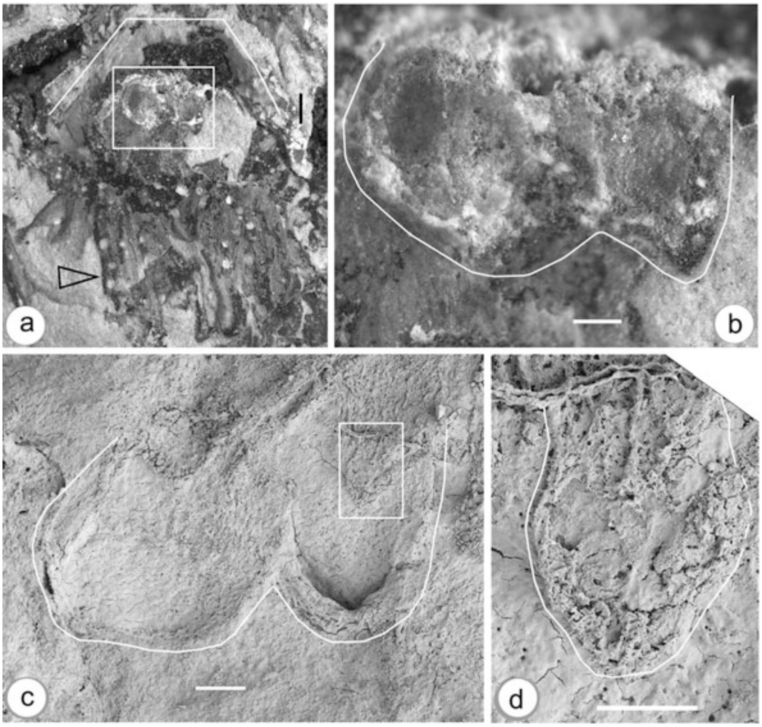


Fig. 6.41 Details of the carpel-like structures and ovule-like structure. **A** Longitudinal view of the "flower" No. 3 in Fig. 6.32b. Note the outline of the peltate head (*white line*), and "tepals" on the *bottom*. Bar = 0.5 mm. **B** Detailed view of the *rectangle* in **A**. Note the impressions *left* by two adjacent carpel-like structures on the sediment (*outlined by the white line*). Bar = 0.2 mm. **C** The same two carpel-like structures in **B**, now under SEM. Note the outline (*white line*) of the carpel-like structures. Bar = 0.2 mm. **D** Detailed view of the *rectangle* in **C**. Note the smooth outline (*white line*) of the ovule-like structure that is attached to the bottom of the carpel-like structure. Bar = 0.1 mm. Courtesy of AGS

of adaxial rim of the peltate head, with in situ monocolpate pollen grains. Pollen wall with a foot layer and a rodlet layer. "Tepals" distinct, alternate, triangular to lingulate in shape, in more than one cycle, attached to the adaxial rim of the peltate head, between the "stamens" and "carpels". Numerous carpel-like structures enclosing ovule-like structure inserted on the adaxial surface of the peltate head.

Etymology: *Solar-* for *solaris*, because of the radial symmetry of the "flowers"; *-anthus* for flower in Latin.

Stratigraphic horizon: the Jiulongshan Formation, Middle Jurassic (>164 MA).

Remarks The words used to describe *Solaranthus* such as inflorescence, flower, tepal and carpel, are put in quotation marks or linked with "-like" because the stamens, carpel-like structures and "tepals" are misplaced in the flower, compared with

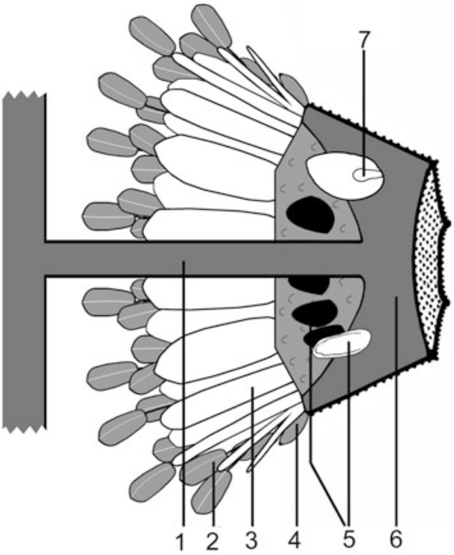


Fig. 6.42 The longitudinal sketch of a "flower". Note the stalk (1), filamentous stamen (2), "tepals" (3), sessile stamen (4), carpel-like structure (5) enclosing ovule-like structure, peltate head (6), and an ovule-like structure (7) in a carpel-like structure. The inflorescence axis is to the *left*. Courtesy of AGS

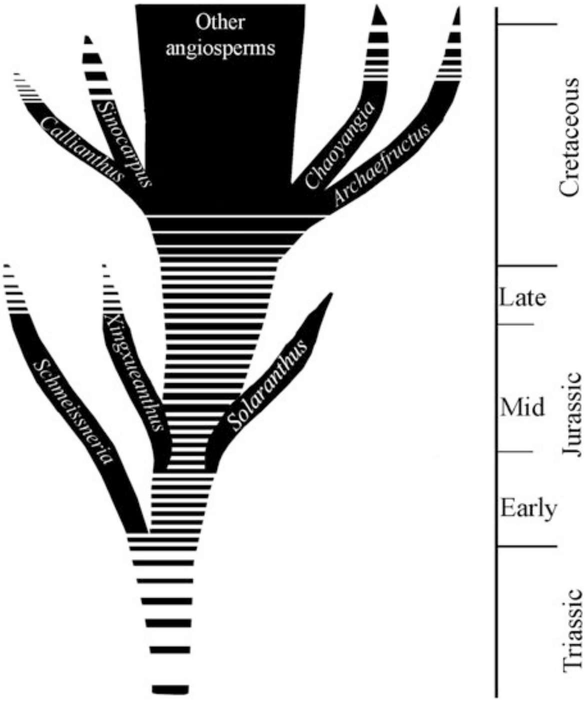


Fig. 6.43 A scenario of diversification of angiosperms in the Mesozoic

living ones (Endress 2008), and the whole “inflorescence” in general organization looks more like a cone.

Solaranthus daohugouensis Zheng et Wang

Diagnosis: Currently the same as that of the genus.

Description: The “inflorescences” are up to 5.7 cm long and 2.2 cm wide, bearing up to 27 “flowers” closely (Figs. 6.31, 6.32, 6.33, 6.34, and 6.35) or sparsely spaced (Fig. 6.33) along an axis. The “flower” includes a stalk, a peltate head, stamen, “tepals”, and carpel-like structures (Figs. 6.31, 6.32, 6.33, 6.34, 6.35, and 6.36b, 6.41a, 6.42). The stalk is about 0.5 mm in diameter, connecting the “flowers” to the “inflorescence” axis. The peltate head is hexagonal (rarely pentagonal) in abaxial view, 2–3 mm in diameter in the distal and 4–4.5 mm in the proximal, about 2 mm high, with a papilla on each polygonal epidermal cell (Figs. 6.36b, 6.41a, and 6.42). The stamens are in grouped in several separate fascicles, distinct, heterandrous, probably bisporangiate (Figs. 6.36d, e, 6.38a–h, and 6.39a–e). Up to three fascicles are on each side of the hexagon/pentagon, inserted on the periphery of the peltate head (Figs. 6.36d, e, 6.38a). The filaments are slender and cylindrical, up to 1.1 mm long and 30–67 μm in diameter (Fig. 6.38c, d, f). The anther of the filamentous “stamen” is bilobate in shape, exserted, 0.7–1.7 mm long and 0.5–0.8 mm wide (Figs. 6.36d, e and 6.38e–g). The sessile “stamen” is close to triangular in shape, about 680 μm high and 530 μm wide at the base (Fig. 6.39a–b). In situ pollen grains are monocolpate, 23–38 μm long and 13–23 μm wide, psilate or with irregular sculpture (Fig. 6.39h, i). The pollen wall is layered, including a foot layer 14–18 nm thick, a rodlet layer 60–70 nm thick, and a vestigial additional layer (Fig. 6.39j, k). The rodlet layer has many rodlets perpendicular to the foot layer (Fig. 6.39j, k). The “tepals” are inserted on the proximal rim of the peltate head, one to three per side (Figs. 6.36b, 6.38b, and 6.41a). The “tepals” are triangular to lingulate in shape, about 1.5–2.7 mm long and 0.6–0.9 mm wide, alternate, in more than one cycle (Figs. 6.36c and 6.37b–d). The gynoecium is up to 3.5 mm in diameter, with numerous carpel-like structures inserted on the proximal surface of peltate head (Fig. 6.40a, d, e). Carpel-like structures are distinct, ellipsoidal, 0.5–1.4 mm long and 0.35–0.88 mm wide (Figs. 6.39f, 6.40a–f, and 6.41b–c). Ovule-like structures are enclosed in carpel-like structures (Fig. 6.40b, c, f, and 6.41a–d). In a large carpel-like structure the ovule-like structure is situated at the “ovary” base, free from the “ovary” wall, 307 μm high and 189 μm wide (Fig. 6.41d). Volcanic ash can enter any non-occluded space (Fig. 6.40f–h) but is absent in the carpel-like structure (Fig. 6.40f).

Holotype: PB21046.

Further specimens: B0179, B0201, PB21107, 47-277, GBM3.

Repository: PB21046, PB21107, in NIGPAS; B0179, B0201, in IVPP; 47-277, in STMN; GBM3, SFLBG.

Etymology: *daohugou-* for the Village of Daohugou, where the specimens were collected.

6.3.4 Affinity

Although both are bisexual, *Solaranthus* has little relationship with Bennettitales since they each have a distinct and different general organization. The reproductive organs in Bennettitales may be dioecious or monoecious. Their monoecia may be comparable to *Solaranthus*, but their ovules/seeds in monoecious plants are borne on a cone-shaped receptacle and dispersed among interseminal scales, surrounded by pollen organs and further by bracts (Rothwell and Stockey 2002; Stockey and Rothwell 2003; Crane and Herendeen 2009; Rothwell et al. 2009). This is distinct from the situation in *Solaranthus*. Therefore this alternative is dropped.

The general organization of the whole structure and arrangement of peltate heads in *Solaranthus* are similar to those of equisetalean cones. However, the presence of filamentous "stamens" and "tepals" in *Solaranthus* makes further comparison impossible.

An enclosed ovule is a feature seen only in angiosperms. Thus this feature can be used as an index feature for angiosperms (see Chap. 3 for details). Usually the existence of such a feature in fossil plants is very hard to confirm. However, the preservation of *Solaranthus* makes this possible. The specimens are preserved in micron-scale fine volcanic ash (Fig. 6.40g, h), which is almost ubiquitous and occur in any accessible cavity, including the miniscule space under the cuticle layer (Fig. 6.40g, h). They are present in space surrounding the carpel-like structures (Fig. 6.40a–c, f), but absent from the ovule-like structure enclosed in the carpel-like structure (Fig. 6.40f), implying the complete enclosure of that ovule-like structure by the carpel-like structure. This inference is in line with the ovule-like structure within the carpel-like structure in Fig. 6.41a–d, where the ovule-like structure is coherently attached to the carpel-like structure. These together prove the existence of an ovule-like structure and its complete enclosure by a carpel-like structure.

The unusual arrangement and orientations of the floral parts in the "flowers" of *Solaranthus* make their homology with living angiosperms difficult. The "flowers" of *Solaranthus* are far beyond the scope of typical flowers seen in living angiosperms though they have their ovule-like structure enclosed, which is a feature unique to angiosperms. An alternative interpretation is that angiospermy had been reached by some seed plants before the occurrence of the angiosperm ancestors that gave rise to the angiosperms living today. Whatever the interpretation, at this time *Solaranthus* cannot be related to any known angiosperm. This leads to another question: "Is angiospermy unique to angiosperms or not?" If yes, *Solaranthus*, without any question, would have to be placed in angiosperms. If no, then the current understanding and definition of angiosperms would need modification to distinguish "real" angiosperms from those seed plants with angiospermy, which may well be a grade of evolution rather than a characteristic feature of a specific group of seed plants.

6.3.5 Implications for the Origin of Angiosperms

The Mostly Male Theory predicts that angiospermous flower may be derived from the male part of Corystospermales, in which the pollen sacs are hanging on the lower surface of a foliar structure, as in *Pteruchus* and *Pteroma* (Frohlich and Parker 2000). This theory may have been realized through diverted development, during which some superfluous parts may evolve to perform new functions (Crane and Kenrick 1997). If some microsporangia in the organs of Corystospermales were metamorphosed into megasporangia, some into "tepals", and their pollen sacs bearing foliar structure into a peltate head, then these transformed microsporophylls of Corystospermales may become something similar to *Solaranthus*. While the Mostly Male Theory lacks fossil data support and is frequently criticized, it appears that *Solaranthus* may lend some support to this theory. In the past, studies based on DNA and those based on morphological data are rarely in good agreement (Frohlich and Chase 2007), but *Solaranthus* may narrow the gap between them. Interestingly, if the stamen and "tepals" of *Solaranthus* were ignored, the peltate head bearing carpel-like structures would look like the seed-bearing peltate head of *Peltasperm* (Peltaspermales), so the relationship among Corystospermales, Peltaspermales and *Solaranthus* (angiosperm) would become an intriguing challenge in the coming years.

If it is an angiosperm, the occurrence of *Solaranthus* in the Middle Jurassic would be surprising to many palaeobotanists. Although this new fossil evidence conflicts with the scientific context in which we have been taught, it is in line with the pre-Cretaceous-angiosperm hypotheses based on Jurassic and Early Cretaceous plant reproductive organs (Wang et al. 2007b, c; Wang 2009, in press; Wang and Zheng 2009; Wang and Wang 2010) and pollen grains (Cornet 1989a; Cornet and Habib 1992; Hochuli and Feist-Burkhardt 2004). First, these fossils are mutually corroborative. More and more Jurassic angiosperm traces are attracting increasing attention, so ignoring them does not contribute anything to science. Probably the best way is to deal with them in an alternative and better way. Second, even if the Jurassic and earlier fossil evidences were ignored, the unexpectedly high diversity in the Yixian Formation (Duan 1998; Sun et al. 1998, 2001, 2002; Leng and Friis 2003; Ji et al., 2004; Leng and Friis 2006; Wang and Zheng 2009), which currently is the oldest strata yielding megafossils of reproductive organs of angiosperms widely-accepted, would be "abominable" and defy an interpretation. It appears most likely that those early angiosperms may have masqueraded in gymnospermous coverage and evaded our attention.

The general organization of *Solaranthus* is similar to the cones of gymnosperms. The "flowers" are spirally arranged along an axis, as bract-scale complexes in coniferous cones. Although the gymnospermous appearance and angiospermous identity of *Solaranthus* may appear paradoxical, it helps to explain the following. First, this makes *Solaranthus* a cryptic angiosperm. Its identity would have remained elusive had not enough attention been paid to its female part. If *Bayeritheca* were later proven to be congeneric to *Solaranthus*, it would remind us of how careful we should be when studying fossil plants. Second, this makes the so-called transition between gymnosperms and angiosperms smoother than previously thought. Probably more careful examination of pre-Cretaceous fossil plants will bring a new perspective on early angiosperms and their history, and more cryptic "pre-historic" angiosperms will be recognized. Third, this non-typical arrangement of floral parts in *Solaranthus* may well represent the fluidity of organization in early angiosperms. Similar fluidity has been seen in the gametophyte of the basal angiosperm *Amborella* (Friedman and Ryerson 2009). According to study on living basal angiosperms, heterandry is not seen in basal angiosperms (Endress 2010). Therefore heterandry appears derived from the perspective of living angiosperms. The presence of heterandry in *Solaranthus* implies that there may have been function differentiation among the stamens, for feeding and pollination (Barrett 2010). This derived-appearing status of *Solaranthus* suggests an earlier origin of angiosperms.

6.4 General Summary

The plant fossils documented in Chaps. 5 and 6 represent a few of many plants from the Jurassic and Early Cretaceous that have demonstrated the character of angio-ovuly. Angio-ovuly currently is a feature only seen in angiosperms and never seen in gymnosperms. If this generalization holds, it appears that angiosperms have occurred in the Jurassic, much earlier than the currently accepted age for angiosperms. This conclusion will influence our perspective on the evolution and history of angiosperms. The so-called "abominable mystery" appears to be a consequence of prolonged interaction between angiosperms and their environments. The presence of angiosperms in the Jurassic also changes the information assemblage on which many evolutionary theories and interpretations are based. For example, one of the reasons to reject Cornet's claims of early angiosperms from the Triassic was the lack of angiosperms in the Jurassic. Although the new data in this book do not necessarily change the affinity of those interesting plants, it does bridge the gap. The earlier occurrence of angiosperms also helps to bring angiosperms closer to their gymnosperm ancestors, in time and morphology, and thus sheds a new light on the systematics of seed plants.

Chapter 7
Trace of Possible Angiosperms in the Jurassic

In addition to those fossil plants that can be put in angiosperms without reservation, there are more fossil plants that are most likely angiosperms, but the current knowledge on them does not allow the author to put them in angiosperms according to the criterion proposed in Chap. 3. In this chapter, two of these plants are briefly documented. These two show combinations of characters that are never seen in gymnosperms, but are frequently seen in angiosperms. Their angiosperm-like traits prompt the author to share their information with the readers. It is hoped that future study will elucidate whether they are angiosperms or just angiosperm-like gymnosperms.

7.1 Taxon A

The specimens of Taxon A include two facing parts of the same flower-like organ (Fig. 7.1a, b). It is distinct from any fossil plants recognized from the region. Although the current information about the plant is not enough to ensure its position in angiosperms, its flower-like appearance is too intriguing to ignore. Due to its strong similarity to angiosperms, angiospermous terms are used below to describe the specimen for the sake of communication since gymnospermous terms, if used, would introduce uncertainty and confusion rather than useful information. However, using angiospermous terms does not mean that the author is committed to assigning it to angiosperms. If future study proves the fossil belongs to a gymnospermous group, the following description should be changed accordingly.

7.1.1 Diagnosis

Taxon A
(Figures 7.1–7.3)

Diagnosis: Organ including more than one cycle of floral parts. All floral parts attached to the receptacle. Distal of sepal-like parts missing, with only

X. Wang, *The Dawn Angiosperms*, Lecture Notes in Earth Sciences 121,
DOI 10.1007/978-3-642-01161-0_7,

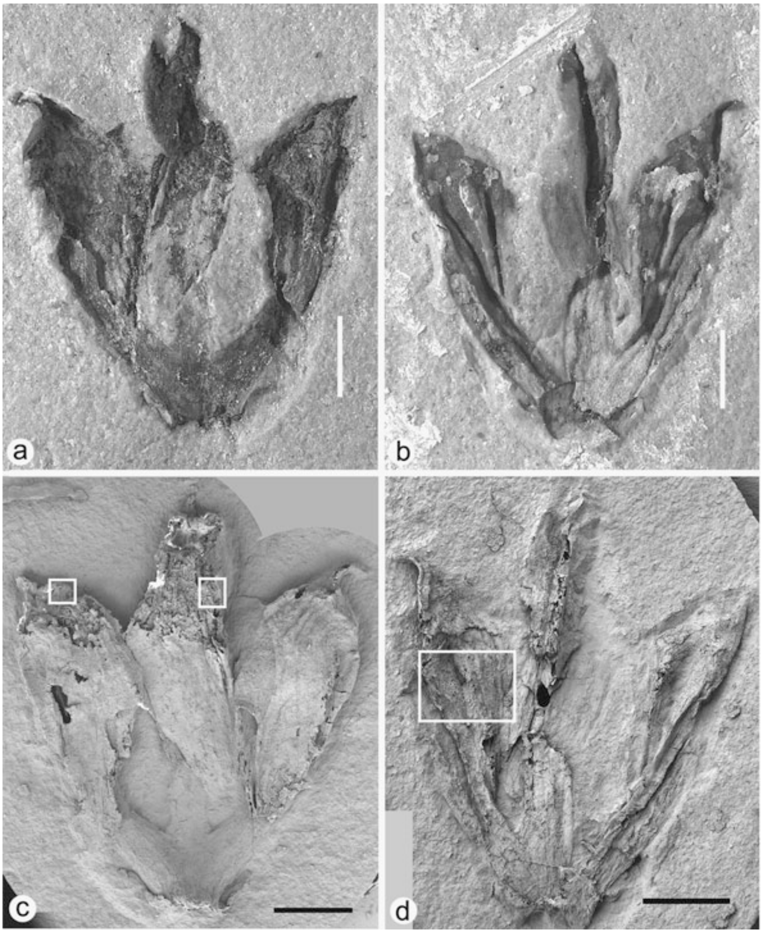


Fig. 7.1 Two facing parts of Taxon A, LM (**A** and **B**) and SEM (**C** and **D**). Note the arrangement of the petal-like parts. The regions in the *rectangles* will be detailed in later figures. Bar = 1 mm

stubs remaining. Petal-like parts probably of two facing pairs, elongate, with pointed tips. Innermost parts branching upward, including at least three individual parts, attached to the receptacle.

