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The Dawn Angiosperms

Uncovering the Origin of Flowering Plants

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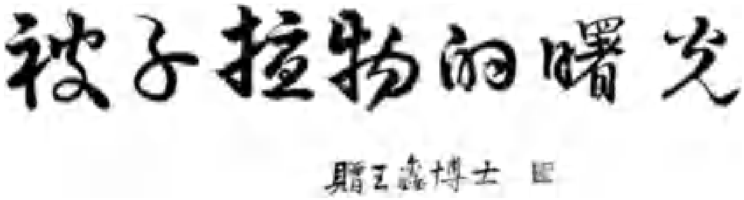

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贈王鑫博士

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ISSN 2197-9545 ISSN 2197-9553 (electronic)
Springer Geology
ISBN 978-3-319-58324-2 ISBN 978-3-319-58325-9 (eBook)
DOI 10.1007/978-3-319-58325-9

Library of Congress Control Number: 2017945088

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Printed on acid-free paper

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The registered company is Springer International Publishing AG
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Dedicated to
the 120th Anniversary of
Peking University

Preface

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

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

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

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

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

Nanjing Xin Wang
March 2017

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 benefited 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, Zhong-Jian Liu, Limi Mao, Frédéric Jacques, Gang Han, Yong Yang, and my advisors have coauthored 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, Shuangxing Guo, Qiang Ji, Jun Wang, Yi Wang, Deming 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, 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, 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, Ian Glasswool, José B. Diez Ferrer, Michael Heads, Douglas McKinnon, Williams Rose, and many unnamed here. Margaret Joyner have helped with English in the first edition of this book. Dr. Christopher Hill has gone through the first edition and given constructive and detailed suggestions. Finally, and most importantly, my family, especially my wife Huijun Ma, have been supportive for my research. I wish to extend my cordial thanks to all of them.

The research is supported by the National Natural Science Foundation of China (41688103, 91514302, 91114201), Strategic Priority Research Program (B) of Chinese Academy of Sciences (Grant No. XDPB05, XDB18000000), the State Key Laboratory of Systematic and Evolutionary Botany at the Institute of Botany, Chinese Academy of Sciences, the Scientific Research Foundation for Returned Overseas Chinese Scholars, State Education Ministry, State Key Laboratory of Palaeobiology and Stratigraphy (Nanjing Institute of Geology and Palaeontology, CAS, No. 053103), and Deep Time RCN. This work is a contribution to IGCP 632.

Contents

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Acronyms

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

List of Figures

xinwang@nigpas.ac.cn

List of Tables

Chapter 1
Introduction

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

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

X. Wang, The Dawn Angiosperms, Springer Geology,
DOI 10.1007/978-3-319-58325-9_1

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

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

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

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

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

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

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

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

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Chapter 2
Suggested Angiosperm Ancestors

There have been many proposals of candidates for the ancestors or closest relatives of angiosperms. Some of the currently most 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 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. Thus the gap between gymnosperms and angiosperms is by no means narrowed. 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 concerned to the origin of angiosperms, 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.

X. Wang, *The Dawn Angiosperms*, Springer Geology,
DOI 10.1007/978-3-319-58325-9_2

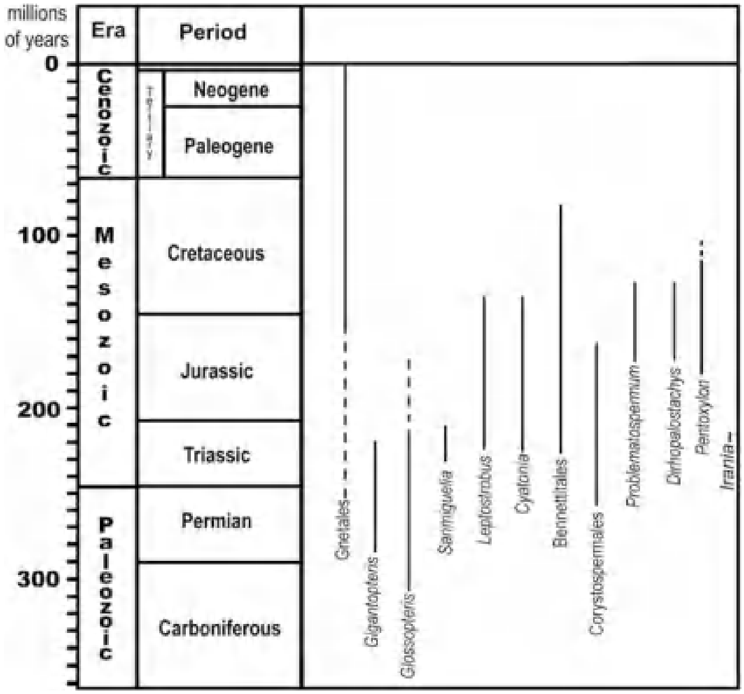

Fig. 2.1 Approximate temporal distribution of the taxa discussed in this chapter. Dashed lines indicate uncertainty

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, opposite and decussate phyllotaxy, vessel elements, circular bordered pits in protoxylem, a terminal ovule with two integuments, micropylar tube, lack of archegonia, ribbed pollen (except for Gnetum) and leaf vein anastomose (except for Ephedra) (Crane 1996; Maheshwari 2007). Among them a micropylar tube is a common feature shared by these three genera, uniquely in living gymnosperms. Recent studies indicate that the micropylar tube is a feature seen in the Bennettitales-Erdtmanithecales-Gnetales clade (Friis et al. 2009). But whether this feature implies a common ancestor for these three groups is still an open question. Gnetales appear to have had their greatest diversity in the past, and Ephedra-like pollen 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

Permian (Delevoryas 1962; Wang 2004). Recent more megafossils of Gnetales have been found from the Early Cretaceous in South America and China (Rydin et al. 2003, 2004, 2006; Tao and Yang 2003; Dilcher et al. 2005; Yang et al. 2005; Guo et al. 2009; Wang and Zheng 2010). But not all of them are well-studied, and sometimes various taxa may be lumped into a single one (Yang et al. 2005). Therefore more detailed studies need to be carried out to elaborate the implications of these fossils. 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; Chamberlain 1957; Martens 1971; Friedman 1990a, b, 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 1990a, b, 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). 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). The relationship between angiosperms and Gnetales becomes more intriguing when a fossil named Pseuodoephedra is taken into consideration. Pseudoephedra is a fossil plant with ephedroid appearance and solid style (rather than micropylar tube) (Liu and Wang 2016). Such a chimerical combination of feature makes previous treatment of fossil Ephedraceae more vulnerable to criticisms (For more, see Chaps. 7 and 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 coal ball material (Li and Yao 1983a, b; 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 et al. (2004) prefer to describe them using angiospermous terms although the authors rule out any relationship between them and angiosperms. These foliar

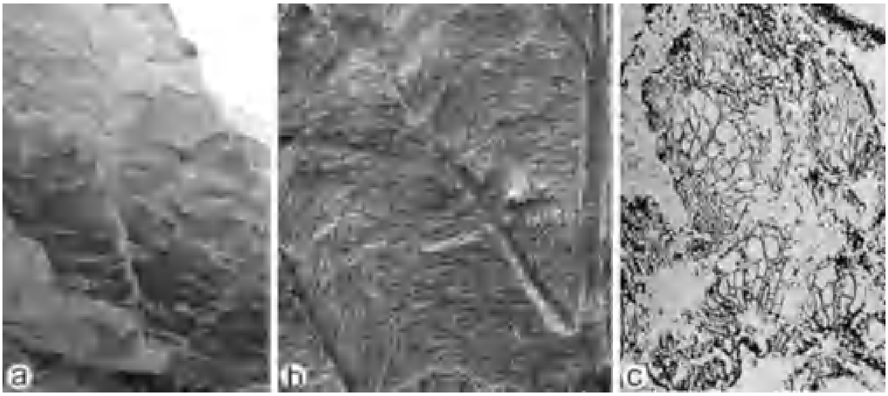

Fig. 2.2 Leaf morphology, venation, and vessel elements of Gigantopterids. (a) Leaf morphology of *Gigantonoclea* (IBCAS). (b) Venation of *Gigantonoclea rosulata* Gu et Zhi (PB4969, NIGPAS). (c) Vessel element of *Vasovinea tianii* Li et Taylor (Courtesy of Dr. Hongqi Li)

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). Typical vessel elements are seen so far only in Gigantopteridales, Gnetales, and angiosperms, making Gigantopteridales especially attractive candidate for angiosperm ancestors. Furthermore, oleanane, a chemical species formerly found only in extant angiosperms, has also been found in Gigantopterids in addition to Bennettitales (Taylor et al. 2006a). This discovery suggests a possible relationship among Gigantopterids and angiosperms as well as Bennettitales (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 (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 Middle Jurassic (Delevoryas 1969; 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).