Description: Organ is about 5.2 mm long and 4.24 mm wide, preserved on two facing slabs (Fig. 7.1a–d). The organ consists of more than one cycle of floral parts (Figs. 7.1a–d and 7.2a, b). The outermost cycle includes relic floral parts, which are probably connated and missing their distal portions (Figs. 7.1b, d and 7.2b). The shape of the whole floral parts is unknown and their stubs are about 0.5 mm long (Fig. 7.2b). Inside of this cycle are probably four petal-like parts in two facing pairs, attached to the receptacle at the base of the organ (Figs. 7.1a–d and 7.2a, b). Each petal-like part is

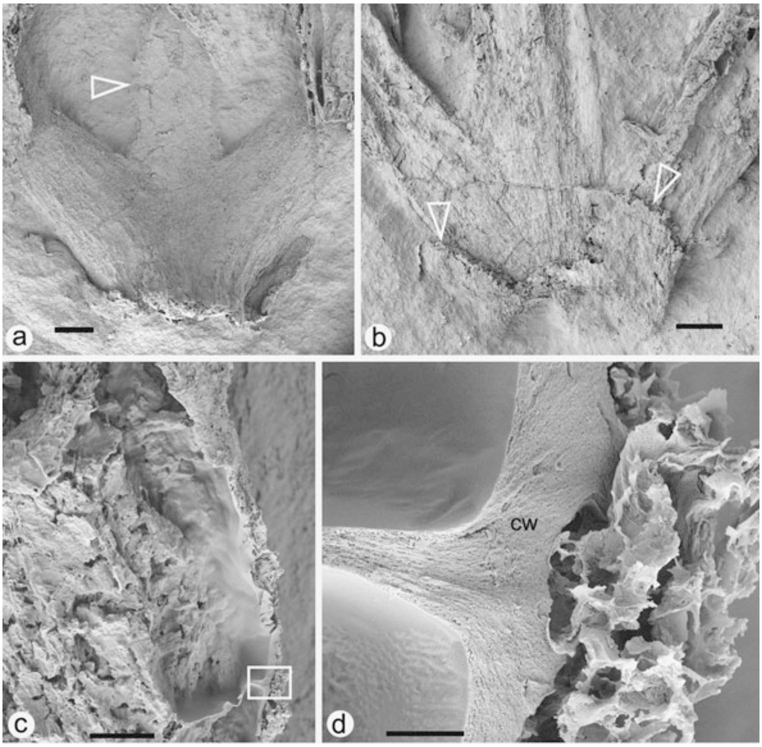


Fig. 7.2 Details of Taxon A, under SEM. **A** A detailed view of the basal portion of the organ shown in Fig. 7.1c. Note the trifid arrangement of the three parts, *arrow* points to the central one. Bar = 0.2 mm. **B** The basal portion of organ shown in Fig. 7.1d. Note there are extra appendages besides petal-like parts. Bar = 0.2 mm. **C** A detailed view of right rectangle in Fig. 7.1c. Note the cell lumen adjacent to the epidermis. Bar = 50 μm. **D** A detailed view of rectangle in **C**. Note, from *right to left*, cuticle, cell wall (cw), and cell lumina. Bar = 5 μm

about 4.2–4.7 mm long and 1.2–1.3 mm wide, probably lanceolate in shape, with a narrow basal portion, widest in the upper middle, with a pointed tip (Figs. 7.1a–d and 7.2a, b). There are longitudinal striations on the surface of the petal-like parts (Figs. 7.2b and 7.3b). Sometimes the cellular details can be seen in the petal-like parts (Fig. 7.2c, d). Innermost are floral parts whose identity is obscure (Fig. 7.2a). These parts are inserted on the apex of the receptacle and include at least three individual parts that branch trifidly (Fig. 7.2a). Possible in situ pollen grains, elliptical in shape, 121 μm long and 70 μm wide, with smooth sculpture (Fig. 7.3a, c). The exact relationship between these pollen grains and other floral parts is obscure.

Remarks All floral parts in Taxon A are attached to the same basal part, probably equivalent to a receptacle. It appears that at least the petal-like parts are arranged in cycles. The extra appendages outside the petal-like parts look like sepal in flowers

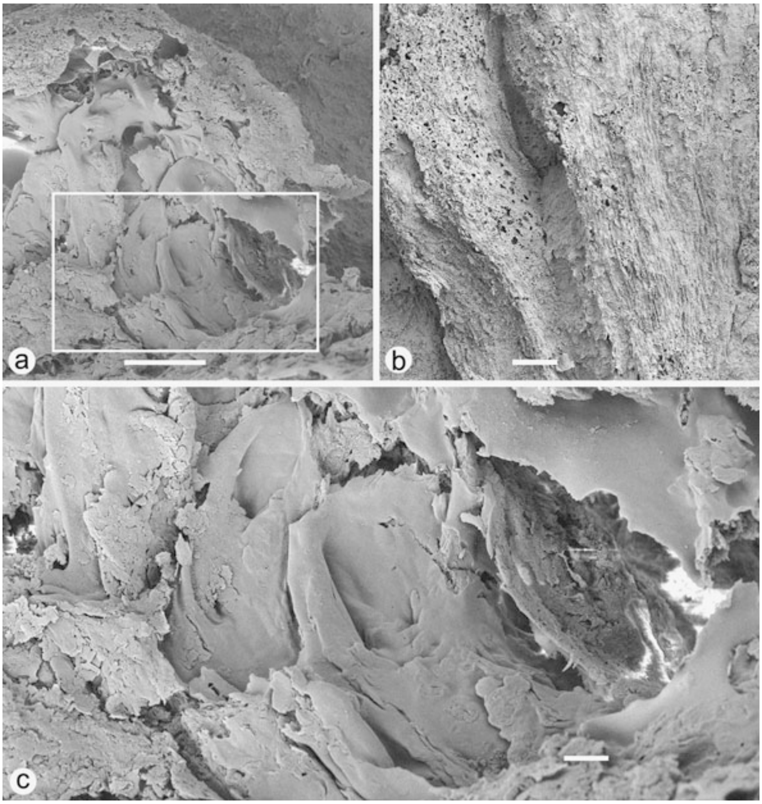


Fig. 7.3 Details of Taxon A, under SEM. **A** Detailed view of the *left rectangle* in Fig. 7.1c. Note the epidermis toward the top, and possible in situ pollen grains. Bar = 50 μm. **B** Detailed view of *rectangle* in Fig. 7.1d. Note the longitudinal striations on the surface of the organ. Bar = 0.1 mm. **C** Detailed view of *rectangle* in **A**. Note the smooth surface of possible pollen grains. Bar = 10 μm

in position and they are probably fused to each other. Three petal-like parts are seen in each of the two facing parts. The opposite positioning of two lateral petal-like parts strongly suggests that these petal-like parts are arranged in two facing pairs. It is very likely that there is an additional petal-like part embedded in the sediment.

The innermost floral parts in the organ are probably three to four in number. It is unknown how the possible in situ pollen grains in Fig. 7.3a, c are related to these parts. If related, then the organ may be a male flower. The possibility that this potential male flower belongs to Gnetales, especially *Ephedra*, is very remote since the sepal-like parts have no counterpart is Gnetales.

As said above, the general organization of the organ appears similar to angiosperms. This situation is rarely, if ever, seen in gymnosperms. However, the possibility that Taxon A belongs to a gymnospermous group cannot be completely eliminated for the following reasons. First, the organ does not show unequivocal enclosed ovules, which is required to ensure the identity of a pre-Cretaceous angiosperms (see Chap. 3). Second, if there were an evolution between gymnosperms and angiosperms, it would be assumed that there be a transitional status in which both angiospermous and gymnospermous characters were present in the same plant. At this time, the author cannot exclude the possibility that Taxon A is such a transitional fossil plant.

Specimens: CNU-Plant-2010-001a&b.
Locality: Daohugou, Ningcheng, Inner Mongolia, China.
Stratigraphic horizon: The Jiulongshan Formation (Daohugou Formation), Middle Jurassic (>164 Ma).
Depository: CNU.

7.2 Taxon B

Specimens of Taxon B include two facing parts of the same fruit-like organ (Fig. 7.4a, b), distinct from any other fossil or living plants known in the region. Limited by currently available information, the plant cannot be placed in angiosperms with confidence. However, its flower-like appearance justifies a documentation. Angiospermous terms are used to describe the specimen because gymnospermous terms cannot convey the information efficiently. This does not mean, however, that the author considers it an angiosperm.

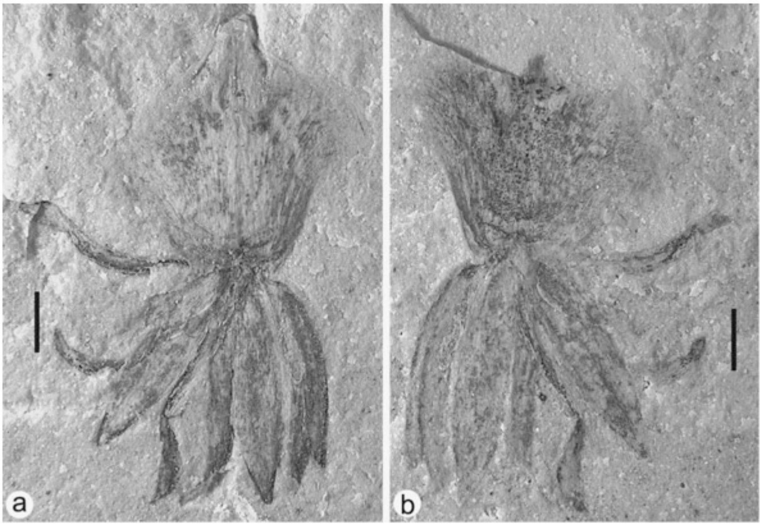


Fig. 7.4 Two facing parts of Taxon B, under light microscope. Note the apical fruit and drooping tepals in the base. All bar = 1 mm

7.2.1 Diagnosis

Taxon B
(Figures 7.4–7.6)

Diagnosis: Organ including an apical fruit-like structure and more than one cycle of drooping tepals at the base.

Description: The whole organ is about 8.1 mm long and 5.8 mm wide (Fig. 7.4a, b). The organ consists of two parts, an apical fruit and cycles of tepals at the base (Figs. 7.4a, b and 7.5a–c). The fruit is about 4.1 mm long and 4.2 mm wide, widest in the upper portion, narrowing rapidly to the apex, with a truncated/broken tip and a base about 2 mm wide (Figs. 7.4a, b and 7.5a–c). There are well defined cellular details on the surface of the fruit (Figs. 7.5c and 7.6a, b). The cells in the apical region are delimited from other regions by evident changes in cell dimension and arrangement (Fig. 7.6a, b). The cells in this region are about 70–162 μm long and 14–38 μm wide, much wider than cells in the adjacent regions. Tepals are about 3.7 mm long and 0.85 mm wide, lanceolate, probably in more than one cycle (Figs. 7.4a, b and 7.5a, b).

Remark The truncated tip of the fruit suggests that the original distal portion of the fruit is missing, implying that there should have been a style-like structure at the top of the fruit. Considering style-like projections are only seen in angiosperms, Gnetales, Erdtmanithecales, and Bennettitales (the latter is apparently out of the question here) and the cellular details at the fruit apex do not show anything similar to the structures around micropylar tubes in Gnetales and Erdtmanithecales (Friis et al. 2009), which usually is bracketed by an outer envelope (a separate layer), Taxon B appears very likely to be an angiosperm element.

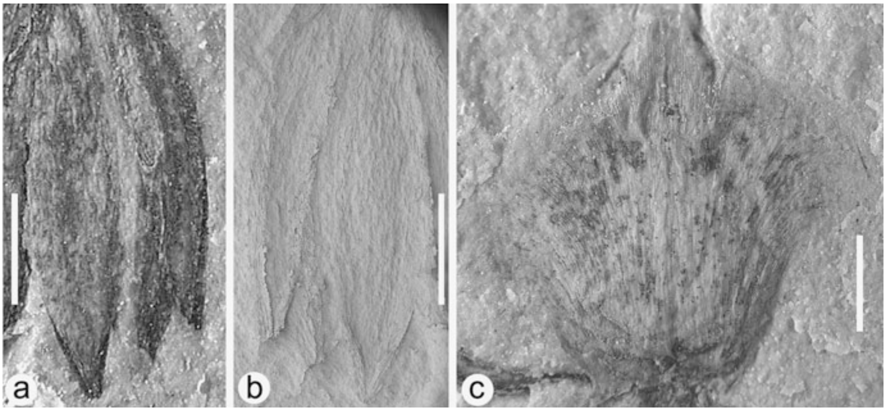


Fig. 7.5 Details of Taxon B. **A** Detailed view of the lanceolate tepals. LM. **B** Mirror image of the same region as in **A**. Note the tepal margins and rugose surface. SEM. **C** Detailed view of the apical fruit. Note the shape and cellular details on the surface. LM. All bars = 1 mm

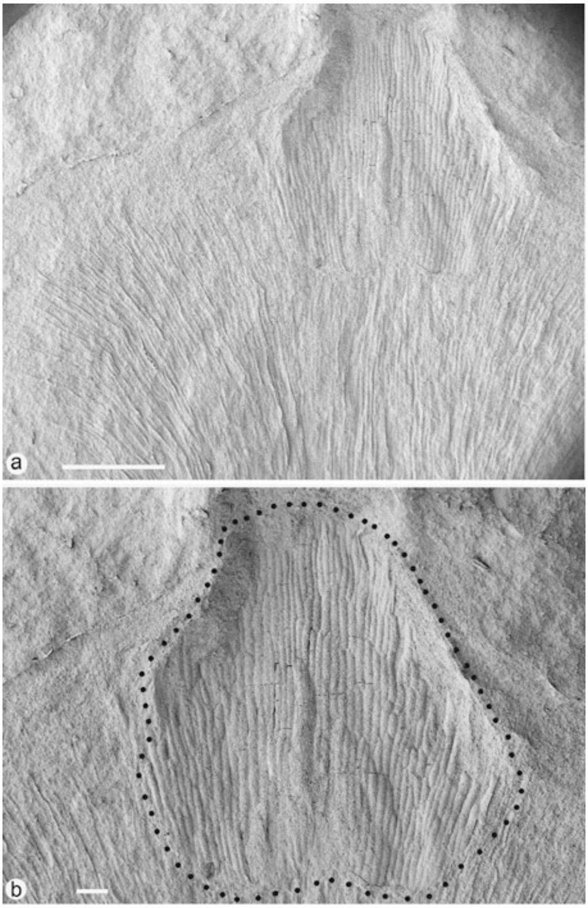


Fig. 7.6 Details of Taxon B. SEM. **A** Further detailed view of the fruit. Note the radial arrangement of cells. Bar = 0.5 mm. **B** Close-up of the apical region of the fruit. Note the cells within the *dotted line* are different from the adjacent cells. Bar = 0.1 mm

The tepals appear to overlap each other (Fig. 7.5a, b), suggesting that there are more than one cycle of tepals in the fruit. Their attachment to the fruit suggests that the fruit is not completely mature. The droopiness of the tepals implies that the tepals are not rigid and lack strong support tissue, which is more frequently seen in gymnospermous leaves or scales. Such arrangement of tepals is never seen in gymnosperms. All these strongly suggest that Taxon B is very likely an angiosperm fruit.

Considering its Middle Jurassic age, Taxon B is put as a fossil plant with a suspected angiospermous affinity.

Specimens: PB21391.
Locality: Daohugou, Ningcheng, Inner Mongolia, China.
Stratigraphic horizon: the Jiulongshan Formation (Daohugou Formation), Middle Jurassic (>164 Ma).
Depository: NIGPAS.

Chapter 8
Making of the Flower

Making of the flower is the key question in the origin of angiosperms. Two rivaling schools in botany have been fighting against each other on the nature of carpel in the past centuries. This prolonged controversy over the carpel may end if placenta is isolated from carpel. This separation is supported by evidence from various fields. Observations of the organization of floral parts in some angiosperms indicate that the formerly assumed primitive carpel may not be so primitive. Extrapolation from the floral organization of Caryophyllales leads to a new hypothesis of flower forming and points to Palaeozoic Cordaitales-related groups for the ancestry of angiosperms. Although this new hypothesis can answer many formerly difficult questions, as a hypothesis, it still needs more evidence to test.

The most characteristic feature of angiosperms is their flower, which distinguishes them from all other seed plants. With carpels the flowers provide much better protection for their ovules. This protection and isolation of ovules from the outside lead to many changes in biological behavior and contribute to the past and current success of angiosperms. Thus the core question in the origin of angiosperms is the appearance of the flower, and the core question in the latter is the occurrence of the carpel.

8.1 Definition of a Carpel

8.1.1 Difficulties for Applying the Classic Definition

Before commencing a detailed discussion, it is necessary to clarify the definition of a carpel, namely what a carpel is, because to a "science which prides itself upon precision of language, any confusion in terms is a reproach" (Puri 1952). Ironically, botanists who have been using the term "carpel" almost everyday for long time cannot reach a consensus on its definition. The classic definition for a carpel is an upward-folded leaf-like organ that bears and encloses ovules (Eames 1931). Although this definition has received some support from morphology of extant angiosperms (Eames 1961; Tahktajan 1980; Cronqist 1988) as well as fossil evidence (Crane and Dilcher 1984; Dilcher and Crane 1984; Dilcher and Kovach

X. Wang, *The Dawn Angiosperms*, Lecture Notes in Earth Sciences 121,
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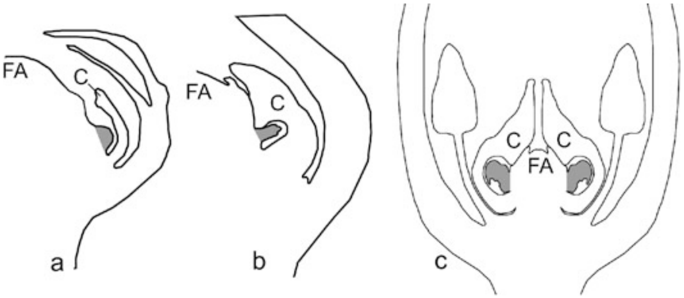


Fig. 8.1 Enclosing ovules by floral apex and carpel in Gyrostemonaceae (**A**, **B**) and Phytolaccaeceae (**C**). Note the ovule (*gray*) and its spatial relationship relative to the floral apex (FA) and enclosing carpel (**C**). **A** and **B** are redrawn after Hufford (1996), **C** drawn after Decraene et al. (1997)

1986; Retallack and Dilcher 1981a; Sun et al. 1998, 2001, 2002; Ji et al. 2004; Leng and Friis 2003, 2006) and has been widely used, it cannot be applied universally to all living angiosperms (Boke 1964; Sattler and Lacroix 1988) (Figs. 8.1a–c and 8.3b–e). According to detailed morphological and anatomic observations, flowers in many families do not fit this definition (Boke 1964; Puri 1952; Sattler and Lacroix 1988). Eames (1961) admits the existence of such cases and interprets some of them as carpel closed by "adnation to receptacle". Sattler and his colleagues think that there are two types of gynoecia in angiosperms, "carpellate" and "acarpellate". In the first type, carpel encloses and bears ovules, while in the second, carpel only encloses but does not bear ovules. Many angiospermous gynoecia are "acarpellate", which have been noted in 11% of the angiospermous families (Sattler and Lacroix 1988). This confliction between classical concept and actuality forces botanists and the author to search for a more applicable definition for carpel.

8.1.2 Converging on a New Definition

According to the developmental genetic studies of model plant *Arabidopsis*, the carpel is derived from eight ancestral cells in a linear arrangement in the floral meristem, supporting the foliar nature of the carpel, while the placenta is a separate part (Bowman et al. 1999). Based on gene expression pattern, Skinner et al. (2004) reach the conclusion that the placenta is a shoot independent of the carpel. This is in agreement with studies of vascular anatomy, which is more conservative and informative (Eames 1926). For example, the carpels and placentae have separated vascular bundles in the Ranunculaceae (Thompson 1934) and many other families (Laubengayer 1937; Puri 1952; Sattler and Lacroix 1988). Fagerlind (1946), Taylor (1991), Doyle (2008), and Rudal and Bateman (2010) also call for effort to relate angiospermous flowers to secondary shoot and subtending bract in gymnosperms. Based on their observations and analyses of various types of gynoecia, Sattler and

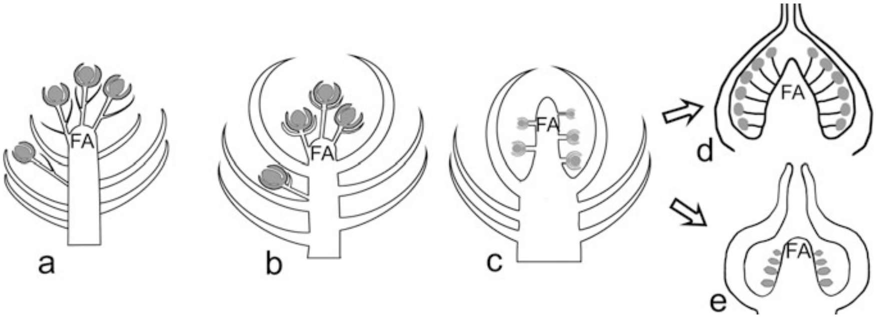


Fig. 8.2 Diagrams of cordaitalean secondary shoots (**A**, **B**) and their derivatives (**C–E**). **A** A secondary shoot of Cordaitales. Note the ovules interspersed with sterile scales, and ovular stalks with bracteoles. **B** Another secondary shoot of Cordaitales. The bracteoles on the ovular stalks aggregate to the ovule as the ovular stalks become shorter than in **A**. **C** An imagined female reproductive organ derived from Cordaitales. The ovules have two integuments and are concentrated at the floral apex. The sterile scales are covering the floral apex. **D**, **E** More reproductive organs possibly derived from Cordaitales-like plants, only the gynoecium portion is shown. Note the arrangement of the ovules on the floral apex and ovular stalks of various lengths. All ovules are in *gray*. FA = floral apex

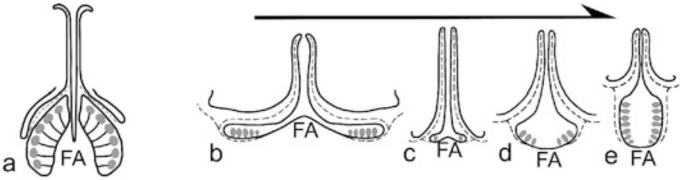


Fig. 8.3 Gynoecia of the Portulacaceae (**A**) and Cactaceae (**B–E**). **A** Gynoecium with free central placentation in the Portulacaceae. Note its similarity to Fig. 8.2d. **B–E** Flowers in Cactaceae. Note the reduction and recession of the floral apex in the series, ovules on the floral apex, as well as little change in the carpels in these longitudinal sections. **B** *Pereskia pititache*. Note its similarity to Fig. 8.2e. **C** *Pereskia aculeata*. **D** *Pereskia sacharosa* or *P. corrugata*. **E** *Opuntia stenopetala*. **B–E** are redrawn after Boke (1964), **A** is redrawn after Payer (1857). The broken lines stand for vascular strands. All ovules are in *gray*. FA = floral apex

Perlin redefined a carpel as “a gynoecial appendage that encloses the ovule(s) but does not necessarily bear them” (Sattler and Lacroix 1988). This treatment is logical if the history of land plants is taken into consideration. Since ovules have been seen in seed plants that are dated back to the Devonian and the record of carpel-bearers (angiosperms) currently is restricted to the Mesozoic (Friis et al. 2005, 2006; Wang et al. 2007b, c; Wang and Wang 2010; Wang and Zheng 2009), ovules and their bearers apparently should have a much longer, distinct history than that of carpels and should be separated from the latter (Bowman et al. 1999).

The enclosure of ovules in angiosperms is accomplished by the ovary wall, which consists of either the carpel alone (Eames 1931, 1961) or both carpel and the floral apex (Boke 1964; Hufford 1996; Sattler and Lacroix 1988; Decraene 1997). According to Sattler and Perlin, the function of the carpel is only to protect the

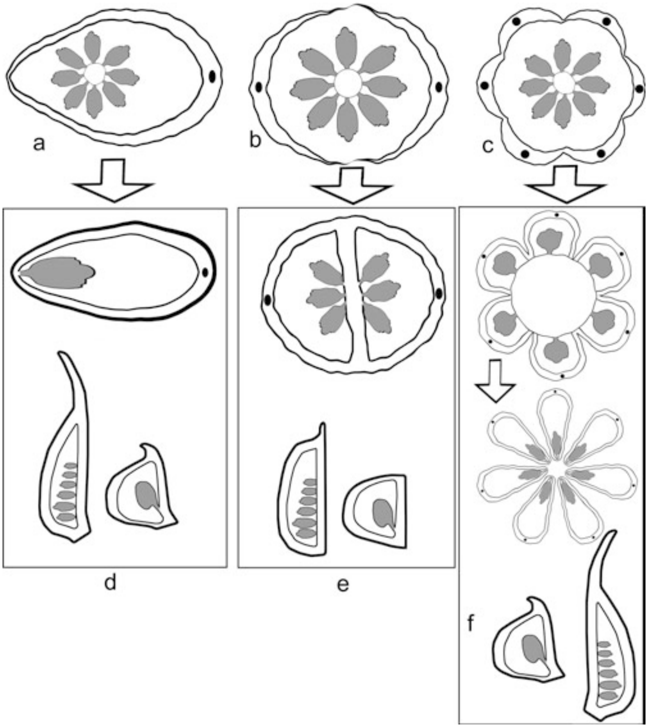


Fig. 8.4 Possible relationship among different placentation. Note the variable number of carpels surrounding the placenta in **A**–**C**. Each of them may give rise to other types of placentation (**D**–**F**) through metamorphoses, following the direction of the *arrows*. All ovules are in *gray*

ovules (Sattler and Lacroix 1988). For example, the Basellaceae does not have a carpel in the classic sense and its ovule is inserted onto the floral apex rather than on either margin of the carpels (Sattler and Lacroix 1988; Fig. 8.5c). In the Gyrostemonaceae, the ovules are borne on the periphery of the floral apex and covered by the carpels that initially only subtend the ovules but latter bend over and surround the ovules (Hufford 1996; Fig. 8.1a, b). In the Cactaceae, numerous ovules inserted on the floral apex are under the coverage of several carpels that converge over the floral apex forming an ovary (Boke 1964; Fig. 8.3b–e), which is simply a hollow under the carpels. In Ranunculus, the carpels also initially subtend rather than enclose the ovules (Fig. 321d, Haupt 1953). Similarly, ovules borne on the central column are gradually covered and enclosed by carpels from bottom up in Caryophyllaceae (Lister 1884; Thomson 1942). This partially explains why Thompson (1934) completely rejects the existence of carpels in traditional sense.

If there is only one ovule to be enclosed by a single carpel, the carpel may surround the ovule at its abaxial and lateral sides (Figs. 8.1a–c and 8.4d–f), as in Ranunculaceae, Gyrostemonaceae, and Phytolaccaceae (Figs. 30–31, Thompson 1934; Figs. 16–22, Hufford 1996, Figs. 6 g, 7a–b, Decraene et al. 1997). When there

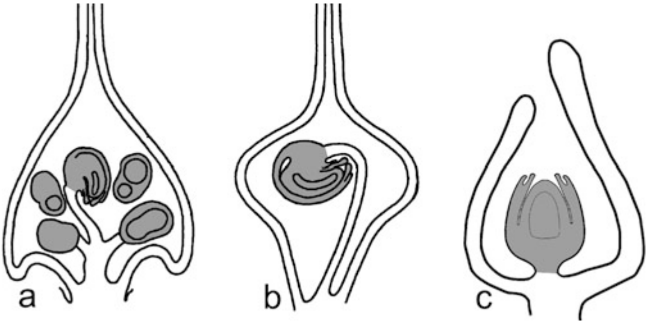


Fig. 8.5 Derivation of a basal ovule from free central placentation. Note the number of ovules is reduced from many to one in the series from **A** to **C**. **A** and **B** are redrawn after the figures of Amaranthaceae in Joshi (1938). **C** shows the ovary with a basal ovule in Basellaceae. All ovules are in *gray*

are numerous ovules to be enclosed by a single carpel and these ovules are borne on the periphery of the floral apex, an ovary with free placentation may come to form, as in *Delphinium consolida* as described by Baillon in 1880 (Vuillemin 1926; Thompson 1934; Puri 1952; Fig. 8.4a). When the floral axis is appressed to the ventral margins of the only carpel, it may form placentation as seen in *Aquilegia, Aconitum, Delphinium* (Ranunculaceae) (Fig. 8, Baillon 1871), Fumariaceae (Judd et al. 1999; Payer 1857), and Fig. 8.4d. When there are numerous ovules to be enclosed by multiple carpels and these ovules are borne on the periphery of the floral apex, these carpels may either collectively converge and cover the floral apex (as in Caryophyllaceae, Lister 1884; Cactaceae, Boke 1964; Figs. 8.3b–e and 8.4c), forming free central placentation, or each carpel contains an ovule or a file of ovules on the floral apex, forming axile placentation. The ovary in Cactaceae is rejected by A. Berger, who thinks that there is no true ovary and the ovules are borne in a hollow at the base of the styles, as in *Pereskia aculeate* (Boke 1964; Fig. 8.3c). Papillae on the carpels may fill up the space between carpels and form the transmitting tissue (Boke 1964; Bowman et al. 1999; Decraene et al. 1997).

Despite the above interpretation, many botanists may still tend to stay with the classic definition of carpel. This is understandable as Lam (Puri 1952) put it, there is “too much inertia to readily abandon the names and concepts with which we have grown up scientifically”. The classic definition of carpel has been well-entrenched and has been taught in classrooms for decades. But it is poorly applicable for Phytolaccaceae because the so-called “continuous adaxial parts” of carpel in *Phytolacca* (Decraene et al. 1997) are actually a part of the floral apex and the “abaxial part” of the carpel (= carpel, in new sense) has an evident border with the floral apex at its base (Fig. 7b, Decraene et al. 1997), which is suggested by the spatial arrangement of the cells. The same can be said of situations in the Cactaceae, Basellaceae, Gyrostemonaceae, and probably other families.

Despite a long history dating back to 1849 (Thompson 1934), the axial theory for carpels has been the subject of criticism. According to Eames (1961), in the

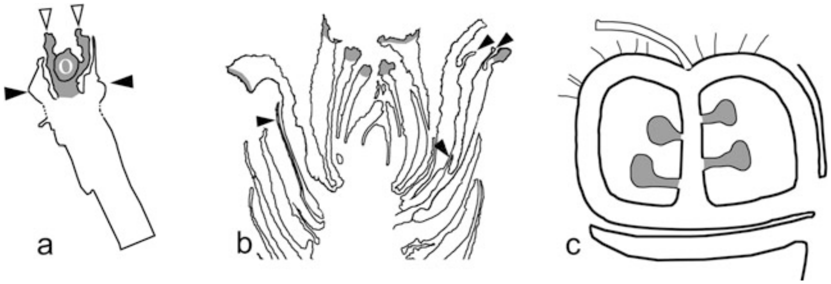


Fig. 8.6 Fossil evidence from the Permian and Jurassic. **A** Ovule of *Cordaianthus duquesnensis* from the Permian. Note the ovule (o) with additional appendages (*black triangles*) besides integument (*arrows*). **B** Secondary shoot of *Cordaianthus duquesnensis* with apical fertile scales bearing ovules. Note bracteoles on the ovular stalks (*black triangles*). **C** Ovary of *Xingxueanthus sinensis*, a Middle Jurassic angiosperm, with free central placentation. **A** and **B** are redrawn after Rothwell (1982). All ovules are in *gray*

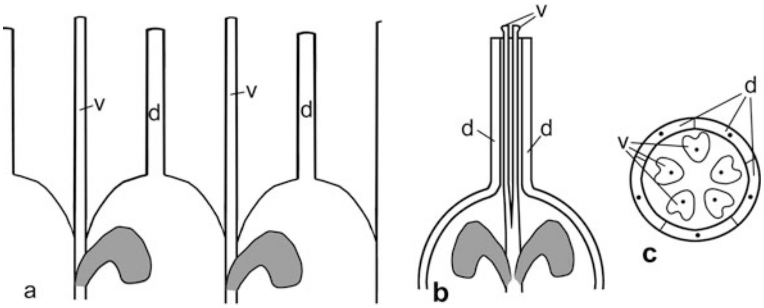


Fig. 8.7 Floral diagrams of *Pyrola elliptica* (Pyrolaceae). **A** Opened gynoecium. Note the ovules (*gray in color*) in the ovary. The so-called "ventral bundle" (v) of the carpel is longer than its "dorsal part" (d) and almost isolated from the rest of the carpel. **B** Longitudinal section of the gynoecium, showing ovules in the ovary, "dorsal parts" (d) of the carpel enclosing their exserted "ventral bundles" (v). **C** Cross section of the style showing the "ventral bundles" (v) of the carpels isolated from the "dorsal parts" (d)

axial theory, "the wall of ovary was considered axial, with carpels merely roofing the ovular chamber and forming the styles and stigmas." Apparently, the flowers in Cactaceae (Boke 1964) are formed exactly in such a way, lending strong support to the axial theory. Furthermore, the appendicular theory for carpels is also undermined by placentae in Amaranthaceae, Juglandaceae, Primulaceae, Portulacaceae, and others (Joshi 1938; Puri 1952). While questioning the axial theory, Eames (1961) says that "If a carpel be considered an axis, it would be a hollow structure containing other axes, the placenta and its branches, the ovules." *Xingxueanthus*, an inflorescence of a Jurassic angiosperm (Wang and Wang 2010), has flowers that have ovaries each with free central placentation inside (Fig. 8.6c). Its organization is almost exactly what Eames (1961) demands his opponents to provide. The occurrence of such evidence in a Jurassic fossil plant, in additional to other evidence from living angiosperms, strongly supports the axial theory for carpels and axial nature of placenta.

Even though the traditional axial theory has gained support from living and fossil angiosperms, it is true that it cannot explain everything, and the dominance of the appendicular theory is not a random event. The latter can account for many phenomena in angiosperms. Actually, both theories emphasize separate aspects and parts of carpels. The distinction between these aspects and parts, unfortunately, are obscured in the classic concept of carpel. This obscurity leads to the conflict between the two schools of thought although both of them are right in their own aspects. If these two parts, carpel and placenta, are separated, it becomes clear that each school of thought is correct about the part it emphasizes. Since apparently every organ in plants was originally derived from dichotomous branches, every plant part is axial in nature in this term, and thus differentiating between axial and foliar nature of plant organ in ancient ancestors would be meaningless. What this book wants to emphasize is that the *immediate* precursor for the carpel was a foliar organ. The classic definition of carpel should be updated and replaced to be in accord with the progress in science. Therefore it is more appropriate to adopt the following definition for carpel:

The carpel is a foliar organ that encloses the placenta, it does not bear ovules.

8.1.3 Derivation of the Carpel

8.1.3.1 Interpreting *Cordaianthus*

Cordaitales are a group of seed plants that flourished in the Carboniferous to Permian (Costanza 1985; Florin 1939; Galtier 2008; Hilton et al. 2009a, b; Rothwell 1982, 1993; Simunek 2007; Wang 1997; Wang and Tian 1993; Wang et al. 2003). Their plant organs are usually preserved as isolated parts and named as organ genera. Thanks to permineralization preservation, many such organs are anatomically well preserved. This allows palaeobotanists to understand the plants, especially their reproductive organs, in detail (Costanza 1985; Florin 1939; Hilton et al. 2009a, b; Rothwell 1982, 1993; Wang 1997; Wang and Tian 1993; Wang et al. 2003). The strobili of Cordaitales include secondary shoots in the axils of subtending bracts arranged either helically, distichously, or tetrastichously along the primary axis. The secondary shoot exhibits determinate growth. Scales, fertile and sterile, are helically arranged along the secondary shoot. The fertile scales are usually found on the distal portion of the shoot, and the sterile ones are proximal. However, there is no distinct border between these two portions, and fertile and sterile scales may be interspersed, or at least so in some taxa (Plate 3, Figs. 19–20, Bertrand 1911; Florin 1944). The fertile scales mature acropetally. Ovules are borne on the distal end of ovular stalks (=fertile scales). The ovules are either exserted or covered by sterile scales. Most of Cordaitales are found living in peat-forming swamp (Costanza 1985; Florin 1939; Hilton et al. 2009a, b; Rothwell 1982, 1993; Wang 1997; Wang and Tian 1993; Wang et al. 2003).

There is an interesting phenomenon in Cordaitales concerning their ovular stalks. Usually ovular stalks are described as longitudinally ribbed and star-shaped in cross section, but sometimes some of them are described as branched or with bracteoles (Florin 1944; Rothwell 1982). Rothwell (1982) has shown that there are additional appendages besides the integuments (Fig. 8.6a) and that there are bracteoles along the ovular stalks (Fig. 8.6b). Florin (1944) thinks that the ovular stalks tend to change from elongated branched into short unbranched (Eames 1952). Bertrand (1911) also demonstrates the existence of bracteoles along the ovular stalk. All these are of pivotal significance in the following derivation of outer integument in angiosperms. Reduction in ovular stalk length promotes such bracteoles to aggregate with the ovule, forming outer-integument-like structure as in Fig. 8.2a–c, which paves the way leading to bitegmic ovules in angiosperms.

8.1.3.2 The Making of Carpels

The carpels in angiosperms can be derived from the scales in ovulate cone of Cordaitales-like plants with the least modifications for the following reasons.

1. The scales in Cordaitales tend to cover, surround, or enclose ovules (Costanza 1985; Florin 1939; Hilton et al. 2009a, b; Rothwell 1982, 1993; Wang 1997; Wang and Tian 1993; Wang et al. 2003). This tendency appears to be a common rule in seed plants, as it has been seen in the evolution of Coniferales (Schweitzer 1963; Wang et al. 2008) and Gnetales (Fagerlind 1946; Eames 1952), suggesting that it may well happen in the ancestors of angiosperms. This may parallel the so-called “Chinese Latern” effect or Inflated-Calyx Syndrome (ICS) seen in Solanaceae (Angiospermae), namely, sepals encapsulating the mature fruit (He et al. 2004; He and Saedler 2005).
2. Female organ of Cordaitales has tens of scales that can be categorized in three types (Wang et al. 2009d). These scales may have the potential to evolve into different organs or floral parts. Some of them may turn into carpels, and others into perianth or various residual organs, such as prophylls (as in Phytolaccaceae, Decraene et al. 1997), arils (as in Papaveraceae, Judd et al. 1999), or hairs (as in Gnetales, Stopes 1918; Fagerlind 1946; Martens 1971).
3. The existence of bracteoles along the ovular stalks and the evolutionary trend of ovular stalks in Cordaitales-like plants make derivation of an outer integument in angiosperms a natural and simple step. As the ovular stalks become shorter, it is possible for these bracteoles to aggregate with the ovule, forming an outer-integument, as in Fig. 8.2a–c. This appears already materialized in some Cordaitales (Rothwell 1982; Fig. 8.6a). This, if correct, would pave the way leading to bitegmic ovules in angiosperms, which, however, have frequently been a challenge for other flower-forming theories. The extra integuments in angiosperms (Eames 1961) can also be derived in this way. Furthermore, the presence of stomata on outer integument (Eames 1961) supports the derivation of integument from a foliar part.