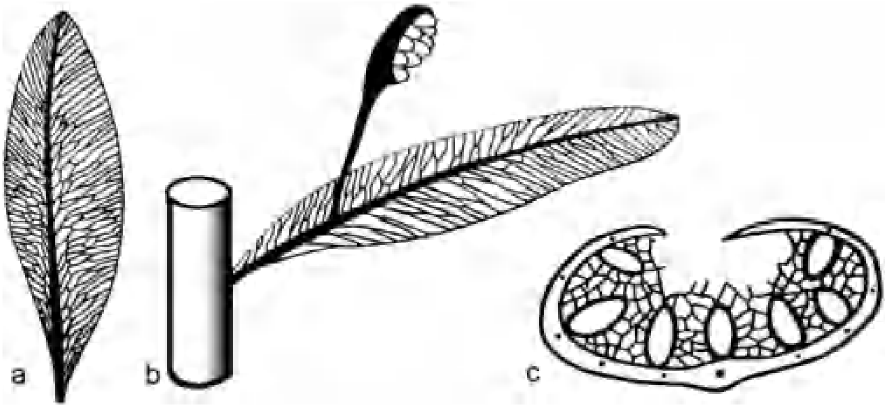

Fig. 2.3 Leaf and reproductive organ of Glossopterids. (a) Leaf. (b) Axis with a megasporophyll. (c) Cross section of cupule showing adaxial arrangement of seeds partially inrolled by the cupule

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 leaf (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 midvein of a modified leaf. The glossopterids have been suggested as potential angiosperm ancestors (Retallack and Dilcher 1981). Theoretically, the glossopterid vegetative leaf could be homologous to an angiosperm′s carpel, and the megasporophyll to the outer integument (Retallack and Dilcher 1981; 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 previously advanced 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 1981). 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 1981; Taylor and Taylor 2009). Moreover, the provenance of stamens and perianth are further challenges for this hypothesis. Meanwhile, it has also been suggested that the Glossopteridales are the ancestors of Caytoniales based on leaf venation, pollen grains and seed structure (Delevoryas 1969; Krassilov 1977b).

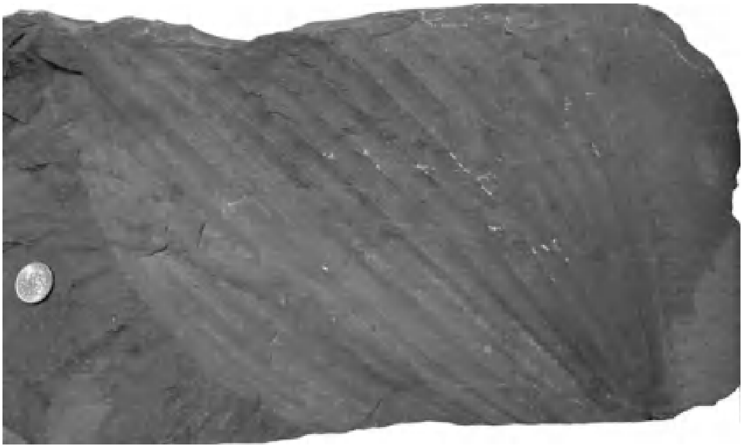

Fig. 2.4 Palm-like pleated leaf of *Sanmiguelia*

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, 1989; Fig. 2.4). The reconstructed plant includes the leaves (*Sanmiguelia*), ovuliferous 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 pollen units yielding monocolpate pollen grains. Cornet (1989) described the transmitting tissue, cotyledons, and developmental pattern in the fossil to prove its angiospermous affinity. 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 determined 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. 2006). It consists of an axis bearing numerous short-stalked, spirally arranged bivalved capsules containing multiple seeds (Krassilov 1977a; Liu et al. 2006; Fig. 2.5). The capsule valves

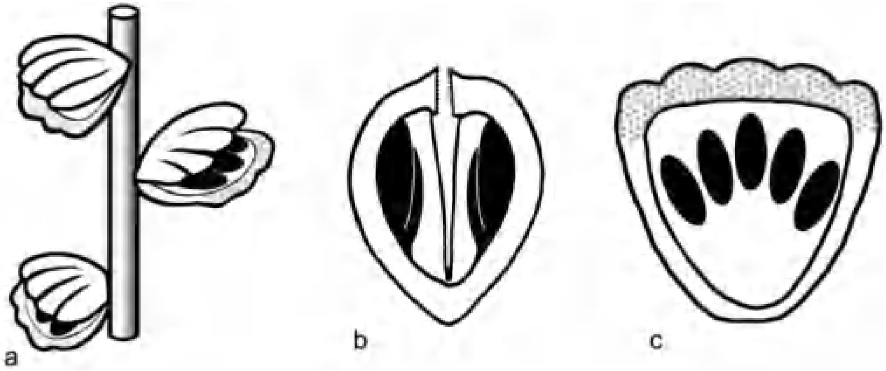

Fig. 2.5 Reproductive organ of Czekanowskiales. (a) *Leptostrobus*, showing capsules attached to an axis. (b) Longitudinal section of capsule showing two identical facing valves forming a capsule. (c) Interior view of a valve of the capsule showing seeds and papillate flange (dotted)

have papillate flanges (or lips), which may have functioned like stigmatic bands (Krassilov 1977a; Fig. 2.5c). Each valve bears 3–5 seeds (Liu et al. 2006; Fig. 2.5b, c). The flange is not seen in *Leptostrobus* specimens from earlier specimens, therefore its presence in later species of the genus may be derived (Krassilov 1977a). Its leaf is of the *Phoenicopsis*-type. 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. 2.6). 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 *Caytonanthus* bears in situ monosulcate bisaccate pollen grains, *Vitreisporites* (Harris 1964; Taylor et al. 2006a, b; Taylor and Taylor 2009). Caytoniales have an axis bearing stalked, rounded, helmet-like cupules. Each cupule is recurved adaxially, 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. 2.6). The micropyles of the ovules are connected to the cupule opening via canals (Harris

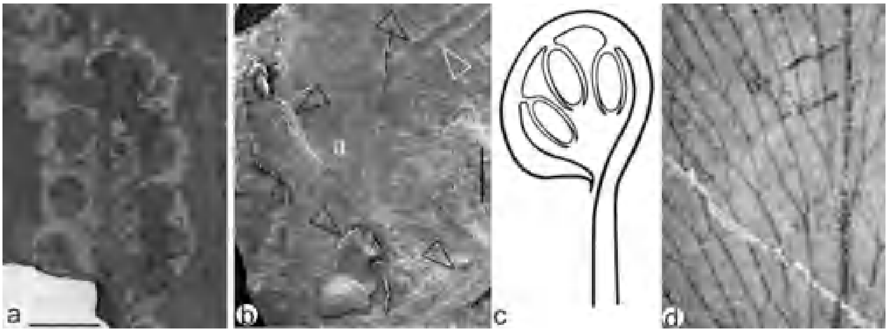

Fig. 2.6 Paracaytonia and Sagenopteris. (a) General view of the reproductive organ. Note the multiple cupules physically connected to the same axis (GBM1, SFLBG). Bar ¼ 1 cm. (b) Detailed view of the cupules helically arranged around the axis. Note the cupule stalks (black arrows) and the stub of another broken one suggesting a helical arrangement along the axis (a). Bar ¼ 1 mm. (c) Idealized longitudinal section of a caytonialean cupule, showing cupule stalk, basal cupule opening, and seeds inside the cupule. (from Wang 2010, courtesy of Journal of Systematics and Evolution). (d) Meshes and midrib (right) in the leaf of Sagenopteris

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, indicated 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 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.