Fig. 8.8 Possible relationships among Cordaitales, Coniferales, Gnetales, and Angiospermae

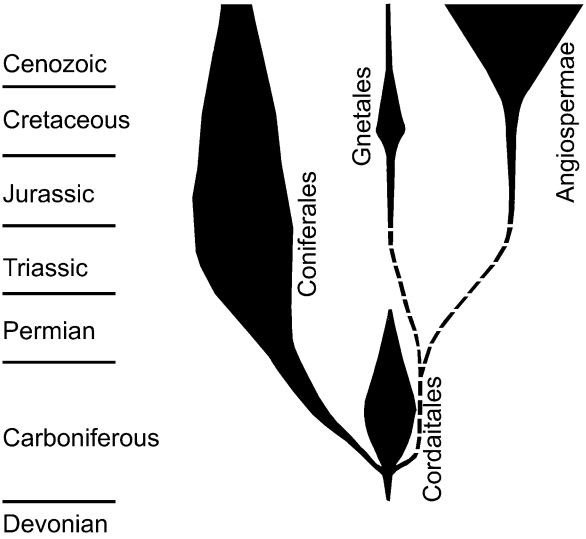
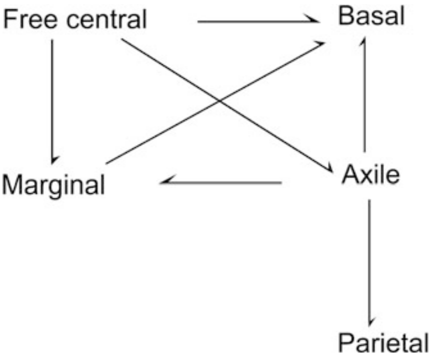


Fig. 8.9 Major evolutionary relationships among various placentation. The arrows mark the directions of the general evolutionary trends, which, however, may be reversed sometimes



4. The aggregation in point 3 has parallel examples in Coniferales and Gnetales (Fagerlind 1946; Florin 1939, 1944, 1951; Schweitzer 1963; Wang et al. 2008). These latter two groups are thought related to or derived from Cordaitales. It is not surprising but rather expected that similar evolutionary rules are applicable in Cordaitales-like plants and their other derivatives.
5. Developmental genetics indicates that carpel and placenta are floral parts of different natures (Bowman et al. 1999; Frohlich 2003; Skinner et al. 2004). The carpel is equivalent to a leaf, while the placenta is equivalent to an ovule-bearing shoot. These parallel with the sterile scales and secondary shoot bearing fertile scales in Cordaitales-like plants. This is in line with the presence of stomata on internal surface of ovary wall (Eames 1961).
6. The organization of flowers in Cactaceae is closely comparable to that in Cordaitales. The floral structure in Fig. 8.3b–e shows a smooth transition from

Fig. 8.3b to Fig. 8.3e. And Fig. 8.3b shows little difference from Fig. 8.2e, which is an imagined status derived from that in Cordaitales-like plants. Both of them have the ovules attached to the floral apex that is covered by the sterile scales or carpels. Note that in the series from Fig. 8.2b to Fig. 8.2e, there is little change in the configuration of the carpels. However, the floral apex undergoes great changes, changing from a columnar ovule-bearing protrusion to a deep concave depression bearing ovules on its wall. The above imagined status in Fig. 8.2e is also very similar to the free central placentation in Portulaccaceae (Judd et al. 1999), which is regarded as the closest relative of Cactaceae according to the molecular outcome based on 12 genes (Brockington et al. 2009).

7. Many families in angiosperms, including Portulacaceae, Primulaceae, Amaranthaceae, and Juglandaceae, have free central placentation in their ovaries, in which the floral apex bears numerous ovules on its surface and is independent from the surrounding ovary wall (Judd et al. 1999; Cronquist 1988).
8. Comparison between carpel, in classic sense, with a subtending bract and its axillary shoot in gymnosperms has been proposed or mentioned by various scholars (Doyle 2008; Fagerlind 1946; Retallack and Dilcher 1981b; Taylor 1991; Rudall and Bateman 2010). As early as in 1857, Payer asserted that the carpel "is formed by an appendicular part, the carpellary leaf, inserted by its base on the two branches of a bifurcated axis which carries the ovules" (Hunt 1937). Taylor (1991) states that "The ovule carpel complex is best interpreted as a short shoot with the gynoecial appendages equivalent to a bract or bracteole, and the ovule being the apical portion of an axillary bud or terminal apex", thus they can be homologous with the bract-bracteole-terminal ovule system in gymnosperms. However, these hypotheses were not elaborated on or well-evidenced previously.
9. Besides the traditional idea about a primitive conduplicate carpel (Eames 1961), ascidiate carpels are taken to be primitive by many authors, including developmental morphologists (van Heel 1981), morphological phylogeneticists (Taylor 1991), molecular phylogeneticists (Qiu et al. 1999; Endress and Igersheim 2000a, b; Doyle 2008; Endress and Doyle 2009; Doyle and Endress 2010). Compared to the traditional one, the latter hypothesis is closer to the new theory proposed in this book. When the number of ovules in the free central placentation is reduced to one, a basal ovule, as in Basellaceae (Sattler and Lacroix 1988), may be derived (Fig. 8.5a–c). Asymmetrical growth may turn an ascidiate carpel into an ascido-plicate and further conduplicate (Taylor 1991). This transition is supported by fossil evidence of a possible ascido-plicate carpel in *A. eoflora* (Ji et al. 2004), *Sinocarpus* (Dilcher et al. 2007; Leng and Friis 2003, 2006), and living angiosperms (Taylor 1991). Deriving carpels with free central placentation from a Cordaitean counterparts through an intermediate status as in *Xingxueanthus* appears not contradicting this conclusion and has the potential give rise to various types of placentation (Fig. 8.4a–f and 8.9).

Based on the above comparison, the author thinks that it *more plausible to derive angiospermous carpels from the sterile scales attached to the reproductive* *secondary shoot*, as in Cordaitales, than from the cupule-subtending leaf in *Glossopteris* or the rachis in *Caytonia.*

8.2 Ovule

Ovule is not a novel structure in seed plants. According to Herr (1995), the nucellus is a sporangiophore of stem origin that bears a terminal megasporangium. The derivation of the ovule from the earliest land plants can be summarized as below, according to Herr (1995), Kenrick and Crane (1997), and Crane and Kenrick (1997).

Early land plants were homosporous and isodichotomous. Later evolution introduced heterosporosity and unequal dichotomy through diverted development. The occurrence of a megaspore paves the way to an ovule. The nucellus is a sporangiophore-sporangium complex. One of the megasporangia takes the apical central position and the other adjacent sporangia take junior peripheral positions. Further evolutionary selection causes the peripheral ones to aggregate with the central apical megasporangium, which absorbs more nutrition and becomes bigger than the peripheral ones. Later these peripheral ones become fused laterally and form a protective structure surrounding the central megasporangium. At the same time, the difference in fertility between the central and peripheral sporangia increases until the peripheral ones lose their fertility completely. The distal parts of these sterilized sporangia become extended and connated to form a more and more complete roof over the apex of the central megasporangium. The central megasporangium and its accessories turn into the so-called nucellus, and the peripheral sterilized sporangia into the so-called integument. This process is illustrated by Kenrick and Crane (1997) in their Fig. 7.23 on p. 294.

This interpretation is supported by detailed anatomic study (Fagerlind 1946; Herr 1995; Johri and Ambegaokar 1984), cladistic analysis (Kenrick and Crane 1997), and diverted developmental theory (Crane and Kenrick 1997). It is apparent that *an ovule is originally a branch system in nature.*

A gymnospermous ovule has only one integument, which, according to the above interpretation, is derived from sterilized sporangia. The ovule in most angiosperms has two integuments, an inner one and an outer one. The derivation of outer integument is one of the key questions in the origin of flowers and angiosperms (Doyle 2006, 2008). Developmental genetics indicates that quite different sets of genes control the development of inner and outer integuments in *Arabidopsis*, suggesting that the outer integument is derived from a precursor different from that of the inner one. The outer integument, like other lateral organs such as sepal, tepal, petal, stamen, requires YABBY gene expression to grow, implying that it is a leaf (phyllome) in nature (Skinner et al. 2004). This conclusion is substantiated by the morphological difference between the outer and inner integuments. For example, the outer integument in *Arabidopsis* does not necessarily completely surround the funiculus, developing on only one side of the latter (Skinner et al. 2004). Stomata on outer integuments (Eames 1961) suggest a foliar nature for their bearers. As there are bracteoles along the ovular stalk in Cordaitales (Bertand 1911; Florin 1944; Rothwell 1982) and some of them even take a position similar to that of an outer integument (Fig. 8.6a), it requires little imagination to conceive that the outer integument in angiosperms may be derived from the bracteoles attached to ovular stalk in Cordaitales (Fig. 8.2a–c) since reproductive structures of plants frequently become more condensed and compressed through aggregation of adjacent vegetative organs (Frohlich 2003).

8.3 Placenta

8.3.1 Isolation of Placenta from Carpel

Placenta should be separated from carpels based on the following reasons.

1. Frequently placentae have vascular bundles separated from those of carpels and the so-called dorsal and median ventral bundles "play little part in the supply of ovular traces" (Hufford 1996; Laubengayer 1937; Puri 1952; Sattler and Lacroix 1988; Thompson 1934, among many) (Fig. 8.3b–e). Since the vascular skeleton is conservative and may be more informative than morphology about the history of organs (Eames 1926), placentae at floral apex with one or more vascular bundles entering them strongly favor a cauline/axial interpretation of placentae (Decraene et al. 1997; Sattler and Lacroix 1988). The so-called cauline origin of placentae (or "acarpellate" gynoecium) may exist in the Nyctaginaceae, Illiciaceae, Piperaceae, Solanaceae, Chenopodiaceae, Polygonaceae, Malvaceae, Urticaceae, Scyphostegiaceae, Salicaceae, Primulales, Juglandaceae, Myricaceae, Santalaceae, Cactaceae, Amaryllidaceae, Onagraceae, Berberidaceae, Basellaceae, Asteraceae, Cyperaceae, Poaceae, and Amaranthaceae (Bogle 1974; Boke 1964; Engler and Prantl 1889; Heywood et al. 2007; Joshi 1938; Laubengayer 1937; Marilaun 1894; Puri 1952; Sattler and Lacroix 1988). The placentae in these families are either enclosed by carpels and floral apex together or have little to do with carpels, and their ovules are not borne on the carpel, unlike assumed in the appendicular theory. Although interpreted otherwise, the figures of Joshi (1938) show a cluster of ovules inserted on a branch-like floral apex in the ovary of *Celosia argentea* (Amaranthaceae, Fig. 8.5a) and a single ovule on a long stalk in *Pupalia lappacea* (Amaranthaceae, Fig. 8.5b). These two examples from the same family at the very least confirm the existence of placenta independent of carpels in Amaranthaceae.
2. Developmental genetics also supports treating carpel and placenta separately (Bowman et al. 1999; Frohlich 2003; Skinner et al. 2004). Study of the model plant, *Arabidopsis*, indicates that the juxtaposition of expression of adaxial (REV) and meristem (STM) factors, characteristic for axillary meristem

formation, is also seen in placenta, implying that placenta is equivalent to a shoot-like structure (Skinner et al. 2004). It is very likely that the ovule is not developed or undetectable in gene expression, and only the shoot meristem and its gene expression are detectable during this early development.

3. Anatomic study of Cactaceous flowers provides evidence of placenta independent of carpels. Eames (1961), a proponent of the appendicular theory, wrote that, according to the axial theory, "the wall of ovary was considered axial, with carpels merely roofing the ovular chamber and forming the styles and stigmas". The situation in Cactaceae is almost exactly what the axial theory predicts and what Eames demands: the ovules in *Pereskia* are inserted on free receptacular tissue (= floral apex) that is covered by a roof composed of multiple carpels, forming an ovary (Boke 1964; Fig. 8.3b–e). This case is very hard to interpret using the appendicular theory. Fagerlind (1946) writes that a placenta in angiosperms is equivalent to a branched shoot, which is apparently supported by figures of Joshi (Joshi 1938; Fig. 8.5a, b). A similar idea is shared among O. Hagerup, M. J. Schleiden, and J. B. Payer. Payer (according to Puri 1952) stated that the margins of carpellary leaf derive their power of bearing ovules from being overlain with outgrowths of the branched floral axis. This appears to be supported by the case of *Pyrola elliptica* (Pyrolaceae, Fig. 8.7) documented by Hunt (1937), although Hunt interpreted it otherwise. The so-called "ventral bundles" bear ovules in Pyrolaceae. They are isolated from the carpels distally, and exsert above the distal ends of the "dorsal parts" of carpels. This configuration makes the "ventral bundles" more likely parts of the placenta rather than ventral margin of the carpels (Fig. 8.7). There are two meristems for each carpel in *Talinum* (Portulacaceae), the adaxial one giving rise to ovules, and the abaxial one to ovary wall (Vanvinckenroye and Smets 1996). In this case the adaxial one is on the surface of and indistinguishable from the floral axis. It is more plausible that the ovules in this case are attached to the floral axis and independent from the ovary wall (= carpel in new sense).
4. Flower development indicates that all primordia of ovules, like those of carpels, stamens, and perianth, are borne on a floral apex. Although belonging to different carpels, the primordia of all ovules follow the same developmental sequences on the floral axis (Figs. 28, 34–36, Thompson 1934). In addition, floral axis bearing clusters of ovules in the ovary (free central placentation) has been seen in Portulaceae, Myrsinaceae (Judd et al. 1999; Payer 1857), Polygonaceae, Chenopodiaceae, Primulaceae (Payer 1857; Puri 1952), Amaranthaceae (Joshi 1938), and many other families. Furthermore, although interpreted otherwise, the placentation in Gyrostemonaceae (Hufford 1996) and Phytolaccaceae (Figs. 6 g, 7a–b, Decraene et al. 1997; Figs. 1a–b, Zheng et al. in press) can be, at least equally plausibly, interpreted as floral axes bearing ovules enclosed by the subtending carpels (leaves).
5. Ovules have a history dating back to the Devonian while carpels have a much shorter history, currently restricted to the Mesozoic. Therefore it is logical that the ovule-bearer (placenta) should be separated from the carpel (Bowman et al. 1999).

6. This suggestion is supported by the recent discovery of *Xingxueanthus* from the Middle Jurassic, an inflorescence of female flowers with free central placentation. The ovules are borne on a central column and have little to do with the so-called carpel (in the new sense) or ovary wall (see Chap. 6 for details).

All these concurringly point to the independence of placenta from carpel.

8.3.2 Origin of Placenta

The appendicular theory for carpels states that placentae are derivation of leaf margin. This theory has led many botanists to search for prototypes of carpels that would have ovules/seeds borne along the leaf margins. For example, megasporophylls of *Cycas* once were a target of interest (Thomas 1931). To make the cupules of *Caytonia* marginal, Doyle (1978, 2006, 2008) (and other scholars) tried to expand the assumed rachis of *Caytonia* to derive a carpel. As mentioned above, these efforts are not as successful as their authors hoped (Frohlich 2003).

Considering the axial nature of the placenta in the Cactaceae, Primulaceae, Portulacaceae, *Arabidopsis* and the secondary shoot in the female organ of Cordaitales, it is logical to correlate the ovules, secondary axillary shoot, and sterile scales in Cordaitales-like plants with the ovules, placenta, and carpels in angiosperms (Figs. 8.2 and 8.3; Table 8.1).

1. The secondary shoot in Cordaitales has already been observed to have a tendency to cover or enclose its ovules with its sterile scales (Hilton et al. 2009a; Rothwell 1982; Wang 1997; Wang and Tian 1993; Wang et al. 2003). As frequently seen in the transverse sections of the ovulate cones of Cordaitales, there are multiple scales surrounding the central ovules. If these sterile scales become connated laterally and the ovules are concentrated onto a short shoot apex in Cordaitales, they can constitute something like flowers in basal Cactaceae of

Table 8.1 The correlation between organs in Cordaitales and possibly related groups

In Cordaitales	In Angiosperms	In Coniferales	In Gnetales
Sterile scale	Carpel, prophyll, perianth	N/A	Outer integument, hairs
Bracteole on ovular stalk	Outer integument	N/A	N/A
Ovule	Ovule	Ovule	Ovule
Integument	Inner Integument	Integument	Inner Integument
Secondary shoot	Placenta	Scale	Ovuliferous unit
Secondary shoot and appendages	Flower	Scale	Ovuliferous unit
Bracteole on ovular stalk	Aril, obturator	N/A	N/A
Bract	Pherophyll, involucral bract	Bract	Bract

angiosperms (Fig. 8.3b). If so, then there appears to be no major block to conclude that the angiospermous placenta may be derived from an ovule-bearing short shoot in a Cordaites-like plant. This is at least circumstantially supported by recent molecular systematics. Brockington et al. (2009) put Portulaccaceae as the closest sister of Cactaceae. Interestingly, the ovules of Portulaccaceae are borne on a protrusion on the base of the ovary, very similar to those in Figs. 2d–e. The occurrence of this feature in the closest outgroup of Cactaceae reinforces that the ovaries with various ovule arrangement in Cactaceae are derived from something resembling the secondary shoots of Cordaitales-like plants.

2. Cordaitales have demonstrated the tendency to form a structure similar to placenta in angiosperms. According to Rothwell (1982), Florin (1944) thought that their ovular stalks tend to change from being elongated, branched into short, unbranched. The existence of such an evolutionary trend in Cordaitales is of pivotal significance because a decrease in ovular stalk length not only promotes the forming of outer-integument-like structure, which paves the way to bitegmic ovules in angiosperms, but also helps to give rise to the placenta, which is a shoot bearing ovules in nature.
3. There is a smooth transition from secondary shoot in Cordaitales to the flowers in Cactaceae (Figs. 8.2 and 8.3). If the sterile scales in Cordaitean plants are symmetrically arranged, their fusion and enclosure will result in a free central placentation, as in Primulaceae and Onagraceae (Marilaun 1894; Judd et al. 1999; Fig. 8.4c). When each individual carpel covers only one ovule on the periphery of floral apex, the placentation as those in Gyrostemonaceae, and Phytolaccaceae (Decraene et al. 1997; Hufford 1996; Fig. 8.1a–c) may be derived.
4. Other types of placentation in angiosperms may be derived from those in point 3 through various transformations. Marginal placentation may come into being when an enclosing carpel surrounds a floral axis bearing numerous ovules and the floral axis becomes appressed and fused with the carpel margin (Figs. 8.4a–d and 8.9). This results in follicle, as in Ranunculaceae and Magnoliaceae (Baillon 1871; Marilaun 1894; Thompson 1934). However, if the number of the ovules to be enclosed is reduced to one, it will end in an achene as in Ranunculaceae (Baillon 1871; Marilaun 1894; Thompson 1934). Axile or pseudoaxile placentation may be derived from free central placentation through the intrusion of the coalesced carpel margins, as once suggested by Tahktajan (1980). It was once proposed that parietal placentation was obtained by a longitudinal splitting of the central placental axis into several branches that diverge and become appressed to the ovary wall along the line of fusing carpellary margins or by failure of partition development (Cronquist 1988; Fagerlind 1946; Puri 1952; Figs. 8.4c–f and 8.9).
5. The variation in number of sterile scales that enclose ovules may result in various types of placentation and their derivations. The number may be one, two, or many, configuring different gynoecia (Fig. 8.4a–f).
6. The basal ovule has been a puzzle for botanists, at least for the appendicular theory proponents (Laubengayer 1937; Puri 1952). The basic reason behind this puzzle is that the ovule is independent of the carpels surrounding it (Sattler and Lacroix 1988). However, according to the theory proposed in this

book, basal ovule can be derived from free central placentation through reduction in number of ovules on the placenta, namely, the number of ovule is reduced to one and the funiculus virtually disappears (Sporne 1974; Fig. 8.5a–c). Therefore, a basal ovule can be taken as the only survivor of a free central placenta, as in Basellaceae, Polygonaceae and Caryophyllaceae (Laubengayer 1937; Sporne 1974; Sattler and Lacroix 1988). This transition series has been seen in Amaranthaceae (Joshi 1938).

7. When the enclosure of placenta is not complete, the ovary may remain open throughout its life as in *Delphinium consolida*. Baillon (1880) once described a virescent flower of *Delphinium consolida* with a free placenta in an open carpel (Puri 1952; Thomas 1931; Vuillemin 1926). When the apex of the ovary was sealed by secretions, it may result in a secretion-sealed carpel/ovary as in some basal angiosperms (Endress and Igersheim 2000a, b; Qiu et al. 1999; Endress and Doyle 2009).
8. Since all different placentation appears to be related to each other or interchangeable (Puri 1952), it is not surprising that the formerly called cauline and carpellary ovules can be closely related or even occur in the same flower (Sattler and Lacroix 1988), which has been a trouble defying an interpretation.
9. Finally and most importantly, all these are in line with the recent recognition of *Xingxueanthus*, an angiosperm, from the Middle Jurassic. *Xingxueanthus* is an inflorescence of female flowers with free central placentation. Its early age and free central placentation suggest that the placenta is originally an ovule-bearing branch.

Based on these points, it may be said that *placenta is a branch, reduced or not, that bears ovules*. It may be derived from an ovule-bearing secondary shoot in the immediate ancestor of angiosperms, which might be related to Cordaitales-like plants.

8.4 Enclosing Ovules

The enclosure of ovules can be accomplished in various ways and by various floral parts. The combination of variations in the ways, parts, and number of parts involved in the enclosure constitutes the foundation for diversified flowers.

1. Floral apex and carpel(s) together enclose the ovules. This is seen clearly in Cactaceae, Gyrostemonaceae, Onagraceae, Primulaceae, and Phytolaccaceae (Boke 1964; Decraene et al. 1997; Hufford 1996; Marilaun 1894; Figs. 8.1 and 8.3). In Cactaceae all of the ovules are borne on the periphery of the floral apex, and the carpels are independently and directly inserted on the periphery of the floral apex. These carpels are connated laterally and eventually cover the ovule-bearing floral apex (Fig. 8.3b–e). The situation in Gyrostemonaceae and

Phytolaccaceae (and probably more families in Caryophyllales) is slightly different (Decraene et al. 1997; Hufford 1996). In these families each carpel covers one of the many ovules along its abaxial and lateral sides, and the ovules are borne on the periphery of the floral apex. Initially the carpels only subtend the ovules. During the late development the carpels bend over the floral apex and isolate the ovule from the outside (Fig. 8.1a–c). The "pseudo-angiospermous" gynoecium (in Meeuse′s sense) of *Engelhardia* (Juglandaceae) is very interesting in that the stigma may be taken as a flared micropyle of integument and the carpel as an outer integument, a situation very similar to that in *Gnetum* (Sporne 1974). Furthermore, Centrospermae may be called "pseudo-carpellate" (in Meeuse's sense), in which the central columnar ovuliferous axis is encased by subtending bracts (Sporne 1974). The later case would be very similar to that in Fig. 8.2e and can be easily derived from Cordaitales-like precursors. Septa develop much late and weakly in Cactaceae (Boke 1964), implying that septa are a derived feature while free central placentation is primitive. Partial septa in *Lychnis viscaria* (Caryophyllaceae) may be interpreted as evidence of incomplete development of septa in the ovary (Sporne 1974).

2. Carpel(s) alone encloses the ovules. According to the traditional orthodoxy, this is very common in so-called primitive angiosperms, such as Magnoliales and Ranunculales. However, according to the new theory in this book, this type of carpel appears derived, except for those formed by enclosing ovules with a single carpel, as seen in Fig. 8.4a, d. It is clear that the placenta in this case is usually completely fused with the carpel margin and thus its own identity is not so obvious.

8.5 Flower

The appendicular theory for carpels states that "The flower morphologically is a determinate stem with appendages, and these appendages are homologous with leaves" (Eames 1931). Except for a subtle difference in the definition of carpel, this idea is generally supported by previous as well as present study. For example, *Aquilegia*'s stamen and carpel are interchangeable (Baillon 1871). Primordia forming tepals, stamens, and carpels in Ranunculaceae follow the same developmental spatial sequences on the floral apex (Figs. 30–31, Thompson 1934). Developmental anatomy indicates that, in *Arabidopsis,* a carpel is derived from eight ancestral cells in a linear arrangement in the floral meristem, supporting the foliar nature of a carpel (Bowman et al. 1999). Pelaz et al. (2000) have proven that a lack of SEP1/2/3 genes will turn all floral parts into sepals (leaves). Abaxial YABBY gene expression in all lateral floral parts in *Arabidopsis* suggests that all these floral parts share certain nature (Skinner et al. 2004). All this evidence suggests that perianths, stamens, and carpels are floral appendages of similar foliar nature.

Thompson (1934) writes that "The basis of a flower is neither more nor less than a sporogenous axis". Based on developmental morphology, he states that "The prototypic axis of the modern Ranunculaceae is supposed to have been of the form of an elongated cone with sporogenous tissue mantling the greater part of its non-emergent surface." Some of the floral apex in Ranunculaceae may remain elongated and the floral parts on it may be widely separated from each other (Zimmermann 1959). The same can be said of the Cactaceae although the floral axis in this case is not so elongated or may even become concave (Boke 1964). The flower-in-gynoecium phenomenon (Sattler and Lacroix 1988) suggests that the terminal portion of the flower (gynoecium) is also a branch system. The author thinks that since ovules, ovary, and gynoecium were originally branch-derived organs, *a flower can be taken as a poly-order reproductive branch system*.

8.6 Angiosperm Prototype and Its Relationship to Other Seed Plants

The bract-scale complex theory proposed by Florin (1939, 1951, 1954) has been used to interpret Cordaitales and the derivation of Coniferales from Cordaitales (Florin 1939, 1954; Rothwell 1982, 1993; Schweitzer 1963; Wang 1997; Wang and Tian 1993; Yang and Fu 2001). It runs into trouble when interpreting the female cone of Podocarpaceae (Mill et al. 2001; Tomlinson 1992; Tomlinson and Takaso 2002; Tomlinson et al. 1991) and Taxaceae (Florin 1954; Wilson 1953), in which it is hard to identify evident bracts and scales. However, recent studies indicate that these two families can be interpreted equally plausibly using the same theory. Wang et al. (2008) demonstrate that, based on anatomy of fossil and living materials, the scale in Podocarpacae is almost completely enclosed by a bract, except for its terminal. This kind of spatial relationship is in line with developmental anatomical genetics. Comparison between the *LFY* gene expression pattern in *Podocarpus* and *Picea* (Vazquez-Lobo et al. 2007) suggests that the gene expressed in the scale of *Picea* is expressed "along the vascular bundle of the bract" in *Podocarpus*, suggesting that the scale is enclosed by the bract in Podocarpaceae. The concurrence of the outcomes from palaeobotany, anatomy and genetics strongly suggests that a bract-scale complex is also seen in Podocarpaceae. In addition, work on a coniferous fossil female cone of *Stachyotaxus* (Arndt 2002; Axsmith et al. 2004; Fagerlind 1946) suggests that the spatial relationship between bract and scale in this taxon may be similar to that in Podocarpaceae. Careful observation of the development and anatomy of *Taxus* indicates that the so-called terminal ovule in the family is actually attached to the terminal of a secondary rather than a primary shoot, and that this ovule bearing secondary shoot overdevelops and suppresses the development of the primary shoot, and thus appears as if the ovule were borne on the terminal of the primary shoot (Dupler 1920; Sporne 1974). With this complement of information, it is simple to derive a *Taxus*-like female structure from that of Cordaitales by reducing the numbers of secondary shoot and of fertile scales both to one, overgrowing its secondary shoot, and suppressing the development of the primary shoot. In this way, using the bract-scale complex theory can unite all Cordaitales and Coniferales seamlessly (Fig. 8.8; Table 8.1).

Fagerlind (1946) has discussed how the female reproductive organs in *Gnetum* may be interpreted as a branch system. From his perspective, the ovuliferous unit in the axil of the bract is a secondary shoot. The outer integument may be correlated to the sterile scales in Cordaitales-like plants. Similarly, Eames (1952) also compares Ephedraceae with Cordaitales and Coniferales. This interpretation parallels with that of Coniferales, although different terms are used. Thus these three groups can be linked to each other based on a similar organization in their cones (Fig. 8.8; Table 8.1).

As mentioned above, a flower in angiosperms may be taken as a poly-order reproductive branch system. If a flower is correlated to a secondary shoot in Cordaitales-like plants, it is not hard to infer that the Cordaitales, Angiospermae, Coniferales, and Gnetales groups sharing such a congruency in organization should be derived from a common ancestor. Interestingly, this conclusion is in line, or at least overlaps, with the outcome based on molecular data, which group Pinaceae and Gnetales together (Bowe et al. 2000; Chaw et al. 1997, 2000; Frohlich 2003; Qiu et al. 2007). Previous morphological studies contradict this (Crane 1985). The theory in this book, if correct, will ease the tension between these formerly conflicting schools of thought. According to this new theory, Caryophyllales should represent, or at least is close to, the most primitive angiosperms. This is supported by the presence of crassinucellar instead of tenuinucellar ovules, diploid perisperm instead of triploid endosperm, hollow styles, poorly defined stigma, intergradation among leaf, bract, sepal and petal, highly diversified wood anatomy, small vessel diameter, raylessness, and diverse pollen morphology in Caryophyllales, all of which are signs of primitiveness in angiosperms (Boke 1963, 1968; Cronquist 1988; Carlquist 1995; Judd et al. 1999; Friedman 2008; Linkies et al. 2010).

This is not the first time that Coniferales and Angiospermae (1926) are related to each other. Vuillemin (1926) has proposed that a carpel is composed of a phyllome and a frondome (Puri 1952). O. Hagerup once tried to connect angiospermous flowers with *Juniperus* and *Gnetum* (Fagerlind 1946). Taylor (1991), Doyle (2008), and Rudall and Bateman (2010) also mentioned the possible homology between angiosperm flowers and bract-bracteole-terminal ovule system in gymnosperms. However, these hypotheses were not elaborated on or well-evidenced. The major difference between the current argument and previous ones lies in the support from a newly discovered Jurassic angiosperm with free central placentation, the aforementioned *Xingxueanthus* (Fig. 8.6c; also see Chap. 6). This fossil provides crucial support and increases the author's confidence in this new theory. Since this theory unifies gymnosperms and angiosperms as well as axial and carpellary theories, it is convenient to call it the Unifying Theory for Flower Formation.

The above evidence from palaeobotany, anatomy, morphology, development, molecular systematics, and genetics justifies the proposing of the new theory. However, it should be stated clearly that this theory is still in its infancy and much more data need to be collected to test its effectiveness and applicable scope.

8.7 Merits of the Unifying Theory

8.7.1 Simplicity and Directness

Deriving carpels from sterile scales on secondary shoot in Cordaitales-like plants is simple because (1) Cordaitales already demonstrate a tendency to enclose ovules with sterile scales, (2) this tendency has also been implemented in Coniferales and Gnetales forming ovule protecting structures, (3) the spatial relationship between the scales and ovule-bearing secondary shoot in Cordaitales requires little transformation or assumptions to give rise to a carpel and placenta in angiosperms (4) Similar enclosure of fruit by sepals has been seen in Solanaceae (Angiospermae).

8.7.2 Evidence from Various Fields

The support for this theory is from various fields, including palaeobotany, developmental biology, developmental genetics, molecular systematics, and developmental anatomy. The factual existence of fossil plants from both the Paleozoic and Mesozoic, joining anatomic and genetic analyses of living angiosperms, lend support to this theory.

8.7.3 Difficulties Negotiated

8.7.3.1 Derivation of Carpel

The provenance of the carpel has been a repeatedly debated topic in the origin of angiosperms. Retallack and Dilcher (1981b) tried to derive it from the leaf subtending cupules in Glossopteridales. Doyle (1978, 2008) tried to derive it from the assumed rachis of *Caytonia*. However, recent study on Caytoniales (Wang 2010) shows a helical instead pinnate arrangement of cupules along the axis in Caytoniales and thus reduces the latter possibility. Now it appears that the derivation of carpels from sterile scales on secondary shoot of Cordaitales-like plants is more plausible.

8.7.3.2 Derivation of Outer Integument

The outer integument is another bottleneck in previous studies. Efforts have been made to show that it was derived from the cupule in Glossopteridales or Caytoniales (Doyle 1978, 2008; Retallack and Dilcher 1981b). Not infrequently more than two integuments have been seen in angiosperms (Eames 1961). If the outer integument was taken as derived from a cupule as assumed, then provenance of these extra integuments constitutes new road blocks for previous interpretations. These challenges disappear if the Unifying Theory is applied: there already are extra bracteoles

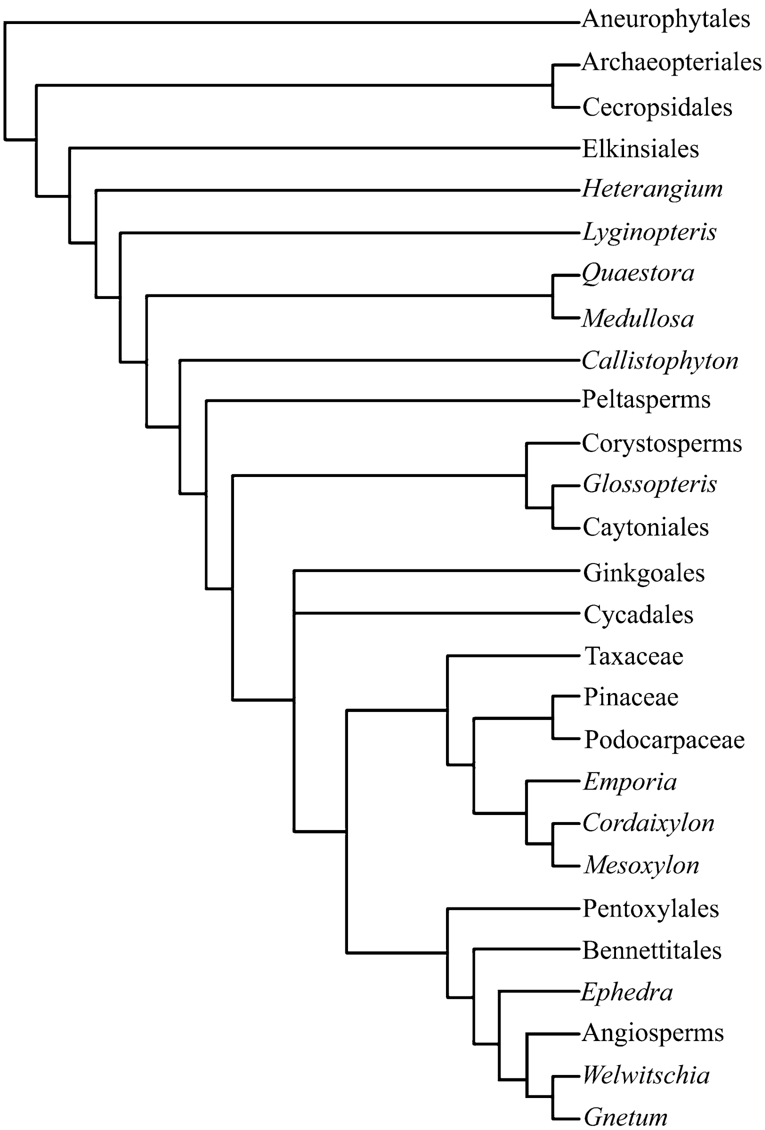


Fig. 8.10 Possible relationship among seed plants. Angiosperms are represented by Caryophyllales

or outer-integument-like structures in Cordaitales (Fig. 8.6a, b) that can give rise to outer integument in angiosperms. In addition, prophylls and pherophylls in inflorescences, arils and obturators in ovaries, and hairs in Gnetales may also be derived from these bracteoles on ovular stalks and sterile scales on the secondary shoot in Cordaitales-like plants (Table 8.1).

8.7.3.3 Clear Definitions of Carpel and Placenta

The classic definition of a carpel is hard to apply in Phytolaccaceae, Basellaceae, Gyrostemonaceae, Cactaceae, Primulaceae and probably many other families. These persisting problems dissolve themselves when the new theory is applied. For example, Boke (1964) has experienced difficulty telling which ovule belonged to which carpel in Cactaceae, because the first ovules appear to arise directly beneath the septa, which is taken as the boundary between two adjacent carpels. Applying the new theory, there should be no strict correspondence between ovules borne on floral apex and carpels because these two are independent parts in flowers originally. In addition, using the classic definition of carpels, Decraene et al. (1997) had to artificially separate the "carpel" in Phytolaccaceae into "abaxial" and "adaxial" parts. In fact, their Fig. 7b clearly shows that the carpel only has what they called "abaxial" parts and the ovule is borne on the periphery of the floral apex rather than on the "adaxial part" of carpel. If they adopt this new definition of carpel, that carpel does not bear ovules, the above separation between adaxial and abaxial parts of carpel becomes superfluous.

8.7.4 Wide Applicable Range

Apparently, the Unifying Theory is applicable in a scope beyond angiosperms. This wide applicability makes it more meaningful to plant systematics because, for the first time, the gap between angiosperms and gymnosperms becomes so narrow or completely filled (Fig. 8.10).

8.7.5 Controversies Settled

Since a flower is a poly-order reproductive branch, an inflorescence is also such a branch system but of higher order. This definition of flower obscures the difference between flower and inflorescence, rendering the debate about whether *Archaefructus* has flowers or inflorescences (Friis et al. 2003; Sun et al. 1998, 2001, 2002) meaningless and unnecessary. In the mean time, the controversy between the traditional axial and appendicular schools can be settled: each of them is right in the part (placenta or carpel) and aspect on which it emphasizes.

8.8 General Regularities in Seed Plant Evolution

8.8.1 Enclosure

Throughout the history of land plants, there is a general trend of enclosing their ovules/placenta in the female organs. The formation of an ovule involves enclosing the central megasporangium. The formation of a carpel involves additional parts forming a container surrounding the ovules/placentae (the so-called angio-ovuly). The formation of inferior ovary involves invagination and enclosure of the tip of the floral axis (Smith and Smith 1942). In some angiosperms this enclosing goes further: carpels are enclosed in a hypanthium (the so-called angio-carpy), as in Monimiaceae (Endress and Lorence 1983; Johri and Ambegaokar 1984; Lorence 1985)

8.8.2 Overgrowth and Reduction

The above enclosure involves the reduction of certain parts and overgrowth of other parts. The intimate coupling between these two tendencies introduces many more novel structures in plants, such as ovules, carpels, and hypanthia.

8.8.3 Sterilization and Neofunctionalization

Almost all branches in the earliest land plants were fertile. Different competition strategies adopted by various individuals made it necessary that some of these branches become sterilized and devoted to ancillary functions, such as protection and support when ovules or other organs form. This is also seen in the formation of integument (concentrating nutrition to the ovule) and endosperm (abortion of extra embryo to provide nutrition to viable embryo).

8.8.4 Fusion

This is frequently seen in the formation of many plant parts due to one simple fact: the earliest land plant was very simple and their branches and sporangia were of the same form. The development of leaf, integument, cupule, carpel, perianth, and marginal placentation all require fusion of some formerly separated parts.

8.8.5 Diverted Development

The homogeneity of organization in early land plants implies that diverted development is necessary to form new plant organs that perform new functions. A similar idea has been proposed by Thompson (1934) and Crane and Kenrick (1997). This is seen in the occurrence of, for example, heterospory (producing different spores) and ovule (producing nucellus and integument). Double fertilization in gymnosperms produces an extra zygote that has to be aborted, during which process it donates its nutrients to the viable embryo. In angiosperms, endosperm is homologous with the embryo and becomes a novel part in the seed, storing nutrition for embryo through diverted development (Friedman 1994; Raghavan 2005).

8.9 Problems Unsolved

8.9.1 From Unisexual to Bisexual

The cones in Cordaitales are unisexual. This raises the question of how to derive the bisexual flowers of angiosperms from the unisexual cones in Cordaitales-like precursors? It is well known that female and male cones in Cordaitales have a similar organization and some of the fertile scales are interspersed with sterile ones (Costanza 1985; Florin 1939; Hilton et al. 2009a, b; Rothwell 1982, 1993; Wang 1997; Wang and Tian 1993; Wang et al. 2003). If some (especially distal ones) of the fertile scales in male cones of Cordaitales-like plants can be metamorphosed into female scales and they are enclosed by the subtending sterile scales, then the condensed secondary shoot of Cordaitales-like plants would look precisely like an angiospermous flower. This can be accounted for by the Mostly Male Theory or gamoheterotopy, although the original authors of the theories favor Peltaspermales or Bennettitales rather than Cordaitales-like plants as the candidates for angiosperm ancestors (Frohlich and Parker 2000; Meyen 1988; Rudall and Bateman 2010).

8.9.2 Boundary Between Cordaitales-Like Plants and Angiospermae

At least some of the flowers in Cactaceae have hollow style lined with papillae that extend from the style tip to ovules in the ovary. So if there are some papillae or trichomes along the margin of the distal sterile scales in cordaitalean secondary shoots, something very similar to cactaceous gynoecium will come into being. Considering the smooth transition between the flowers of Cactaceae and the female cones of Cordaitales-like plants (Fig. 8.3a–e), drawing a boundary between Cordaitales-like plants and angiosperms, especially in the fossil record, appears to be a new challenge for botanists.

8.9.3 Prediction and Test

According to Hoffmann (2003), whether or not a theory in science is accepted depends on several factors. First, it explains. Second, the explanation is better to be simple. Third, most importantly, it predicts. The ultimate value of a theory lies not in its capability explaining things, but in its capability predicting future and providing guidance for people.

The Unifying Theory proposed here satisfies first two criteria, at least appears so to the author. Then whether or not it can predict the occurrence of some type of fossils intermediate between angiosperms and Cordaitales-like plants in the early Mesozoic will be the touchstone to test its validity.