According to the previous interpretations, there is a contrast between Caytonia and angiosperms as the Caytonia cupule is derived from megasporophyll that has become folded or recurved transversely while the conduplicate carpel in angiosperms is thought folded longitudinally (Taylor et al. 1994; Taylor and Taylor 2009). This contrast becomes less strong if the way of carpel forming in some non-mangoliaceous angiosperms (e.g. Amborella and Centrolepdiaceae, in which the carpels are not conduplicate) is taken into consideration. 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, b, 1987; Doyle 1998, 2006; Taylor et al. 2006b; Taylor and Taylor 2009). Since an angiospermous ovule usually has two 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). 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*, unequivocally demonstrates that the arrangement of cupules along the axis is spiral rather than pinnate (Wang 2010; Fig. 2.6), suggesting that the so-called rachis is a true axis rather than a true rachis, as had been commonly thought (Doyle 2006; 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; Taylor and Taylor 2009). Thus the Chinese material at least widens the gap between Caytoniales and angiosperms, or more likely, it reduces the probability of carpel derivation in this way.

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. 1989; 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 funiculus, 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 male parts bearing pollen sacs on their adaxial surfaces containing monocolpate pollen grains. Outermost are numerous 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 1907; 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; Doyle and Donoghue 1987). The presence of oleanane in Bennettitales adds further evidence as to 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. 1989). Based on the similarities of seeds with micropylar tubes, Friis et al. (2009) proposed that Bennettitales, Erdtmanithecales, and Gnetales be grouped into 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 different to be ancestral for carpels of angiosperms. However, Rothwell and Stockey′s (2010) report of Foxeoidea from the Early Cretaceous suggests a possible ovule-enclosure different than previously assumed. It is more intriguing that it appears that such an ovule-enclosing appears to realized in Zhangwuia, a fossil reproductive organ that spans Bennettitales and angiosperms (for more, see Chap. 7).

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 organ in Corystospermales is called Umkomasia (Fig. 2.7). Based on strong evidence of association in the field, it is believed that the pollen organ is Pteruchus, which produce bisaccate pollen grains. The connected leaf is Dicroidium (Axsmith et al. 2000; Taylor and Taylor 2009). It was 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, China, and Mongolia) (Kirchner and Müller 1992; Zan et al. 2008; Shi et al. 2016). 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; Shi et al. 2016; Fig. 2.7). Each lateral axis bears pairs or whorls of stalked, abaxially recurved, helmet-like cupules. Unlike Caytoniales, each cupule of Umkomasia contains only one or two ovules, and usually its curved bifid micropyle protrudes beyond the cupule opening. Recent study indicates that, at least in U. mongolica, the ovules are borne on the terminals of axes and more or less covered by two foliar structures (Shi et al. 2016). The abaxial position of the ovules alienates Corystospermales from most angiosperms and Petriellales as well as Caytoniales, which bear adaxial ovules (Klavins et al. 2002; Taylor and Taylor 2009). But this conclusion becomes tentative as a new type of gynoecium is found in a Jurassic angiosperm (Yuhania), in which the ovule is not situated in the axil but on the floral axis and abaxial relative to the concerned ovule-enclosing structure (Chap. 6). Although requiring further confirmation, this discovery reduces the gap between angiosperms and Umkomasia. 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).

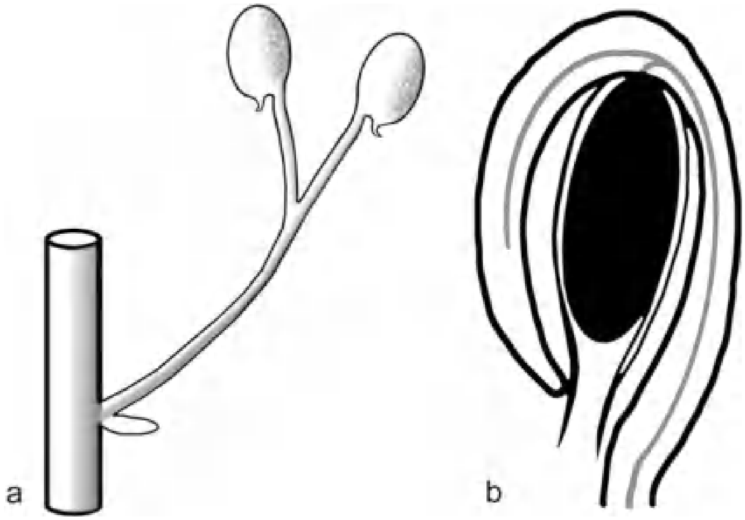

Fig. 2.7 *Umkomasia* and its details. (a) Reconstructed branch bearing a pair of cupules. (b) Longitudinal section showing cupule surrounding a seed with a protruding micropyle. Gray color stands for vascular bundles

2.9 Problematospermum

Problematospermum is reported from the Middle Jurassic to Lower Cretaceous of Kazakhstan, Mongolia, and China (Fig. 2.8). 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 rows and files. Its apical projection is straight, with a central canal. Its seed coat is composed of epidermal cells and three types of sclerified cells. Inside the seed coat is endosperm of parenchyma. This fossil plant has frequently been classified as an angiosperm or proangiosperm (Krassilov 1973a, b, 1977a, 1982; Liu 1988; Wu 1999), and it was lumped into Ephedraceae (Figs. 7–9 of Yang et al. 2005). However, recent work indicates that these conclusions are inconclusive and that this plant may well bridge gaps among several groups (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 comprises helically attached elliptical to obovate cupules each dehiscing along a ventral suture. Each cupule has an elongated beak-like extension and a ventral

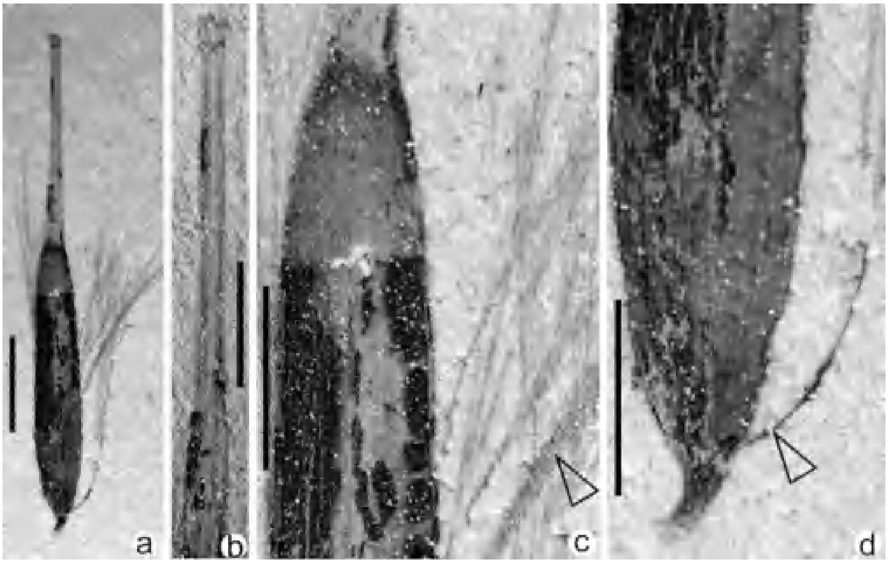

Fig. 2.8 Seeds of Problematospermum ovale (PB21392, NIGPAS). (a) Complete seed. Bar ¼ 2 mm. (b) Seed with an apical projection. Bar ¼ 1 mm. (c) Seed with filamentous appendages (arrow). Bar ¼ 1 mm. (d) Seed body with filamentous appendages attached (arrow). Bar ¼ 1 mm

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 related Dirhopalostachys to the capsule of the angiosperms Trochodendrocarpus (1977a) and Kingdonia (Krassilov 1984). Little is known about the pollination/fertilization of this plant (Krassilov 1984), therefore it is hard to know whether or not it is truly an angiosperm.