8.10 Implications for Seed Plant Phylogeny

The phylogeny of seed plants relies on interpretation of homology of plant organs, even in this cladistic age. To test the effect of the new theory in this book, a cladistic analysis is performed using heuristic search in the Paup software (Swofford 2002). Two equally parsimonious trees of 195 steps are obtained. The data matrix is from Rothwell and Serbet (1994), and only the data about angiosperms are altered according to the theory proposed here: Caryophyllales is taken as the representative of angiosperms. Outgroup is designated as Rothwell and Serbet (1994) did. The data include 65 total characters of 27 taxa plus 1 ancestor group. Character-state optimization is done using accelerated transformation (ACCTRAN). The consistency index (CI) is 0.5128, homoplasy index (HI) is 0.4872, Retention index (RI) is 0.7156, and Rescaled consistency index (RC) is 0.3670. The strict consensus tree of these two trees is shown in Fig. 8.10. For the matrix, refer to Appendix 10.5.

The result indicates that angiosperms are nested within Gnetales in the strict consensus tree. The angiosperm-Gnetales group is sistered by Bennettitales and Pentoxylales in the order. This group is sistered by a group consisting of Coniferales and Cordaitales. This angiosperm-Gnetales-Bennettitales-Pentoxylales plus Coniferales-Cordaitales group composes a polytomy with Cycadales and Ginkgoales (Fig. 8.10).

This result, at least partially, supports a relationship among Cordaitales, Coniferales, Gnetales and angiosperms, which is suggested by the new theory in this book (Fig. 8.8). Although different from the representative tree given by Rothwell and Serbet (1994), it is in general agreement with one of the five phylogenetic scenarios obtained by Rothwell and Serbet (1994, Fig. 2a). The nesting of angiosperms within Gnetales is in agreement with Eames (1952) on the separation of Ephedraceae from Gnetaceae and Welwitschiaceae. The association of Angiospermae, Gnetales and Coniferales is also in agreement with the analyses of Hill and Crane (1982) and Nixon et al. (1994). It is interesting to note that, if two of the fossil groups (Bennettitales and Pentoxylales) are ignored, this result favors the proposal of close relationship between Coniferales and Gnetales and separation of Ephedraceae from Gnetaceae and Welwitschiaceae (Eames 1952; Bowe et al. 2000; Chaw et al. 1997, 2000; Frohlich 2003; Qiu et al. 2007; Rydin and Korall 2009). It is noteworthy that the result shown in Fig. 8.10 is a strict consensus tree of two most parsimonious trees rather than simply one of many most parsimonious trees. It implies that the new information from the theory proposed here helps to make the phylogeny of seed plants more stable. However, it should be kept in mind that this is just a preliminary result, and the data about Coniferales and Gnetales in the original matrix are not coded under the light of this new theory. Therefore future analysis might show a slightly different result.

Chapter 9
General Conclusions

Origin of angiosperms has been and will continue to be a topic that promotes vigorous debate in botany. Despite efforts, many questions remain unanswered. With new fossil records from the Jurassic, research in this direction becomes more promising. The current status of studies is briefly summarized here.

9.1 Origins and Ancestors of Angiosperms

9.1.1 Time of Origin

There is no consensus on when the angiosperms originated. Based on various evidence, some scholars believe that angiosperms originated in the Carboniferous or Permian (Wieland 1926; Eames 1961; Long 1977a, b), some think in the Triassic and Jurassic (Darrah 1960; Cornet 1986, 1989a, b, 1993; Hochuli and Feist-Burkhardt 2004; Lu and Tang 2005; Smith et al. 2010), still others think in the Early Cretaceous (Cronquist 1988; Friis et al. 2005, 2006). Even using similar tools and data, the same lack of consensus exists among molecular phylogeneticists (Martin et al. 1989a, b; Soltis et al. 2004, 2008; Mathews 2009; Mathews et al. 2010).

No matter how early or late these estimates are, there are limitations to deducing conclusions only based on data from living plants (Axsmith et al. 1998; Lev-Yadun and Holopainen 2009; Mathews 2009), partly because there is no simple roadmap to follow and partly because simplicity is not always equal to primitiveness in the evolution of angiosperms (Eames 1961). Another reason is that molecular sampling can only be done on living plants, and what is dated is the age of the crown groups, rather than the stem group. An evident example is the assumed young age of *Ephedra* (Huang and Price 2003; Huang et al. 2005), which is refuted by fossil evidence from the Early Cretaceous (Rydin et al. 2004, 2006a; Wang and Zheng 2010). Apparently, fossil plants are the final data source on age.

The controversy over the origin time of angiosperms is also due to the lack of an agreed upon criterion for angiosperms. This is why there is a whole chapter, Chap. 3, devoted to refining a definition of fossil angiosperms.

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The angiosperms documented in Chaps. 5 and 6 satisfy the criterion for angiosperms proposed in Chap. 3: an enclosed ovule at or before pollination. This, I believe, makes all the claims in this book more conservative. *Angiosperms exist at least in the Early Jurassic* since *Schmeissneria* is from the Liassic alpha in Germany. If this is correct, then the development and evolution of angiosperms can be divided into three stages.

1. Early stage: the Jurassic and earlier age
   This is the originating period for angiosperms. Pioneering angiosperms during this stage are experimenting with various possibilities. Failures and extinctions are common. Many features typical of angiosperms may have occurred and scattered in various plants. Some of them may have reached angiospermy. Many, if not all, of them have gone extinct and cannot be related to living angiosperms.
2. Middle stage: the Cretaceous
   This is the developing and radiating period for angiosperms. Angiosperms during this stage are more successful than their predecessors. They managed to rise to a dominating position by the end of the Cretaceous. Many of them have demonstrated character assemblage typical of angiosperms and many, if not all, can be related to living angiosperms.
3. Late stage: the Cenozoic
   Angiosperms dominate in this period. They play more and more important roles in various types of vegetations. Ecologically, angiosperms develop more coherent and mutually beneficial relationships with animals, especially insects, birds, and mammals. The co-evolution between angiosperms and animals results in many specialized features in both.

9.1.2 Location and Habitat of Early Angiosperms

There is no consensus on the location of angiosperm origin. This is frequently linked to such questions as when angiosperms originated from which group.

C. Darwin thought angiosperms originated in a remote, now vanished continent, and did not appear on other continents until full-fledged. Retallack and Dilcher (1981b) and Cronquist (1988) stated that angiosperms originated from the Gondwana lands. A. C. Seward proposed an arctic origin for angiosperms (Brenner 1976). People who believed in an earlier origin of angiosperms frequently thought that angiosperms originated in remote, bleak highland, where the harsh environment (including strong ultraviolet rays) is conducive to gene mutation and speciation, and early angiosperms were missing from the fossil record because their environment were not conducive to preservation (Xu 1980). Hutchinson (1926) thought angiosperms originated in temperate areas and later moved to the tropics, while others thought that angiosperms originated in the tropics and gradually moved to higher latitude (Doyle 1977, 1978; Hickey and Doyle 1977; Brenner 1976).

Recent progress on fossil angiosperms from the Early Cretaceous suggests that some angiosperms lived in aquatic habitats (Retallack and Dilcher 1981c; Sun et al. 1998, 2001, 2002; Ji et al. 2004; Friis et al. 2010). This partly agrees with conclusions based on ecological phylogenetic analyses of living angiosperms (Feild et al. 2003; Feild and Arens 2005). Based on ecological systematic analysis of basal angiosperms in terms of molecular data, Feild et al. (2003) thought that the earliest angiosperms lived in dimly lit, disturbed forest understory habitats and/or shady stream-side settings.

However, considering the high diversity of angiosperms in the Yixian Formation (Early Cretaceous) and the occurrence of *Schmeissneria* in the Early Jurassic, many of the above statements are open to question.

In short, there is no consensus on the origin place for angiosperms, but there are a few points worth mentioning. First, *Schmeissneria* has been found in the Early Jurassic both in Germany and Poland. The plant may have lived very close to a water body (Van Konijnenburg-Van Cittert and Schmeissner 1999). Second, if the theory in Chap. 8 is correct, works about the anatomy and ecology of Cordaitales, such as Rothwell (1977, 1993), Wang et al. (2003), and Hilton et al. (2009a, b), are worth of future attention.

It appears the above statements tend to converge on a close-to-water habitat for early angiosperms. However, it is hard to say that they lived there exclusively. This impression is possibly due to the fact that most fossil plants are found in fluvial or lacustrine sediment, which is closely related to water. Whether early angiosperms lived in other habitats is still an open question. Information related to this question can only be extracted by studying other types of sediments not closely related to water, for example, volcanic sediments.

9.1.3 Ancestors

Various hypotheses on ancestors of angiosperms have been proposed based on various kinds of evidence. Engler and Prantl (1889) claimed that Amentiferae were the most primitive angiosperms. This idea was refuted by Hutchinson (1926) and Eames (1926). Hutchinson (1926), Eames (1961), Takhtajan (1969, 1980), and Cronquist (1988) named *Magnolia* as the most primitive angiosperm, overlapping with the conclusion of Feild et al. (2003) and supported by Cretaceous fossil evidence (Retallack and Dilcher 1981a; Crane and Dilcher 1984; Dilcher and Crane 1984; Dilcher and Kovach 1986; Sun et al. 1998, 2001, 2002). Wieland (1926) thought that angiosperms were derived from the *Williamsonian* tribe. Taylor and Hickey (1990) thought that early angiosperms are “small, rhizomatous perennials, which had diminutive reproductive organs subtended by a bract-bracteole complex.” Elsewhere, early angiosperms have been variously characterized as drought-adapted early succession shrubs (Doyle 1977; Hickey and Doyle 1977), sun-loving semi-herbaceous rhizomatous plants of disturbed sites (Taylor and Hickey 1992, 1996), and aquatic herbs (Sun et al. 1998, 2001, 2002; Ji et al. 2004). The previous failure to recognize protoangiosperms may be due to the diminutive habit of early angiosperms and an “incorrect search image” (Taylor and Hickey 1990).

According to the criterion in Chap. 3, *Schmeissneria* currently is the oldest record of angiosperms. However, according to the new theory in Chap. 8, the ancestor should belong to a Cordaitales-related group that occurred in the Palaeozoic. However, this hypothesis apparently needs more data to test.

9.2 Monophyly or Polyphyly

Angiosperms are thought polyphyletic by many (Wieland 1926; Hutchinson 1926; Hughes 1994; Krassilov 1977a). According to Krassilov (1977a), several lines of angiosperms have simultaneously entered the fossil record. However, if these records are restricted to the Jurassic and Cretaceous, they may have less to say about the mono- or polyphyly of angiosperms.

The present dominating doctrine states that angiosperms are monophyletic, with *Amborella* sistering all remaining angiosperms (Qiu et al. 1999; Soltis et al. 2004, 2008; Doyle 2006, 2008; Graham and Iles 2009; Chase and Reveal 2009). This is supported by molecular data and some morphological analysis (Doyle 2006, 2008).

The author proposed a new theory predicting angiosperm relatives back to the Palaeozoic in Chap. 8. The long gap between the Permian and Early Cretaceous allows for the diversification from a single ancestor to many varieties of angiosperms. Future fossil evidence will test whether this is correct.

9.3 Animals and Plants

Insects have a long history of interaction with plants (Ren 1998; Hasiotis et al. 1995, 1998; Hasiotis 1998; Hasiotis and Demko 1998, Van Konijnenburg-Van Cittert and Schmeissner 1999; Vasilenko and Rasnitsyn 2007; Ren et al. 2009). Evidence suggests that plant and animal interactions were already established by the Early Carboniferous (Taylor and Archangelsky 1985). Although there might possibly be some host specificity between some insects and plants (Pott et al. 2008), it is possible that these insects, unlike their living descendants working closely with flowers, might have also lived on the reproductive organs of gymnosperms (Ren et al. 2009). How much animals contributed to the success of angiosperms is an open question, as there were few changes in insects and reptiles corresponding to the changes in angiosperms during the Cretaceous, according to Hughes (1994).

Dragonfly's eggs have been found in leaves of *Schmeissneria* (Van Konijnenburg-Van Cittert and Schmeissner 1999). Although it is unknown what role did dragonfly played in the pollination and dispersal of *Schmeissneria*, it suggests that *Schmeissneria* lived in an aquatic or semi-aquatic environment.

The fleshy fruits in *Callianthus* from the Early Cretaceous suggest that they may have been dispersed by animals. This is in agreement with the conclusion drawn by Eriksson et al. (2000) based on study of Cretaceous fruits and seeds from Portugal.

The significance of animal dispersal in the Early Cretaceous may have been underestimated (Eriksson et al. 2000). However, the small seeds and non-fleshy fruits in *Schmeissneria* suggest that the situation in the Early and Middle Jurassic may have been different.

9.4 Road to Success

It now appears that the feature angiospermy has appeared much earlier than the dominance of angiosperms. Namely, the traits promoting angiosperm diversification arose well after the origin of the lineage (Stuessy 2004; Feild and Arens 2005). It appears that angiospermy alone cannot account for the success of the angiosperms. It may have been the combination of many features as well as biotic and abiotic factors that have contributed to the success of angiosperms since the Middle Cretaceous (Magallon and Castillo 2009). These features may include but are not restricted to polyploidy (Soltis et al. 2009), gene duplication (Flagel and Wendel 2009; Xu et al. 2009), vessels, low-carbon-cost-for-shoot physiology, reticulate leaf venation, more efficient light usage, rhizomatous and lianoid habits, extensive vegetative propagation, high photosynthetic rates, plant-insect relationships, plant-dinosaur interaction, unique ability to response to high CO_2 levels, climate change (Feild and Arens 2005; Sultan 2009), higher vein density (Boyce et al. 2009; Brodribb and Feild 2009), fast growth rate, weedy habit (Royer et al. 2010), plant-bacteria association (Johri and Ambegaokar 1984), short reproductive cycle (Williams 2009), high speciation rate and low extinction rate, chemical defense mechanism (Doyle and Donoghue 1986a), occurrence of endosperm (Friedman 1992b), landscape connectivity (Riba et al. 2009), environment influence (Wake 2010), and horizontal gene transfer (Krassilov 1973a, 1977a), which has been found among more and more organisms (Diao and Freeling 2006; Richardson and Palmer 2007; Williamson and Vickers 2007; Rumpho et al. 2008; Pace et al. 2008; Sanchez-Puerta et al. 2008).

9.5 The Idiosyncrasy of Angiospermae or a Grade of Evolution?

Among the living plants, angiospermy appears to be a feature unique to angiosperms since no other living plants demonstrate it. According to the current “angiospermy = angiosperms” concept, those plants documented in Chaps. 5 and 6 satisfy the criterion for angiosperms adopted in this book and they should be placed in angiosperms. These plants challenge the currently well-accepted evolutionary theories, many of the polarities of character in cladistic analyses will be forced to be reoriented, and the existing system of angiosperms will need a revision. However, if these plants were not accepted as angiosperms although they satisfy the criterion for angiosperms, then angiospermy should be taken as a grade of evolution rather than the idiosyncrasy of Angiospermae. This is also possible because, theoretically, some other seed plants may have reached the status of angiospermy independently, and Angiospermae represented by living angiosperms may simply be the survivors among many peer competitors. The ensuing problem more perplexing than the origin of angiosperms is how to differentiate the angiospermy in such "gymnosperms" and in true angiosperms.

9.6 Digging Deeper

Fossil plants have two ways to leave a mark in the history, one way is to leave tangible fossils, the other is to leave living progeny ("*living fossils*"). Both of these are filtered and thus altered records of fossil plants, and neither can reflect the fossil plants completely faithfully. Tangible fossils can preserve the morphology and anatomy, but they are susceptible to preservation filtration and may lose labile information in the fossil plants. Conversely, "living fossils" have the advantage of preserving labile information. But this preservation is also not as faithful as assumed. Rather, over time the original information has inevitably been altered and filtered in one way or another since the plants must have had adapted to new environment that is different from those of their ancestors and change themselves more or less accordingly (Wake 2010). Thus the information embodied in living plants cannot reflect the original status of their ancestral fossil plants. Therefore it is no wonder that different or even conflicting conclusions may be drawn based on such altered molecular and morphological information. Considering all this, to solve the problem of the origin of angiosperms, we need to take advantage of the information contained in both tangible fossils and "living fossils". The final answers about early angiosperms lie in the tangible fossils. The only way to answer the question of the origin of angiosperms is to dig deeper, with the preliminary guidance from the information gleaned from living plants.

Chapter 10
Appendix

10.1 List of Morphological Characters Used for Cladistic Analysis

The following are the 123 morphological characters and their coding used in the cladistic analysis in Chap. 5. Morphological characters No. 1–4 are new, No. 5–15 are the characters No. 2–8, 10–12 and 14 from the dataset of Sun et al. (2002), No. 16–123 are the characters No. 1–108 from the dataset of Doyle and Endress (2000). For detailed discussion, see the original references.

1. Seed-enclosed (0) no, (1) yes.
2. Floral-symemetry (0) radial, (1) bilateral.
3. Double-fertilization (0) absent, (1) present.
4. Micropylar-tube (0) absent, (1) present.
5. Pachycaulous-stems (0) absent, (1) present.
6. Axillary-buds (0) absent, (1) present.
7. Short-shoots (0) absent, (1) present.
8. Primary-vein-form (0) dichotomous, (1) anisotomous, (2) solitary/unbranched.
9. Vein-orders (0) one, (1) at least two.
10. Laminar-vein-form (0) dichotomous, (1) non-dichotomous.
11. Vein-fusion (0) nonanastomosing, (1) anastomosing.
12. Tectum (0) absent, (1) clearly-defined.
13. Compound-megastrobilus (0) absent, (1) present.
14. Carpel (0) absent, (1) present.
15. Leaves (0) simple, (1) compound.
16. Habit (0) tree or shrub, (1) rhizomatous, scandent, or acaulescent.
17. Stele (0) eustele, (1) (pseudo) siphonostele, (2) monocottype (atactostele).
18. Inverted cortical bundles (0) absent, (1) present.
19. Protoxylem lacunae (0) absent, (1) present.
20. Cambium (0) present, (1) absent.
21. Storied structure (in tracheids and axial parenchyma, phloem) (0) absent, (1) present.

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22. Tracheary elements (0) tracheids, (1) vessel members with typical perforations.
23. Vessel grouping (0) predominantly solitary, (1) mostly pairs or multiples.
24. Vessel perforations (end-wall pits in vesselless taxa) (0) scalariform, (1) scalariform and simple in the same wood, (2) simple.
25. Fiber pitting (lateral pitting of tracheids in vesselless taxa) (0) distinctly bordered, (1) minutely bordered or simple. Scored? when there is no secondary xylem or fibers are replaced by pervasive axial parenchyma.
26. Rays (0) narrow (generally not more than four cells wide), (1) wide.
27. Paratracheal parenchyma (0) absent or scanty, (1) well developed. Pervasive (Asaroideae, Ranunculaceae) scored?
28. Tangential apotracheal parenchyma bands (0) absent, (1) present.
29. Pith (0) uniform, (1) septate (plates of sclerenchyma).
30. Secondary phloem (0) simple, (1) stratified (fibers in small tangential rows or bands several cells thick).
31. Sieve tube plastids (0) S-type (starch), (1) PI-type, (2) PII-type.
32. Pericycle (including modified protophloem) with (0) separate fiber bundles, (1) more or less continuous ring of fibers (or fibers and non-U-shaped sclereids), (2) fibers alternating with U-shaped sclereids,
(3) no sclerenchyma.
33. Laticifers in stem (0) absent, (1) present.
34. Raphide idioblasts (0) absent, (1) present.
35. Phyllotaxy (0) spiral, (1) distichous (at least on branches), (2) opposite.
36. Nodal anatomy (0) multilacunar, (1) unilacunar onetrace, (2) unilacunar two-trace (leaf traces derived from two adjacent stem bundles or protoxylem areas, may split or fuse in petiole), (3) trilacunar.
37. First appendage (s) on vegetative branch (0) paired lateral prophylls, (1) single distinct prophyll (adaxial, oblique, or lateral). This coding was wrong in Doyle and Endress (2000) but was corrected in Doyle (2006).
38. Stipules (0) absent, (1) adaxial/axillary, (2) interpetiolar.
39. Axillary squamules (0) absent, (1) present.
40. Leaf blade (0) bifacial, (1) unifacial.
41. Leaf shape (0) obovate to elliptical to oblong, (1) ovate, (2) linear.
42. Major venation (0) pinnate with secondaries at more or less constant angle, (1) palmate (actinodromous or acrodromous) or crowded (pinnate with crowded basal secondaries, upward decreasing angle). “Parallel” scored?, since this is correlated with linear shape.
43. Base of blade (0) not peltate, (1) peltate.
44. Leaf dissection (0) simple, (1) lobed or compound.
45. Marginal teeth (0) absent, (1) chloranthoid, (2) monimioid, (3) platanoid.
46. Stomata (predominant type on leaf) (0) paracytic, (1) laterocytic, (2) anomocytic, (3) tetracytic.
47. Midrib vasculature (0) simple arc, (1) arc with adaxial plate, (2) ring.
48. Palisade parenchyma (0) absent (mesophyll homogeneous), (1) present (mesophyll dorsiventral).

49. Asterosclereids in mesophyll (0) absent, (1) present.
50. Oil cells in mesophyll (0) absent, (1) present.
51. Mucilage cells in mesophyll (0) absent, (1) present.
52. Inflorescence (0) solitary or occasionally with one to two additional lateral flowers, (1) spike, raceme, or botryoid, (2) richly branched (panicle or compound inflorescence of spikes, racemes, botryoids). Ordered.
53. Sex of flowers (0) bisexual, (1) bisexual and unisexual (usually male), (2) unisexual.
54. Floral base (0) hypanthium absent, superior ovary, (1) hypanthium present, superior ovary, (2) inferior ovary.
55. Perianth phyllotaxy (0) spiral, (1) whorled.
56. Perianth whorls (series when phyllotaxy is spiral) (0) more than two, (1) two, (2) one, (3) absent.
57. Perianth number (merosity) (0) irregular, (1) in threes, (2) in twos, fours, or fives.
58. Outer perianth cycle (series) (0) not clearly differentiated (or continuum of forms), (1) sepaloid. Taxa with one cycle scored?
59. Outermost perianth whorl (series) (0) separate or basally fused, (1) fused most of length (usually calyptrate).
60. Nectar petals (0) absent, (1) present.
61. Androecium phyllotaxy (0) spiral, (1) whorled, (2) irregular.
62. Stamen number (0) irregular, (1) in threes, (2) in twos, fours, or fives.
63. Stamen fusion (0) free, (1) connate.
64. Stamen base (0) short (<length of anther) and wide (typical laminar), (1) long (>length of anther) and wide (>1/2 width of anther), (2) narrow (<1/2 width of anther) and either long or short (typical filament).
65. Paired basal stamen glands (0) absent, (1) present.
66. Connective apex (0) extended, (1) truncated or smoothly rounded. Peltate scored as extended.
67. Microsporangia (0) four, (1) two.
68. Pollen sacs (0) protruding, (1) embedded.
69. Orientation of dehiscence (0) introrse, (1) latrorse, (2) extrorse.
70. Mode of dehiscence (0) longitudinal slit, (1) H-valvate, (2) valvate with upward-opening flaps.
71. Connective hypodermis (0) unspecialized, (1) endothecial or sclerenchymatous.
72. Tapetum (0) secretory, (1) amoeboid.
73. Microsporogenesis (0) simultaneous, (1) successive.
74. Pollen unit (0) monads, (1) tetrads.
75. Pollen shape (0) boat-shaped, (1) globose.
76. Aperture type (0) monosulcate (including monoulcerate and disulcate, with distal and proximal sulcus), (1) inaperturate, (2) sulculate, (3) trichotomosulcate, (4) tricolpate.
77. Pollen size (average) (0) large (>50 μm), (1) medium, (2) small (<20 μm). Ordered.

78. Infratectum (0) granular (including “atectate”), (1) intermediate, (2) columellar. Ordered.
79. Tectum (0) continuous or microperforate, (1) perforate (foveolate) to semitectate (reticulate), (2) reduced (not distinguishable from underlying granules).
80. Striate muri (0) absent, (1) present.
81. Supratectal spinules (smaller than the width of tectal muri, when present) (0) absent, (1) present.
82. Prominent spines (larger than spinules, easily visible with light microscopy) (0) absent, (1) present.
83. Aperture membrane (0) smooth, (1) sculptured.
84. Nexine (in extra-apertural regions) (0) footlayer only, (1) footlayer and endexine, (2) absent or discontinuous.
85. Inner staminodes (0) absent, (1) present. Unisexual taxa scored?
86. Carpel number (0) more than one, (1) one.
87. Carpel form (0) ascidiate up to stigma, (1) intermediate (both plicate and ascidiate zones present below the stigma) with ovule (s) on the ascidiate zone, (2) completely plicate, or intermediate with some or all ovule (s) on the plicate zone.
88. Carpel sealing (0) by secretion, (1) partial postgenital fusion with continuous unfused canal containing secretion (=type 2 of Endress and Igersheim 2000a), (2) postgenital fusion to apex with partial canal containing secretion (p type 3), (3) complete postgenital fusion without canal.
89. Pollen tube transmitting tissue (0) not prominently differentiated, (1) one layer prominently differentiated, (2) more than one layer differentiated.
90. Style (0) absent (stigma sessile or capitate), (1) present (elongated apical portion of carpel distinctly constricted relative to the ovary, including cases in which the apical portion is mostly or entirely stigmatic).
91. Stigma (0) extended (all around ventral slit or far down on both sides, half or more of the style-stigma zone), (1) restricted (above slit or around its upper part). Syncarps scored 0 when stigmas almost reach the center of the gynoecium; extreme parasyncarps (without separate styles) scored?
92. Stigma papillae (0) unicellular only (or stigma smooth), (1) some or all uniseriate pluricellular, (2) some or all pluriseriate pluricellular (including multicellular protuberances).
93. Extragynoecial compitum (0) absent, (1) present. Unicarpellate taxa scored? Syncarps with an intragynoecial compitum scored?
94. Carpel fusion (0) apocarpous (including pseudosyncarpous), (1) parasyncarpous, (2) eusyncarpous (at least basally).
95. Oil cells in carpels (0) absent or internal, (1) intrusive.
96. Septal nectaries (0) absent, (1) present.
97. Ovule number (0) one, (1) mostly two (occasionally one or a few more than two), (2) more than two.
98. Placentation (0) linear (including one lateral or median), (1) laminar-diffuse.
99. Ovule direction (0) pendent, (1) horizontal, (2) ascendant.
100. Ovule curvature (0) anatropous (or nearly so), (1) orthotropous (including hemitropous).

101. Integuments (0) two, (1) one.
102. Outer integument shape (0) semiannular, (1) annular. Scoring based on bitegmic taxa. Orthotropous taxa scored?
103. Outer integument lobation (0) unlobed, (1) lobed.
104. Outer integument thickness (at middle of integument length) (0) two cells, (1) two and three to four, (2) four and five, or more. Ordered.
105. Inner integument thickness (0) two cells, (1) two and three, or three, (2) three and more. Ordered.
106. Chalaza (0) unextended, (1) pachychalazal, (2) perichalazal.
107. Nucellus (0) crassinucellar (including weakly so), (1) tenuinucellar or pseudocrassinucellar.
108. Fruit wall (0) fleshy, (1) fleshy with hard endocarp (=drupe), (2) dry.
109. Fruit dehiscence (0) dehiscent, (1) indehiscent.
110. Testa (0) slightly or nonmultiplicative, (1) multiplicative.
111. Exotesta (0) unspecialized, (1) palisade or shorter sclerotic cells, (2) tabular (wider than underlying cells).
112. Mesotesta (0) unspecialized, (1) sclerotic, (2) fibrous, (3) sarcotesta, (4) spongy.
113. Endotesta (0) unspecialized, (1) single lignified layer (cells with thin walls but fibrous endoreticulum), (2) multiple lignified layer (with fibrous endoreticulum), (3) tracheidal (or similar tangentially elongate but nonlignified cells), (4) palisade of thick-walled prismatic or shorter sclerotic cells.
114. Tegmen (0) unspecialized, (1) both ecto- and endotegmen thick-walled, (2) exotegmen fibrous to sclerotic (intergrade in Myristicaceae).
115. Ruminations (0) absent, (1) present.
116. Operculum (0) absent, (1) present.
117. Aril (0) absent, (1) present.
118. Endosperm development (0) cellular, (1) nuclear, (2) helobial.
119. Endosperm in mature seed (0) present, (1) absent.
120. Perisperm (0) absent, (1) present.
121. Embryo (0) minute (less than 1/2 length of seed interior), (1) large.
122. Cotyledons (0) two, (1) one.
123. Germination (0) epigeal, (1) hypogeal.

10.2 Morphological Matrix

The following are the 123 morphological characters of 38 fossil as well as living taxa used in the cladistic analysis in Chap. 5.

Cycas

0100100100000001000010 0--
(01)(01)??00?31100?00000010?21001?2????????0?????000?0(01)000100000
01??????????????111???2?01010(12)0?000?00101

Bowenia

0100100110000010000100--
(01)0??00??1000?0000001??01001?2????????0?????000?0?00010000001????
??????????111???2?0101010?000?00101

Zamia

0100100100000010000100--
(01)0??00??1100?0000001??21000?2????????0?????000?0?00010000001????
??????????111???2?0101010?000?00101

Ephedra

0?1101020??11000100001000100 01??0022?0002?000???1?1?2???????12110
110???0001120000001?--------?0?2101020?0101010?000?10100

Pinus

010001120??010001000000–00??01?31001?0002?000??00?1?2--------?----
10?0?000?1000000010------------001---2?0201210?000?10100

Ginkgo

000001100?000000100000--00??01??1102?0000?010??1001?2-----
21020110100000000100000001?-----------211---2?0101010?000?00001

Chaoyangia

10?0?1020111010????1??????????????2?????2?000??????220??????10?????0
?????1001?000000?002?11??0??0?21???????31??????????????

Euptelea

101001011111?10000000100110100010001000000(01)003221000000?3????10
02000?1110001412101 01?001300000000(01)000000210020020400000000000

Platanus

101001011111?1000000010(01)0100000000 1001?0010131110001201(12)200
01202000(01)111000141210001100231100000010010?112002(01)001000001
00100

Trochodendron

101001011111?100000000?001?0000100030(01)0011001101(01)0010(01)11
2?0?1(02)020101111000141211001 1002(23)11000200200000(01)02002102?
40000000001

Amborella

101001011111?100000000?000?0000(12)00120000100010000000(12)2100000000010000000??0101100101000000002100000010?11100100000000?00000

Aristolochia

111001011111?101000011(01)2010000110013100011000201010002121?0?111?010020?0(01)0111200(01)0??002300?0?200201000(01)0100211(01)?(04)2000000000

Asarum

101001011111?10100001112?1??002(01)00131000110002010100021111001102000020000001(01)12(01)0001100231101020020100(01)01002100?02000000000

Austrobaileya

101001011111?1010000010000?0000100220000100000000100000000000000000000000101210001110001100100020100002120001030010 0?00000

Brasenia

101001011111?10100?101?0????????1?0??00111100?210000001111001102 0100(12)0-010001200000100011 10(01)0000112000??0?021?1???01000100?

Calycanthus

100001011111?10011000112100000120022 0000(01)000000001000100000000000000200000121210000110230110 1?0010200(01)(01)22002010030000010100

Idiospermum

101001011111?10011000112100 1??12002200?00000000??1000100000000000000200??0121?0000??1(01)230012?0001020000220?200????000?10101

Canella

101001011111?1001000010000(01)0001(01)000300?000000(02)0(01)010(12)001011001(01)1?0100200000101210000000211 0?0?100(12)0100101100000100000(01)?0000?

Chloranthus

111001011111?1010000001000100?00000220200000001 10?01010??3??????(01)1010(01)0000001?12101011010 0000(02)?01000010?(01)220000(01)0012000000000

Hedyosmum

111001011111?10(01)000001(01)01100?0?00022?2?00000110001?(12)22?21
?0???000101001?001312101010?1000(01)00?00000010?11100(12)00000000
000000?

Degeneria

101001011111?10000000110110111100010?000000000100100000001100000
000012100000000000000211231001?000201001021000110320100000000

Eupomatia

101001011111?100000001101100001000101000000000011010001?2??1?001
00001010000121000000210?310111?00201000021000010200100?00000

Illicium

101001011111?1001000010000000000000100000000(01)00011000000000000
1010000000013121000110011110010100020011 2(12)0021(01)1100000000000

Liriodendron

101001011111?1000000011(01)(01)00111(01)000(01)00?00000000011110000
10(01)(01)0000000001(02)(01)00000001000000002201(01)00000101000021
002(01)10(03)20000000000

Piper

111001011111?1010000111(12)(01)1000?0(01)00(01)011?011000301010100
?3????11020101(01)00000102?00101000?30(01)?0?1100?210?(01)1(12)00
(01)000001000(01)01000

Schisandra

101001011111?10110000101000000001000100?00000100?1110200000000110
100(02)000001312100011000010001010101000(01)21000001100000000000

Ceratophyllum

101001000001?1?1?0?1000??????003002-?00-
2?012???000020122?0000000010(12)0?1(01)0111?2000?10100?100000001011?
??0?021??000000001100

Acorus

101001011111?1012001???0????0?2(13)001011112?0000?001010011100011
02010000000100012000000100121010?2(01)02?010?0100100000002000001010

Gyrocarpus

101001011111?100000001021(01)10??120001?000110(01)002101?202120?0
?100211112201101111??0?1??01132110?00000000000220010104300000010101

Saururus

101001011111?1010000?11001??0001001011001100030101?100?3????1102
0101100000102200001100230100011 0(12)0110?10100(02)(01)00?01000001000

Saruma

101001011111?10100001112?1??002(01)0013100011000201010002111 1001
10200002000001(01)12(01)00011002311010200201000(01)01002100?02000
000000

Spathiphyllum

101001011111?1012001?1?0????0?2(13)(01)11010(01)0(12)1000(02)0100?
10011(12)0001(12)01010020?1100012(01)0000?0(01)(01)010(01)(01)?20000
(02)(01)(01)00220000000?0000200111

Xanthorhiza

101001011111?1010000111(12)11?00?01000(03)?0?0110112(02)1000(01)00
(01)(12)(12)101(01)0020100100000 1412(01)010110023111 00000(12)0?00
(01)(01)(12)2012101000000100000

Sabia

101001011111?1(01)110?00101?00?????010??00000000(02)???00200112100
120101(01)0(02)000?01422100011000 1?11002011?(12)11???2?011???0000?
20?100

Gnetum

01110101111110001000 01(01)2000001?31020?00010000?01111?2???????12
110110???00011200010010----------?0?1101022?0101010?000?10100

Welwitschia

010111020101100000000101000001?-
0122?0002?0000?1101?2???????121101?020?0?01010000001?----------
?0?1101022?0101010?000?10100

Archaefructus

11?001010001-
111??????????????????00?0??1?010??????000??????0200??1110???0001???00??
?02??00??0??2021????????0??????????????

Hydatella

10100?0201010101??11?1?0????0?23000??0??2?0002?0000120?3??????020
10?100??10022001000?10??0?0??000?000??00002(01)01?000100010?1

10.3 List of Fauna Elements

10.3.1 The Jiulongshan Fauna

10.3.1.1 Conchostracans

Euestheria ziliujingensis, E. haifanggouensis, E. luanpingensis, E. jingyuanensis, Triglypta pingquanensis (Deng et al. 2003; Huang et al. 2006).

10.3.1.2 Ostracodes

Darwinula sarytirmenensis, D. impudica, D. cf. *magna, Timiriasevia* cf. *armeniacumiformis, T.* cf. *catenularia* (Deng et al. 2003).

10.3.1.3 Bivalves

Eolamprotula subquadrata, E. cf. *obovoidea, E. yangyuanensis, Psilunio dongchengensis, Cuneopsis sichuanensis, C. johannisboehmi, C.* sp., *Ferganoconcha sibirica, F. subcentralis* (Deng et al. 2003).

10.3.1.4 Insects

Samarura gigantean, Mesobaetis sibirica, Mesoneta antiqua, M. beipiaoensis, Platyperla platypoda, Ctenoblattina dignata, Permocicada beipiaoensis, Palaeontinopsis cf. *latipennis, Chifengia batuyingziensis, Pycnophlebia obesa, Sinoinocellia liaoxiensis, Mesohelorus haifanggouensis, Rhipidoblattina* (*Canaliblatta*) *hebeiensis, R. liugouensis, R. longa, Sogdoblatta haifanggouensis, Rectonemoura yujiagouensis, Sinoprophalangopsis reticulata, Isfaroptera*? *yujiagouensis, Brunneus haifanggouensis, Anthoscytina longa, Paracicadella beipiaoensis, Palaeontinodes haifanggouensis, Mesocercopis longa, Jurassonurus amoenus, Fortiblatta cuspicolor, Archaeopelecinus tebbei, A. jinzhouensis, Yanliaocrixa chinensis, Jurosyne liugouensis, Samaroblatta nova, Aboillus asticus, A. chinensis, Dioroplachutella sinica, Procercopina longa, Mesocimes brunneus, M. sinensis, Mesoscytina burnnea, Sinocoris oblonga, S. ovata, Trichopsocus beipiaoensis, Mesopsocus divaricatus, Sinopsocus oligonvenus, Pseudopsocus parrus, Parapsocus pectinatus, Mesaplus beipiaoensis, Beipiaocarabus oblonga, Leicarabus pravus, Prostaphylinus mirus, Parandra beipiaoensis, Beipiaopsychops triangulata, Sinosmylites pectinatus, Xutipula longipetalis, Fera jurassica, F. parva, Eohesperinus gracilis, Archilycoria haifanggouensis, Lycoriomimodes oblongus, L. producopoda, Ancylobolbomyia haifanggouensis, Cathaypelecinus daohugouensis, Brianina longitibialis, Protostephylinus mirus, Paucirena elongata, Megathon brodskyi, Protorhyphus neimonggolensis, P. liaoningicus, Megarhyphus rarus, Mesosciophila eucalla, Paraoligus exilus, Paramesosciophilodes ningchengensis, Platyplecia suni, P.*? *parva, Laemargus yujiagouensis, Leptoplecia laevis, Beipiaoplecia malleformis, Paraplecia ovata, Arcus beipiaoensis, Sinoplecia liaoningensis, S.*? *longa, S. parvita, Sinorhyphus arcuatus, Limnorhyphus* *haifanggouensis, Mesosolva parva, Prosolva huabeiensis, Nygmatius beipiaoensis, Beipiaosirex parva, Sinocephus haifanggouensis, Mesoplecia sinica, M. mediana, Epimesoplecia shcherbakovi, E. elenae, Mesobunus martensi, Daohugopilio sheari, Ashangopsis daohugouensis, Sinosepididontus chifengensis, Megasepididontus grandis, Patarchaea muralis, Sinaranea metaxyostraca, Cheirolgisca ningchengensis, Olgisca angusticubitis, Juramantophasma sinica, Archipsylla sinica, Zygokaratawia reni, Sinojuraphis ningchengensis, Juralibellula ningchengensis, Juraperla daohugouensis, Sinokaratawia prokopi, Mongolbittacus daohugouensis, Jurocercopis grandis, Ningchengia aspera, N. minuta, Suljuktocossus coloratus, Shuraboprosbole daohugouensis, S. minuta, S. media, Daohugounectes primitivus, Gracilicupes crassicruralis, G. tenuocruralis, Mesocupes angustilabialis, M. latilabialis, M. collaris, Brochocoleus magnus, B. validus, B. applanatus, Menopraesagus explanatus, M. oxycerus, M. grammicus, Homocatabrycus liui, Loculitricoleus tenuatus, L. flatus, Lasiosyne euglyphea, Brachysyne plata, Pappisyne lasiospatha* (Wang 1987a; Deng et al. 2003; Huang et al. 2006, 2008a, b, c, 2009; Huang and Nel 2007a, b, 2008a, b; Petrulevicius et al. 2007; Zhang 2007a, b, c; Zhang and Lukashevich 2007; Nel et al. 2007, 2008; Lin and Huang 2008; Lin et al. 2008; Selden et al. 2008; Wang and Zhang 2009a, b; Wang et al. 2009a, b, c; Fang et al. 2009; Tan and Ren 2009).

10.3.1.5 Vertebrates

Liaosteus hongi, Jeholotriton paradoxus, Chunerpeton tianyiensis, Liaoxitriton zhongjiani, Yabeinosaurus tenuis, Jeholopterus ningchengensis, Pterorhynchus wellnhoferi, Scansoriopteryx heilmanni, Epidendrosaurus ningchengensis, Pedopenna daohugouensis, and *Liaotherium gracile* (Deng et al. 2003; Ji et al. 2005; Huang et al. 2006).