2.11 Ktalenia

The ovule-baring structure named Ktalenia (Fig. 2.9) 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, abaxially recurved, with their openings pointing proximally, 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 (although this feature has been seen in some Jurassic angiosperm,

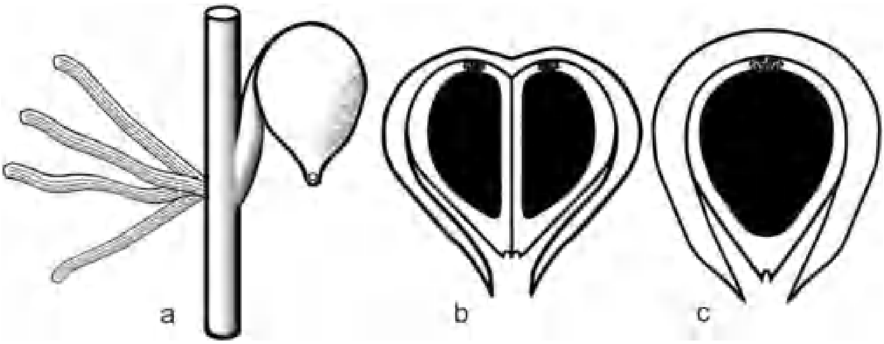

Fig. 2.9 Reconstructed Ktalenia. (a) Fertile axis bearing cluster of a bract at left and cupule at right. (b) Cross section of a cupule containing two ovules. (c) Cross section of a cupule containing one ovule

see Chap. 6), it is hard to take Ktalenia as an angiosperm ancestor because the pre-Aptian age of megafossil angiosperms including Yuhania, Chaoyangia, Archaefructus, Sinocarpus, and Callianthus (Duan 1998; Sun et al. 1998, 2001, 2002; Leng and Friis 2003, 2006; Wang and Zheng 2009; Liu and Wang 2017. see also Chaps. 5 and 6) reduces the probability for Ktalenia to give rise to angiosperms, if the latter are monophyletic.

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 flourished 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 ovules and associated 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 Irania

Irania is the type genus for the order Iraniales established in 1977 by Schweitzer. Irania is a hermaphroditic reproductive structure of the Late Triassic of northern Iran (Schweitzer 1977). It was interpreted as "flowers", consisting of an axis bearing helically arranged clusters of microsporangia. The pollen is unknown. Narrow, dichotomizing, secondary axes arise from the main reproductive axis, each bearing a flattened, heart-shaped structure (capsule). A ridge of delicate tissue is seen on the edge of the capsule. The ridge of tissue may be interpreted as an integumentary wing of a flattened seed, and the pointed tip may be the micropylar end of the seed. The associated Desmiophyllum type foliage in the same rocks was interpreted as suggestive of affinities with the Czekanowskiales.

2.14 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). These plants, at least, require further effort to be related to angiosperms.

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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 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 or before the time of fertilization 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 Messy Definitions of Angiosperms

Defining angiosperms is more much difficult than it appears. The following interactions between my colleagues and me reflect this fact.

Interaction 1 Years before I gave a talk about an early angiosperm, *Schmeissneria*, in a European palaeobotanical meeting. After I had a brief communication with Dr. A. Dr. A disagreed with my treating *Schmeissneria* as an angiosperm, since that, although an interesting fossil, “double fertilization is not seen in *Schmeissneria* . . .” Later I realized that she was right, however, double fertilization had never been seen in any fossil plants, including those documented by Dr. A. Therefore according to Dr. A, there were no fossil angiosperms in this world!

Interaction 2 Once Dr. B gave two talks about fossil angiosperms and their evolution in Nanjing. After the first talk, I asked Dr. B, what were the criteria he used to identify angiosperms in the fossil world. He answered, three features, tetrasporangiate anther, bitegmic ovule, and enclosed ovules, were needed to identify an angiosperm. After the second talk, I asked him to demonstrate how to apply his definition by giving an example. He could not find an angiosperm passing his test. Apparently, he used a secret criterion that he refused to disclose to others.

X. Wang, *The Dawn Angiosperms*, Springer Geology,
DOI 10.1007/978-3-319-58325-9_3

Interaction 3 In May of 2016 Dr. C participated a meeting in Nanjing. In a late afternoon in May, Dr. C came into my office and expressed his interest in discussing my research on early angiosperms. Generally, he disagreed with my conclusions on early angiosperms but he had a will to discuss with me on a better way to do the research. I humbly agreed to take a lesson from him. I asked what I should do. He informed me that I should search for anatomical features. "What kind of anatomical feature defines angiosperms?" I asked. He replied with silence. Then he asked me, how I defined angiosperms. I said, "Literally, angiosperms are defined by enclosed seeds." Dr. C briskly interrupted, "No. Seeds in some conifer cones are also enclosed!" I explained, "That is what average people think. What I used is ovule enclosed before pollination." Again, as briskly as before, Dr. C responded, "I got up very early this morning, and I have been in the meeting all the day. Now I am tired. I still have to modify manuscripts for my students. I need go back to my hotel and have a rest." I let him go.

The common things underlying these three superficially different interactions are (1) that different scholars adopt different definitions and frequently they assume that others agree with them implicitly, (2) that scholars may be requiring others to accept their rules that they rarely apply themselves, (3) that different scholars designate different things when they use exactly the same word "angiosperm".

Such a messy status of defining angiosperms at least partially contributes to the controversies over early angiosperms.

3.2 Angiospermous Characters

Almost every student of biology appears to know what a flower is. But this easy-appearing question turns out to be extremely difficult 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 a science that categorizes and puts like with like, whether they be botany, zoology, or geology. Phytotaxonomy is the branch of such science that deals with plants. Like in other branches of taxonomy, type specimens play a crucial role. 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 from 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.

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, 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 of them are seen in a plant, it is safe to declare it as an angiosperm. However, nature is never as simple as we like. 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.

3.2.1 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 et al. 2003; Archangelsky et al. 2009), thus, unsurprisingly, it is frequently used as an index feature of angiosperms. This character, related to the efficiency of material transport within plant bodies, may have contributed to the success of angiosperms in their competition 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 great, 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 1981; 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 1981; 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 early angiosperms

Archaefructus, *Juraherba*, *Yuhania* (Sun et al. 1998, 2002; Wang and Zheng 2012; Han et al. 2016; Liu and Wang 2017). It appears that the presence or absence of reticulate venation in a plant can neither ascertain nor negate a possible affinity to angiosperms.

3.2.2 Vessel Elements in the Xylem

Vascular plants are distinguished from non-vascular plants by their special and efficient water conducting system, vascular bundles. The evolution of the land plants is, besides other aspects, reflected in the organization and composition of the vascular bundles. During the past hundreds 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. Gnetales, Selaginellales, and some ferns also have vessel elements in their xylems (Eames 1961; Martens 1971; Carlquist and Schneider 2001; Schneider and Carlquist 1998, 2000). 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; Chamberlain 1957; Eames 1961; Martens 1971; Sporne 1971; Cronquist 1988; Li et al. 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.

3.2.3 Closed Carpel, or Enclosed 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). 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 fertilization. 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 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 et al. 2004, 2007; Maheshwari 2007; Zan et al. 2008; Taylor and Taylor 2009). At the same time, not all angiosperms have their seeds physically enclosed, including members of the Amborellaceae, Schisandraceae, Austrobaileyaceae, Trimeniaceae (Endress and Igersheim 2000), and Magnoliaceae. Furthermore, carpels in *Reseda* (Resedaceae) (Hill and Crane 1982) and *Delphinium consolida* (Ranunculaceae) (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 2000). 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 this, 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 strict line between gymnosperms and angiosperms in this term.

3.2.4 Bitegmic Ovule

The so-called integument is a protective layer of tissue surrounding the nucellus. Its existence can be traced back to the earliest ovules/seeds of the Devonian. 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 Zhang 2013 and Chap. 8 for further information). The cupule of *Caytonia* is frequently compared to the outer integument of angiosperms, but this comparison faces the challenge of deriving carpels at the same time (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 identifying feature of angiosperms. For example, the claimed two integuments of *Monetianthus* cannot be demonstrated clearly even with technology of synchrotron radiation X-ray tomography (Friis et al. 2009). Consequently, this character cannot, at least at present, be used as the index character of fossil angiosperms although it works well in most instances of living plants.

3.2.5 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 1992). Double fertilization, resulting in the formation of a (usually) triploid endosperm tissue, is 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 1992). However, within angiosperms, double fertilization does not occur in *Cortaderia jubata* (Gramineae) (Johri and Ambegaokar 1984), Podostemaceae (Raghavan 2005; Maheshwari 2007), and *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 1990a, b, 1991, 1992; Yang et al. 2000; Friedman and Williams 2004; Raghavan 2005).

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

3.2.6 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, as is the case seen in *Euanthus panii* from the Middle Jurassic (Liu and Wang 2016), it is clear 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.

3.2.7 Pollen Tube

The 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 the pollen tube in angiosperms is believed to be related to the enclosure of ovules by ovarian wall, which protect ovule against desiccation, predation, and self-fertilization (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 (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 character distribution among vascular plants, the presence of a pollen tube does not appear to be a synapomorphy of angiosperms since a pollen tube may be a common character shared by many seed plant groups, including angiosperms. Furthermore pollen tube is, most time, not preserved in fossil materials.

3.2.8 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 fertilization, 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, 2013; Maheshwari 2007; Archangelsky et al. 2009). Many such pollen grains are indistinguishable from angiosperms even after careful examination using a TEM. However, at least some of them 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 record based on this character alone has met some resistance. 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. On 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, either. Therefore although tectate-columellate pollen grains cannot definitely determine the occurrence of angiosperms in the pre-Cretaceous, they may direct more attention to more promising research on their mother plants, the affinity of which may be easier to determine with more confidence in palaeobotanical practice.

3.2.9 Developmental Pattern

The formation of nutritional storage tissue in seeds follows different patterns in angiosperms and gymnosperms (Leslie and Boyce 2012). In gymnosperms it is derived from the female gametophyte, which typically forms before fertilization (pre-fertilization allocation of nutrients to the embryo-nourishing tissue, according to Friedman (2008)). In angiosperms the endosperm does not form until after fertilization. This manner of endosperm development in angiosperms does not waste too much nutrition on ovules that may not be fertilized or later abort, as is frequently seen in gymnosperms. For example, cycadalean ovules accumulate much nutrition, but may not ever be fertilized at all and thus waste much nutrition and resources (Cronquist 1988). This economic strategy might have contributed partially to the success of angiosperms in competition with their gymnospermous peers. Cornet (1989b), working on *Sanmiguelia*, has attempted to use its developmental pattern as evidence favoring 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 fertilization in Bennettitales appears to have occurred when the ovule was small (Pedersen et al. 1989b), implying that the endosperm may not have started forming before fertilization, 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 fertilization, a typical gymnospermous trait (Friedman 2008). Therefore the boundary between angiosperms and gymnosperms overlap in this term, so it is not universally valid to use such a character to identify an angiosperm, especially from the fossil record.

3.2.10 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 chemophytotaxonomy (Judd et al. 1999). For example, betalains are restricted to the Caryophyllaceae 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 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 in the angiosperms, was recently found to be present in *Selaginella* of Lycophyta (Weng et al. 2008). Similarly, oleanane, formerly thought restricted to the angiosperms, has been found in Palaeozoic and Mesozoic non-angiospermous plant fossils (Taylor et al. 2006a, b). The variable value and difficulty of extracting information on chemical compounds in fossil plants make them unlikely to be a safe consistent index character of angiosperms.

3.3 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 is based on several characters or an assemblage of characters, sooner or later a case will appear only a subset of the assemblage occurs in a plant. What do we do then? Either accepting or rejecting it will be criticized by someone, and this would cast doubt 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.

3.4 Criterion for Fossil Angiosperms

It is apparent from the foregoing that several characters have been used 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 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 then. Using all of these characters to identify an angiosperm would only result in no angiosperms at that time. 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 allow recovering all these characters from one 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 angiospermous affinity 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 a 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 unsurprising that people working on leaves prefer reticulate leaf venation, those working on wood 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 in palaeobotany. To expel the controversy inflicting this research, aligning with one or another so-called 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 judgment. This normal thinking works only when the key character is secured. Marginal characters help, but less than assumed. For example, Gigantopteris has three characters (reticulate venation, vessel elements, 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 enhances the confidence. But the initial acceptance is based on a single feature, namely, enclosed seeds. From the negative side, Caytonia is rejected as an angiosperm also based on a single character: pollen grain within cupule, suggestive of exposed ovules. In both cases the conclusion is hinged with 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, 2002; Leng and Friis 2003, 2006; Wang et al. 2007a, b; Wang and Wang 2010; Wang and Han 2011; Han et al. 2013, 2016, 2017). The number of characters should be taken into consideration, but the value of such characters vary.

Reproductive characters or floral features should be among 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 of angiosperms acquired their characters. Evolutionarily, all characters in organisms, from 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 the starting point for the evolution to be continued in the future. The characters that appear stable in living plants may be simply snapshots of the on-going evolution that has lasted million years. The origin and development of a character in plants is a function of time and other factors. 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; Maheshwari 2007; Doyle 2008), even 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

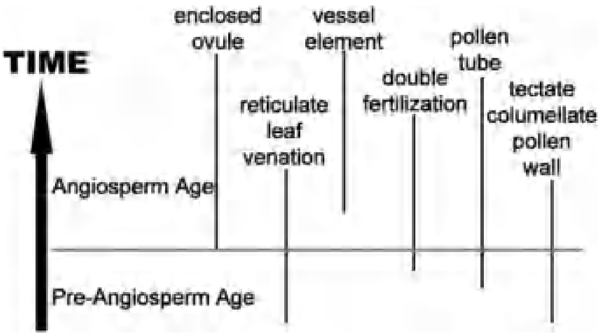

Fig 3.1 A possible scenario for the acquisition of characters typical of angiosperms in the geological history. All these characters could not be acquired at once in a plant. Picking a specific index character for angiosperms is conducive to minimizing controversy among scholars. The author prefers to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

angiosperms came into existence in the geological record. Otherwise 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 fertilization is of critical significance. Except for the case of secretion sealing, for the sake of accuracy, an ovule physically enclosed before or 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 criterion will make the recognized list of angiosperms above suspicion. Triaperturate pollen grains are the most competitive candidate for such index character because their presence can also ensure the existence of angiosperms. However, since the core feature of angiosperms is angio-ovuly, the author prefers enclosed ovules as the index feature. 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.

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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 for a complete 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 North 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: Northern Hebei-Western Liaoning, Erlian-Yinshan, Xingʹan, 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).

X. Wang, *The Dawn Angiosperms*, Springer Geology,
DOI 10.1007/978-3-319-58325-9_4

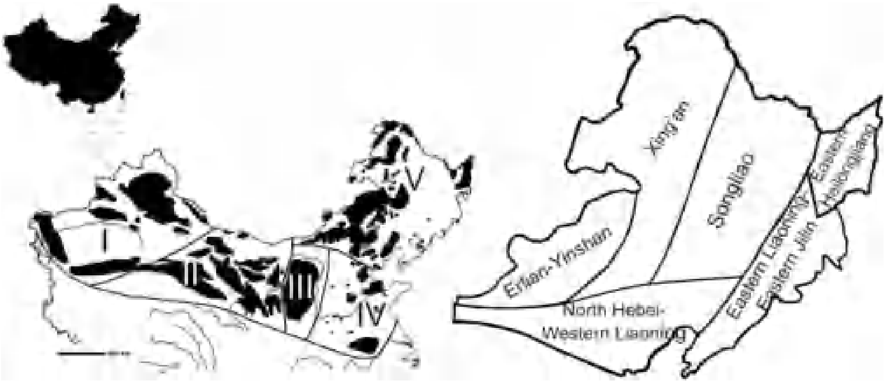

Fig. 4.1 Geographical distribution of the Jurassic strata (including Early Cretaceous Yixian Formation) in China. Upper left is a map of China. Lower-left shows the five regions in North China. Right shows the six zones in Northeast China (after Deng et al. 2003)

The Jurassic strata are represented mainly by fluvial and swampy coal-forming facies of northeastern 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 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 has 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. 4.4). For the sake of simplicity and consistency, in the following text all of these local stratigraphic names 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 and 4.5). 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 has yielded a large number of fossils, including