10.3.2 The Yixian Fauna

10.3.2.1 Conchostracans

Eoestheria aff. *middendorfii, E. jingangshanensis, E. qingquanensis, E. changshanziensis, E.? elliptica, E. persculpta, E. triformis, E. lingyuanensis, E. sihetunensis, E.* aff. *opima, E. cericula, E. guijialingensis, E. ovata, E. primitiva, E. ovaliformis, E. peipiaoensis, E. elongate, Clithrograpta lingyuanensis, C. ovata, C. polyreticulata, C. xiaodonggouensis, C. reticulata, C. guijialingensis, C. songyingensis, Chaoyangestheria yanjiagouensis, C. diformis, C. xiasanjiaziensis, C. zhaojiagouensis, C. luanpingensis, Filigrapta producta, F. corpulepta, F. jianshangouensis, F. phalosana, F. taipinggouensis, F. zhuanchengziensis, F. ovata, F. equilateralis, Dongbeiestheria? ematocomperta, D. fuxingtunensis, D. expleta, D. yushugouensis, D. naketaensis, D. tereovata, D. siliqua, D.* cf. *siliqua, D. bella, Diformograpta vera, D.* cf. *pudica, D. gongyingziensis, D.* aff. *middendorfii, D. opipera, D. lahaigouensis, D. gibba, D. donggouensis, D. ramulosa, D. minor, D. fengningensis, D. longiquadrata, D. takechenensis, D. heshanggouensis,* *D. radiate, D. weichangensis, D. shangshixiaensis, D. triformis, D. persculpta, Diestheria yixianensis, D. lijiagouensis, D. yixianensis, D. abnormis, D. hejiaxinensis, D. jeholensis, D. dadianziensis, D. ovata, D. dahuichangensis, D. longinqua, D. suboblonga, D. shangyuanensis, Isoestheria yanbizigouensism, I. qingquanensis, Asioestheria meileyingziensis, A. firma, A. nanyingpanensis, A. hamakengensis, A. damiaoensis, A.* cf. *sandaogouensis, Yanjiestheria? beipiaoensis, Y. duolunensis, Y. fengningensis, Y. dabeigouensis, Y. subquadrata, Taeniestheria qingquanensis, T. reticulate, T. suboblonga, T. subquadrata, Jiliaoestheria nematocomperta, J. clitheroformis, J. polyreticulate, J. corpulepta, J. ovata, J. longipoda, J. libalanggouensis, J. hengdaoziensis, J. huangbanjigouensis, J. heitizigouensis, J. beipiaoensis, J. zhangjiawanensis, J. striaris, J. floravalvaris, Neimongolestheria* sp., *N. damiaoensis, N. chifengensis, N. zhangjiagouensis,* and *Cratostracus?* (Wang 1987b; Deng et al. 2003; Wang et al. 2004; Li et al. 2007).

10.3.2.2 Ostracode

Cypridea (*Cypridea*) *liaoningensis, C.* (*C.*) *reheensis, C.* (*C.*) *priva, C.* (*C.*) cf. *tubercularis, C.* (*C.*) *laogonggouensis, C.* (*C.*) *yingwoshanensis, C.* (*C.*) *sandaohaoensis, C.* (*C.*) *xitaiyangpoensis, C.* (*C.*) *sihetunensis, C.* (*C.*) *zaocishanensis, C.* (*C.*) *arquata, C.* (*C.*) *placida, C.* (*C.*) *deplecta, C.* (*C.*) sp., *Cypridea* (*Ulwellia*) *sihetunensis, C.* (*U.*) *beipiaoensis, Damonella ovata, D. circulata, D. subsymmetrica, D. sublongovata, D. formosa, D. extenda, Lycopterocypris infantilis, L. debilis, Darwinula leguminella, D. contracta, D. oblonga, D. mashenmiaoensis, D. liaoxiensis, D. lahailiangensis, D. dadianziensis, Yanshania dabeigouensis, Y. elongata, Y. postitruncata, Luanpingella postacuminata, Eoparacypris dadianziensis, Mongolianella palmosa, M. subtrapezoidea, M. longula, M. yixianensis, M. breviscula, M. sandaohaoensis, M.*? *laogonggouensis, Clinocypris scolia, C. parascolia, Yumenia cadida, Y. heitizigouensis, Y. shangyuanensis, Limnocypridea subplana, L.* sp., *Djungarica camarata, D.* sp., *Rhinocypris echinata, R. jurassica, R. subechinata, Candona yingwoshanensis, Jinzhouella longissima, Mantelliana* cf. *purbeckensis, M. cirideltata, M. beipiaoensis, M. suboblonga, Timiriasevia jianshangouensis, T. polymorpha* (Deng et al. 2003; Wang et al. 2004).

10.3.2.3 Bivalves

Arguniella yanshanensis, A. lingyuanensis, Sphaerium anderssoni, S. selengiense, S. jeholense, S. subplanum, Ferganoconcha sibirica, F. cf. *burejensis, F. lingyuanensis, F. quadrata* (Yu et al. 1987; Jiang et al. 2007; Sha 2007).

10.3.2.4 Gastropods

Probaicalia vitimensis, P. gerassimovi, Galba aff. *pseudopalustris, G. minuta, G.* sp., *Gyraulus* sp., *Reesidella robusta, Ptychostylus* cf. *philippi, P. harpaeformis, Viviparus*? cf. *matumotoi, Bithynia haizhouensis, Zaptychius* (*Omozaptychius*) *angulatus* (Yu 1987; Deng et al. 2003).

10.3.2.5 Insects

Ephemeropsis trisetalis, Aeschnidium heishankowense, Sinoeschnidia cancellosa, Rudiaeschna limnobia, Liogomphus yixianensis, Mesocordulia boreala, Chrysogomphus beipiaoensis, Hagiphasma paradoxa, Nipponoblatta acerba, Rhipidoblattina decoris, R. laternoforma, R. sp.*, Karatavoblatta formosa, Blattula* sp. 1, B. sp. 2, *Habrohagla curtivenata, Liaocossus beipiaoensis, L. hui, L.* sp., *Anthoscytina aphthosa, A.* sp., *Anomoscytina anomala, Lapicixius decorus, Karataviella pontoforma, K. chinensis, Parablattula cretacea, Clypostemma xyphiale, Mesolygaeus laiyangensis, Schizopteryx shandongensis, Notocupes laetus, Tetraphalerus laetus, Geotrupoides* sp., *Protorabus* sp., *Aethocarabus levigata,*? *Fengningia* sp., *Sophogramma papilionacea, S. plecophlebia, S. eucalla, Kalligramma liaoningensis, Lasiosmylus newi, Oloberotha sinica, Lembochrysa miniscula, L. polyneura, Choromyrmeleon othneius, Mesascalaphus yangi, Siniphes delicates, Megabittacus colosseus, M. beipiaoensis, Sibirobittacus atalus, Orthophlebia liaoningensis, Parachorista miris, Protoscarabaeus yeni, Alloraphidia anomala, A. longistigmosa, A. obliquivenatica, Xynoraphidia shangyuanensis, X. polyphlebas, Caloraphidia glossophylla, Palaepangonius eupterus, Eopangonius pletus, Allomyia ruderalis, Orsobrachyceron chinensis, Oiobrachyceron limnogenus, Pauromyia oresbia, Baissoptera euneura, B. grandis, Rudiraphidia liaoningensis, Sibopera fornicata, Phiradia myrioneura, Mesoraphidia heteroneura, M. sinica, M. amoena, Alleremonomus liaoningensis, A. xingi, Protapiocera megista, P. ischyra, Lepteremochaetus lithoecius, Protempis minuta, Helempis yixianensis, H. eucalla, Lycoriomimodes* sp., *Paroryssus suspectus, Gurvanotrupes stolidus, G. exiguous, G. liaoningensis, Liaoserphus perrarus, Alloserphus saxosus, Scalprogaster fossilis, Steleoserphus beipiaoensis, Saucrotrupes decorosus, Ocnoserphus sculptus, Protocyrtus validus, Spherogaster coronata, Liaoropronia leonina, L. regia, Sinowestratia communicata, Coptoclava longipoda, Chironomaptera gregaria, Palaeopleciomima illecebrosa, Protonemestrius beipiaoensis, P. jurassicus, Florinemestrius pulcherrimus, Alloxyelula lingyuanensis, Procretevania exquisite, P. vesca, P. pristina, Angaridyela robusta, A. exculpta, A. suspecta, A. endemica, Lethoxyela excurva, L. vulgate, Ceratoxyela decorosa, Liaoxyela antiqua, Heteroxyela ignota, Sinoxyela viriosa, Isoxyela rudis, Pelecinopteron* sp., *Trematothoracoides liaoningensis, Nodalula dalinghensis, Gigantoberis liaoningensis, Turanophlebia sinica, Sinosharaperla zhaoi, Sinomodus spatiosus, S. peltatus,* and *S. macilentus* (Deng et al. 2003; Wang et al. 2004; Liu et al. 2006a; Huang and Lin 2007; Lin et al. 2007; Liu et al. 2007b; Zhang et al. 2007; Huang and Nel 2009; Wang et al. 2009c).

10.3.2.6 Vertebrates

Peipiaosteus fengningensis, P. pani, Yanosteus longidorsalis, Protopsephurus liui, Sinamia zdanskyi, Lycoptera davidi, L. sinensis, L. muroii, Jinanichthys longicephalus, Liaobatrachus grabaui, Callobatrachus sanyanensis, Mesophryne beipiaoensis, Laccotriton subsolanus, Manchurochelys manchouensis, M. liaoxiensis, *Yabeinosaurus tenuis, Dalinghosaurus longidigitus, Jeholacerta formosa, Monjurosuchus splendens, Hyphalosaurus lingyuanensis, Eosipterus yangi, Haopterus gracilis, Dendrorhynchoides curvidentatus, Hoopterus gracilis, Sinosauropteryx prima, Gegepterus changi, Beipiaopterus chenianus, Protarchaeopteryx robusta, Caudipteryx zoui, C. dongi, Sinovenator changii, Sinornithosaurus millenii, Incisivosaurus gauthieri, Yixianosaurus longimanus, Jeholosaurus shangyuanensis, Microraptor zhaoianus, Beipiaosaurs inexpectus, Psittacosaurus yangi, Jinzhousaurus yangi, Liaoceratops yanzigouensis, Luanpingosaurus jingshangensis, Confuciusornis sanctus, C. chuanzhous, C. suniae, C. dui, Jibeinia luanhera, Jinzhouornis zhangjiyingia, Changchengornis hengdaoziensis, Eoenantiornis buhleri, Liaoxiornis delicatus, Liaoningornis longiditris, Repenomamus robustus, Jeholodens jenkinsi, Gobiconodon* sp., *Sinobaatar lingyuanensis, Mirimordella gracilicruralis*, *Microprobelus liuae, Archaeoperla ratissimus, Liaotaenionema tenuitibia, Parvinemoura parvus, Zhangheotherium quinquecuspidens* (Smith and Harris 2001; Deng et al. 2003; Zhang and Wang 2004; Wang et al. 2004; Ji et al. 2005; Liu et al. 2007, 2008; Wang et al. 2007d).

10.4 List of Flora Elements

10.4.1 The Jiulongshan Flora

Hepaticites shebudaiensis, Thallites clarus, Selaginellites asiatica, S. chaoyangensis, S. drepanoformis, S. sinensis, S. spatulata, Lycopodites magnificus, Equisetum ferganensis, E. gracilis, E. guojiadianense, E. ilmijense, E. lamagouense, E. laterale, Equisetites naktongensis, Neocalamites carrerei, N. haifangouense, Marattia sp., *Todites denticulata, T. williamsoni, Clathropteris elegans, C. meniscioides, C. obovata, Hausmannia leeiana, H. rara, Coniopteris burejensis, C. hymenophylloides, C. karatiubensis, C. bella, C. minturensis, C. nerifolia, C.* cf. *sewardi, C. simplex, C. tyrmica, Dicksonia changheyingziensis, Eboracia lobifolia, Pteridiopsis shajingouensis, Cladophlebis argutula, C. asiatica, C. coniopteroides, C. haiburnensis, C. hsiehiana, C. nalivkini, C. nebbensis, C. oligodonta, C. punctata, C. shansiensis, C. spinellosus, C. sulcata, C. tarsus, Raphaelia diamensis, R. stricta, Sagenopteris bilobata, S.* sp., *Ptilophyllum* cf. *pectinoides, Anomozamites angulatus, A. kornilovae, A.* cf. *nilssoni, A. nitida, A.* cf. *major, A. sinensis, A. haifanggouensis, A.* (*Tyrmia*) sp., *Pterophyllum festum, P. firmifolium, P. lamagouense, P. pumilum, Tyrmia grandifolia, T. mirabilia, T. pterophylloides, T. valida, Jacutiella denticulata, Cycadolepis nanpiaoensis, C.* sp., *Cycadocites nilssonervis, Zamites gigas*, *Weltrichia daohugouensis, Nilssonia* cf. *compta, N. liaoningensis, N. orientalis, N. tenuicaulis, N.* sp., *Beania chaoyangensis, Ctenis chinensis, C. delicatus, C. leeiana, C. lingyuanensis, C. niuyingziensis, C. pontica, C. sulcicaulis, Pseudoctenis eathiensis, P. brevipennis, Ginkgo lepida, G.* cf. *obrutschewi, G. sibirica, Ginkgoites* sp., *Baiera asadai, B. concinna, B. czekanowskiana,* *B. furcata, B. gracilis, B. lindleyana, Sphenobaiera angustiloba, S. colchica, S. paucipartita, S.* cf. *pulchella, Czekanowskia rigida, C. setacea, Solenites* cf. *vimineus, Phoenicopsis angustifolia, P. angustissima, P. manchurica, P. speciosa, Leptostrobus cancer, Ixostrobus lepidus, I. groenlandicus, Antholithus fulongshanensis, Yimaia capituliformis, Pityocladus acusifolius, P.* sp., *Pityophyllum lindstroemi, P. longifolium, Eoglyptostrobus sabioides, Pityospermum braunii, P.* cf. *maakianus, Podozamites lanceolatus, P. gramineus,* cf. *Aethophyllum niuyingziensis, Yanliaoa sinensis, Schizolepis* cf. *moelleri, S. micropetra, S. planidigesita, S. trilobata, Elatocladus* (*Cephalotaxopsis*) *krasseri, Nanpiaophyllum cordatum, Desmiophyllum* sp., *Problematospermum ovale, Schmeissneria sinensis, Solaranthus daohugouensis, Xingxueanthus sinensis* (Pan 1977; Zhang and Zheng 1987; Wang et al. 1997; Deng et al. 2003; Li et al. 2004; Wang et al. 2007a, b; Zhou et al. 2007; Wang and Wang 2010, Zheng and Wang 2010; Wang et al. 2010).

10.4.2 The Yixian Flora

Thallites jianshangouensis, T. riccioites, T. dasyphyllus, T. sp., *Metzgerites multiramea, Muscites meterioides, M. tenellus, M. drepanophyllus, Hepaticites* sp., *Selaginellites fausta, Equisetites exiliformis, E. longevaginatus, E. linearis, E.* sp., *Lycopodites faustus, Coniopteris burejensis, C. angustiloba, C. simplex, C. spectabilis, C. tatungensis, Botrychites reheensis, Dictyophyllum*? sp., *Eboracia lobifolia, E. uniforma, Gymnogrammitites ruffordioides, Onychiopsis elongate, Todites major, Xiajiajienia mirabila, Cladophlebis asiatica, Sphenopteris hymenophylla, Taeniopteris* sp., *Cycadites yingwoshanensis, Tyrmia acrodonta, Otozamites anglica, O. beani, O. turkestanica, Zamites yixianensis, Neozamites verchojanensis, Rehezamites anisolobus, Weltrichia huangbanjigouensis, Williamsonia bella, W. exiguous, W.* sp. 1, *W.* sp. 2, *W.* sp. 3, *Williamsoniella jianshangouensis, W.* sp., *Bucklandia* sp. 1, *B.* sp. 2., *Ginkgo apodes, Ginkgoites* sp. 1, *G.* sp. 2, *G.* ex gr. *sibiricus, Baiera furcata, B. gracilis, B. borealis, B. manchurica, B. lindleyana, B. valida, B.* sp., *Sphenobaiera* sp. 1, *S.* sp. 2, *Eretmophyllum* sp. 1, *E.* sp. 2, *Pseudotorellia* sp., *Stenorachis beipiaoensis, Antholithus ovatus, A.* sp. 1., *A.* sp. 2, *A.* sp. 3, *A.* sp. 4, *Czekanowskia rigida, C.*? *debilis, C. setacea, Phoenicopsis angustissima, P.* sp., *Solenites murrayana, S. orientalis, S.* sp. 1, *S.* sp. 2, *Sphenarion parilis, S.* sp., *Leptostrobus sinensis, L.* sp., *Ixostrobus delicatus, Eoglyptostrobus sabioides, Pityophyllum lindstroemi, P. longifolium, P. staratschini, P. nanseini, Pityolepis larixiformis, P. pseudotsugaoides, P.* sp., *Pityocladus densifolius, P. abiesoides, P. jianshangouensis, Schizolepis chilitica, S. moelleri, S. jeholensis, S. beipiaoensis, S.* sp., *Cupressinocladus heterophyllum, Cyparissidium blackii, C. rudlandium, C. opimum, Scarburgia hilli, Araucarites minor, Athrotaxopsis* sp., *Cephalotaxopsis leptophylla, C. sinensis, Podocarpites reheensis, Brachyphyllum longispicum, B. rhombicum, B.* cf. *japonicum, Pagiophyllum beipiaoense, P.* sp., *Liaoningcladus boii, Elatocladus liaoxiensis, E. leptophyllus, E. pinnatus, E.* sp. 1, *E.* sp. 2, *Podozamites lanceolatus, P. graminues, P.* sp., *Pityanthus* sp. 1, *P.* sp. 2, *Khitania columnispicata, Ephedra archaeorhytidosperma, Ephedrites* *chenii, E. guozhongiana, E. hongtaoi, E.? elegans, Amphiephedra rhamnoides, Membranifolia admirabilis, Problematospermum beipiaoense, P. ovale, Strobilites interjecta, S. taxusoides, Conites longidens, C.* sp., *Carpolithus multiseminalis, C. pachythelis, Paracaytonia hongtaoi, Chaoyangia liangii, Archaefructus liaoningensis, A. sinensis, A. eoflora, Beipiaoa spinosa, Sinocarpus decussatus, Callianthus dilae* (Wu 1999; Sun et al. 2001, 2002; Leng and Friis 2003, 2006; Ji et al. 2004; Wang et al. 2004; Zheng and Zhou 2004; Yang et al. 2005; Wang and Zheng 2009, 2010; Guo et al. 2009; Wang 2010; Wang et al. 2010).

10.5 Morphological Matrix for Seed Plant Cladistics

From Rothwell and Serbet (1994), with the data of angiosperms modified.

ANC

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ANE

00?000?0?????000?00000000??0?0000?00?????0??0000000????0?????????

ARC

10?0103000?0?10100010010000200010010?????0??000000000??0??0??????

CEC

11??103?0000?10000000010000200010010?????0??00010?000??0??0??????

ELK

11??120?00???0000000010001000100102100?0010000000000????1000??0?

HET

11??120?0000?10000010100110?010?1022000000100000000?00????10?0??0?

LYG

11?112010000?1010001020011000100102200000100000000000??001000??0?

CAL

11?1130100???10100010200110100021022010112011011110?00?1?10?0??0?

QUA

11?12????????100200103?0??0??00???220000020?10??????0????1000??0?

MED

11?1120?0000?101201103001100000010220000020110010000??011000??0?

GIN

110110310000011111010240510000?0022010002010111010100011100010 10

EMP

11?111200000?1110001015251001001002200?22010001110?0?????0?0??1?

PIN

1101132100000111010103525122100200220102321201111101001121000201 1

POD

1101133100000111010103525122120200220102021201111101001121000201 1

TAX

11011321000001110101032051100300002201010012011001011111210002011

CRD

11?113310000011100010161310000000002201011201 10?1110?00???10?0??0?

MES

11?213310000?1110001016151000000000220101120 1100?110?0???10?0??0?

CYC

110?13110000011110010330410000020022010002011011010100011100010?0

CRS

11?112110000?1?110010200110202020022011 2020?1111110?1???????????

PEL

11???30100?0??????0???001101000200 22?????2???1110?0?0???????????

GLO

11?113111000?1?1?00100001102020?0022010?1211?011111?0???????0????

CAY

11?113111010?1????0???0011020202002 20?01??1?0011110?1???????????

BEN

11?113110001?111?0000340?10003011122110200?2111102011?????0?0??1?

PEN

11?113110000?101101000?021000?000?220102????1111020?0????????????

EPH

11122321000011111101106050000010112211120212111102111011210000011

WEL

1112233111011111?1011360?01000101122111100121111021111120111011 1

GNE

1112231111011111110?1060?0100010?12211100212011?02?11111201110111

ANG

1111(12)3111110111?1001(23)405010?2101022001?2012?1100200?2?120010001?

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