Epoch	Stage	Formation	Volcanic Eruption (Ma)
K2	Cenomanian	Qingshankou Fm	100
K1	Albian	Quantou Fm Fuxin Fm Shahai Fm	113
	Aptian	Jiufotang Fm	126
	Barremian		
	Hauterivian	Yixian Fm	134
	Valanginian		139
	Berriasian		145
J3	Tithonian	Baiyingaolao Fm	152
	Kimmeridgian	Manitu Fm Manketouebo Fm	157
	Oxfordian	Tuchengzi Fm	164
J2	Callovian	Tiaojishan Fm	
	Bathonian		
	Bajocian	Jiulongshan Fm	
	Aalenian		174
J1	Toarcian	Beipiao Fm	
	Pliensbachian		
	Sinemurian		
	Hettangian	Xinglonggou Fm	201

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

conchostracans, ostracodes, bivalves, insects, vertebrates, and plants (Pan 1983; Kimura et al. 1994; Wang et al. 1997; Ji and Yuan 2002; Ren and Oswald 2002; Zhang 2002, 2006, 2007a, b, c; Zhang et al. 2008, 2009; Shen et al. 2003; Zheng et al. 2003; Li et al. 2004; Liu et al. 2004; Ji et al. 2004, 2005; Wang et al. 2004, 2007a, b; Huang and Lin 2007; Huang and Nel 2007a, b; Zhang and Lukashevich 2007; Zhou et al. 2007; Huang et al. 2008a, b, c; Liu and Ren 2008; Liang et al. 2009; Shih et al. 2009; Wang and Ren 2009; Wang and Wang 2010; Huang 2016). 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 161.8 ± 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; Ji et al. 2005; Gao and Ren 2006; Chang et al. 2009b, 2014). 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 4.6) (Wang et al. 2004). It is

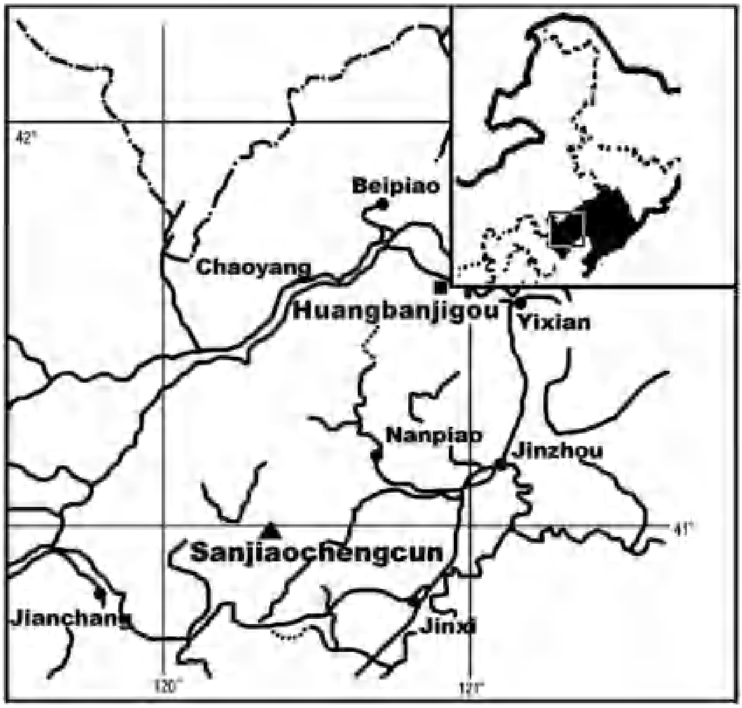

Fig. 4.3 Geographical locations of Sanjiaochengcun (triangle, 40°58′N, 120°21′E) and Huangbanjigou (square, 41°12′N, 119°22′E) in western Liaoning Province, which is shown as the black area in the inset map of northeast China. (Modified from Wang et al. 2007a)

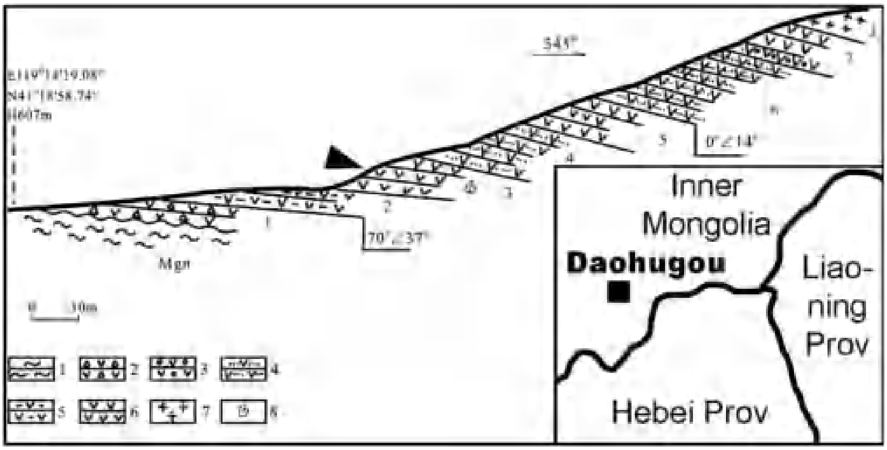

Fig. 4.4 The geographical position of Daohugou Village (square in the inset, 41°19′N, 119°14′E) in Inner Mongolia, China. Note its position close to the borders between Inner Mongolia, Liaoning and Hebei Provinces. Layer 3 (black triangle) in the geological section is the major fossil yielding stratum. (Modified from Tan and Ren 2009, courtesy of Science Press)

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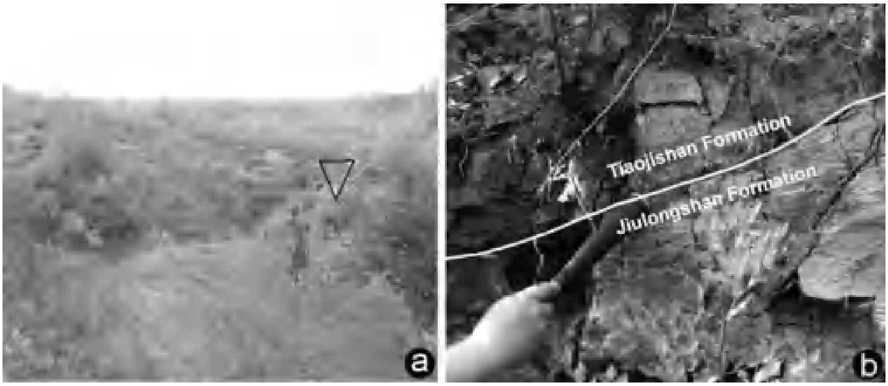

Fig. 4.5 The Jiulongshan Formation. (a) Outcrop of the Jiulongshan Formation (=Haifanggou Formation). (b) Boundary between the Haifanggou Formation and the overlying Tiaojishan Formation near Sanjiaochengcun in Jinxi, Liaoning, China. Courtesy of Acta Geologica Sinica

Fig. 4.6 Outcrop of the Yixian Formation near Huangbanjigou in Beipiao, Liaoning, China

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 basal tuffaceous conglomerate (Wang et al. 2004; Sha 2007). 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. 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. 2004a, b) 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. 2004a, b).

4.2 Faunas

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

4.2.1 The Jiulongshan Fauna

In this region, conchostracans are distributed in all three members of the Jurassic and especially widespread in the Middle Jurassic. The Jiulongshan Formation yields the Euestheria ziliujingensis conchostracan fauna, including five species in two 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 lower 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 five species in two 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 nine species in four 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 18 orders: Ephemeroptera, Odonata, Blattaria, Orthoptera, Dermaptera, Grylloblattodea, Plecoptera, Psocoptera, Hemiptera (including Heteroptera), Megaloptera, Rhaphidioptera, Neuroptera, Mecoptera, Coleoptera, Trichoptera, Diptera, Hymenoptera, and Lepidopetra (Huang et al. 2006). The formation has yielded 134 species in 108 genera of insects (Wang 1987; 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; 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; 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 1987; 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 ten species in three 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, 2009c; Huang and Lin 2007; Lin et al. 2007; Liu et al. 2007, 2008; Zhang 2007a, b, c; Tan and Ren 2009; 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; Wang et al. 2004, 2007c; Ji et al. 2004; Liu et al. 2006a, b, 2007, 2008; 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; Dong et al. 2016). 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, and Lycopodales (Zhang and Zheng 1987; Dong et al. 2016), including 140 species in 57 genera (Zhang and Zheng 1987; Wang et al. 1997, 2007a, b, 2010; Deng et al. 2003; Li et al. 2004; Zhou et al. 2007; Wang and Wang 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, Callianthus, Liaoninganthus, Baicarpus, and Nothodichocarpum (Duan 1998; Sun et al. 1998, 2001, 2002; Leng and Friis 2003, 2006; Ji et al. 2004; Wang and Zheng 2009; Wang and Han 2011; Han et al. 2013, 2017). 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, Caytoniales, and Angiospermae, in descending order of abundance. The documented plant fossils include 151 species in 75 genera (Duan 1998; Wu 1999; Sun et al. 1998, 2001, 2002; Leng and Friis 2003, 2006; Ji et al. 2004; Wang et al. 2004, 2010; Zheng and Zhou 2004; Yang et al. 2005; Wang and Zheng 2009, 2010; Guo et al. 2009; see Appendix 10.4.2 for the species list).

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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 of this age. Chaoyangia, Archaefructus, Sinocarpus, Callianthus, Liaoningfructus, Baicarpus, and Nothodichocarpum are 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 detailed. 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, Callianthus, Liaoningfructus, Baicarpus, and Nothodichocarpum. 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 advanced in this book before being accepted.

X. Wang, The Dawn Angiosperms, Springer Geology,
DOI 10.1007/978-3-319-58325-9_5

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 on the *Science in China Series D: Earth Sciences*, and attracted certain attention, its affinity was challenged and undervalued, especially after the description of the so-called "first flower", *Archaefructus*, which 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 or never 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 fructifications and physically connected parts, have been collected. Unfortunately, the information in these specimens is rarely explored and the affinity of *Chaoyangia* remains unresolved.

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 are related to this holotype

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), 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 an identification.

The characters, including urceolate coating layer, hairs on its surface, monocolpate pollen grain, close spatial relationship between female and male flowers, three carpels/fruits in the coating layer, 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, 5.3, 5.4, 5.5, 5.6, 5.7, 5.8, 5.9, 5.10, 5.11,

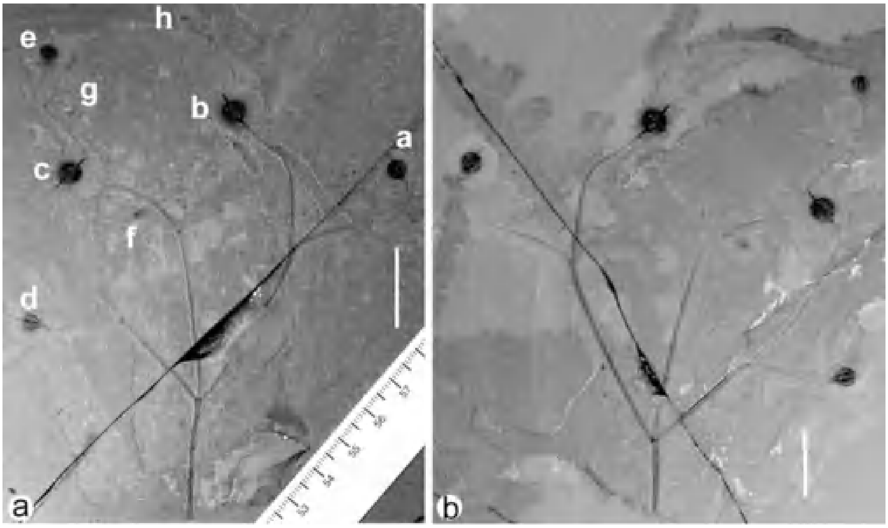

Fig. 5.2 The holotype of Chaoyangia. The flowers/fructifications are labeled with letters. (a) and (b) are two facing parts of the same specimen (9341a&b, IBCAS)

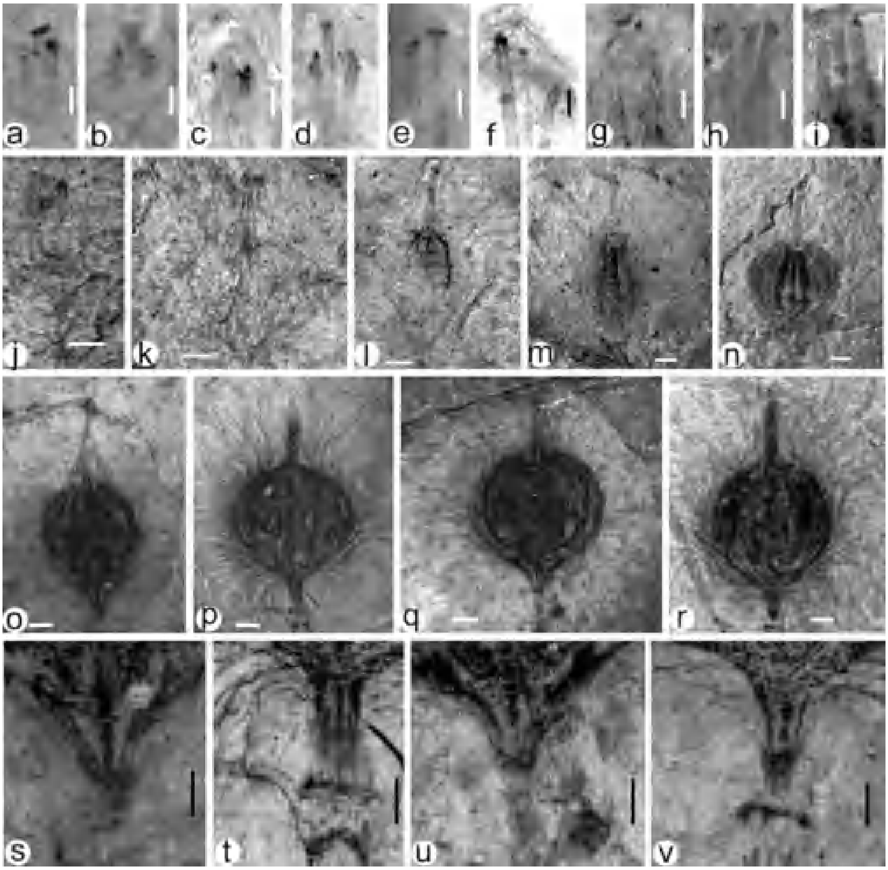

Fig. 5.3 Details of the styles, flowers/fructifications. (a–i) Styles of the flowers/fructifications labeled i, g, h, f, e, d, b, a, and c, in that order, in Fig. 5.2a. Bar = 0.2 mm. (j–r) The flowers/fructifications labeled i, g, h, f, e, d, b, a, and c, in that order, in Fig. 5.2a. Bar = 1 mm. (s–v) The stalks of the flowers/fructifications labeled d, b, a, and c, in that order, in Fig. 5.2a. Bar = 0.5 mm

5.12, 5.13, and 5.14). Important features of the Welwitschiaceae, such as well-defined cone, polyplicate 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 three assumed seeds, as in *Chaoyangia*. The wing-like structure around the fructifications of *Chaoyangia* is an artifact of degaging to expose the hairs on its surface (Fig. 5.5a). The so-called wing in *Chaoyangia* has no actual boundary (Fig. 5.3j–r, 5.4a, b, 5.6a, 5.7a, b, and 5.11a–f, i), as would be expected in a typical 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

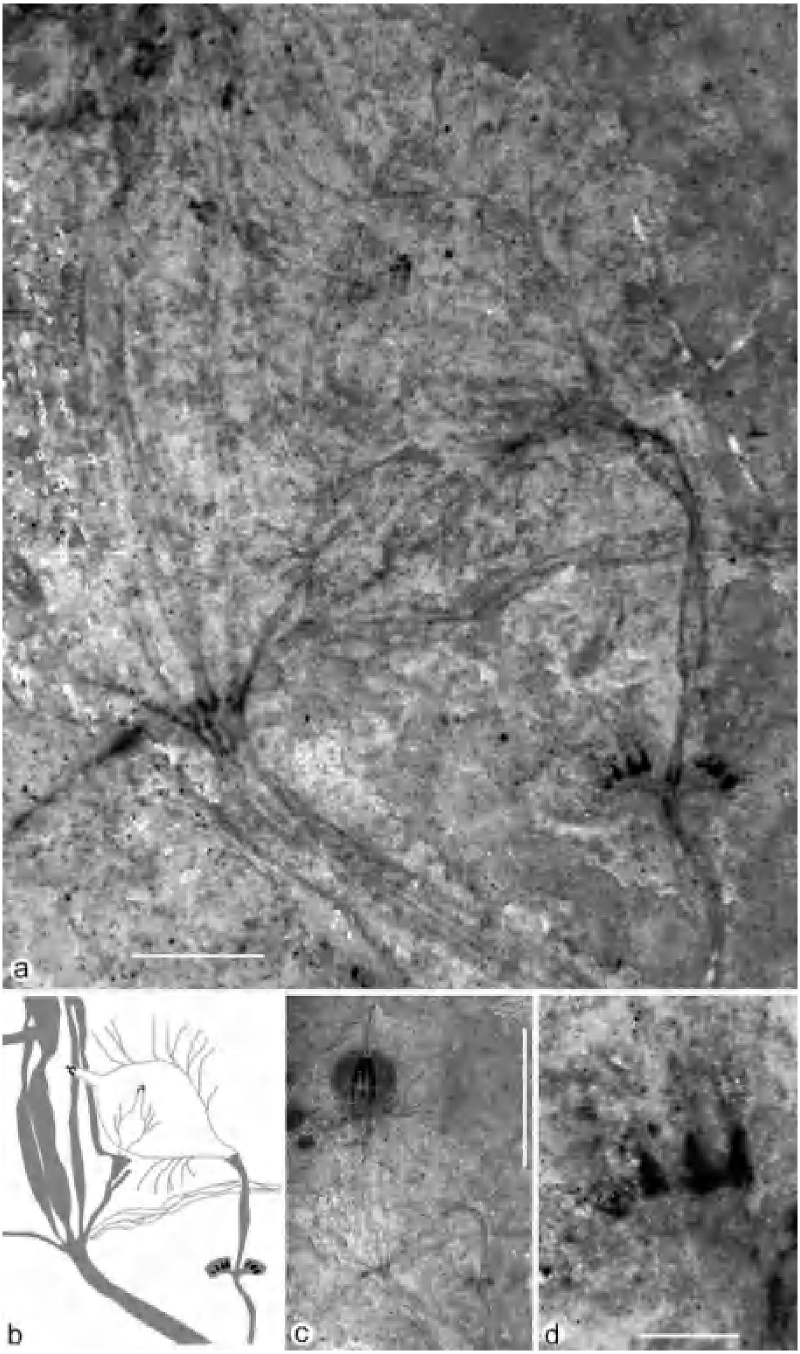

Fig. 5.4 Details of connected floral parts. (a) Details of the lower central portion in (c). Note the connection between the male flower at the lower right and its female flower at upper center, and that there is another smaller flower overlapping this larger female flower. Bar = 2 mm. (b) Line-

reflects the lack of both evidence and confidence 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 fructifications of Chaoyangia the styles are appressed against each other by hairs on the coating layer (Figs. 5.5a, 5.13b, and 5.14c). In short, Chaoyangia shares too few characters of taxonomic significance with Gnetales 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 fructification surface. These two differences alone are enough to distinguish Chaoyangia and Gurvanella, plus bisexuality vs unisexuality, respectively. 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 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 any further modification. Actually, the truth may be revealed by simply putting Krassilov′s publications (1982, 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 the presence of male flowers, enclosed seeds, young female flowers with well-defined styles, and physically connected male and female flowers on the same branch in Chaoyangia. 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. 5.4 (continued) 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

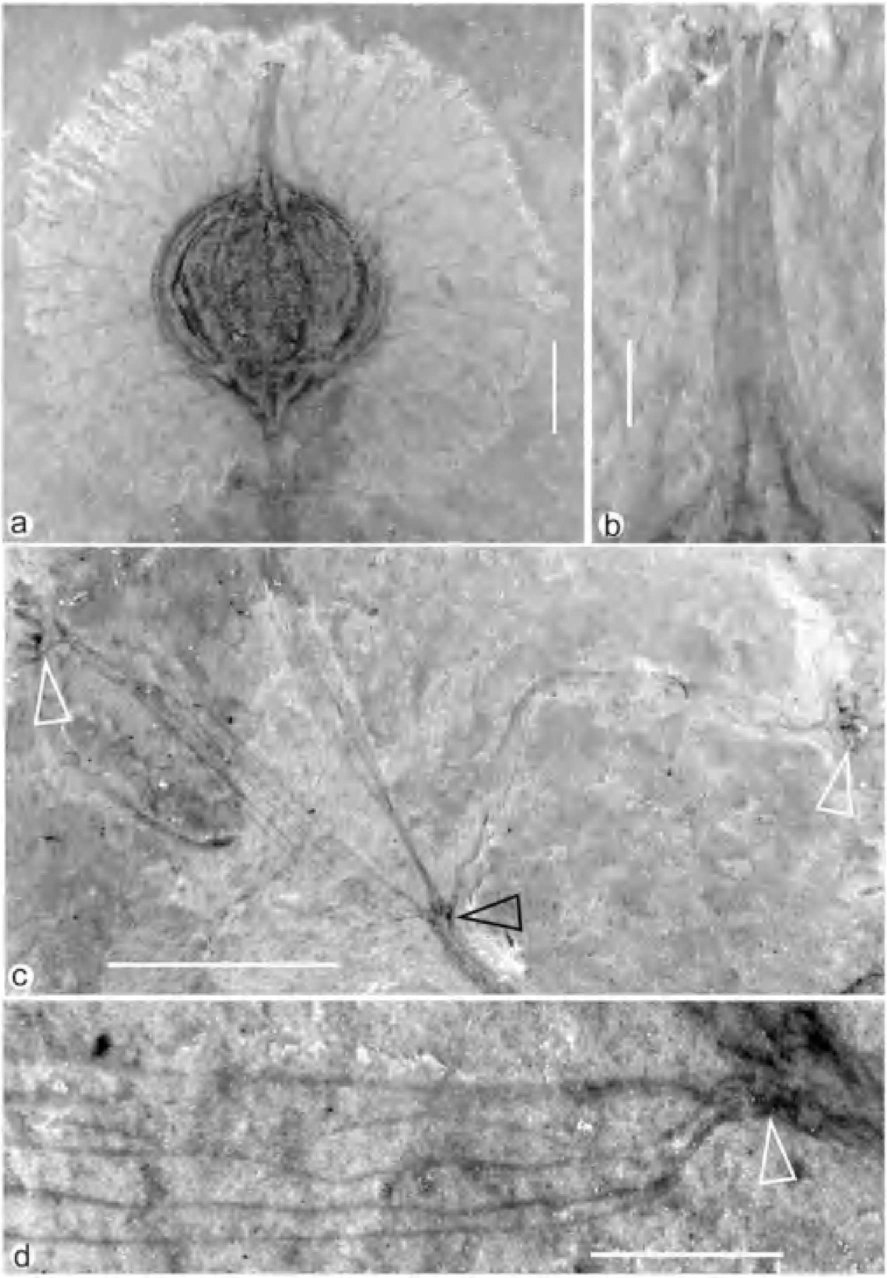

Fig. 5.5 Female flower A in Fig. 5.2b. (a) Whole female flower. Note the coating layer enclosing the ovaries, forked hairs on its surface, and hairs in their early stage forming an envelope around the style. Bar = 2 mm. (b) Three straight styles at top, and dark stigmas on the terminal of the styles. 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)

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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 its 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 was finally identified. As seen in Figs. 5.4, 5.6, 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. Figures 5.6a and 5.7a 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 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 on male parts of Chaoyangia, tentative at that time, and also helps to narrow the scope about sexual nature and affinity of Chaoyangia.

Fig. 5.5 (continued) 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

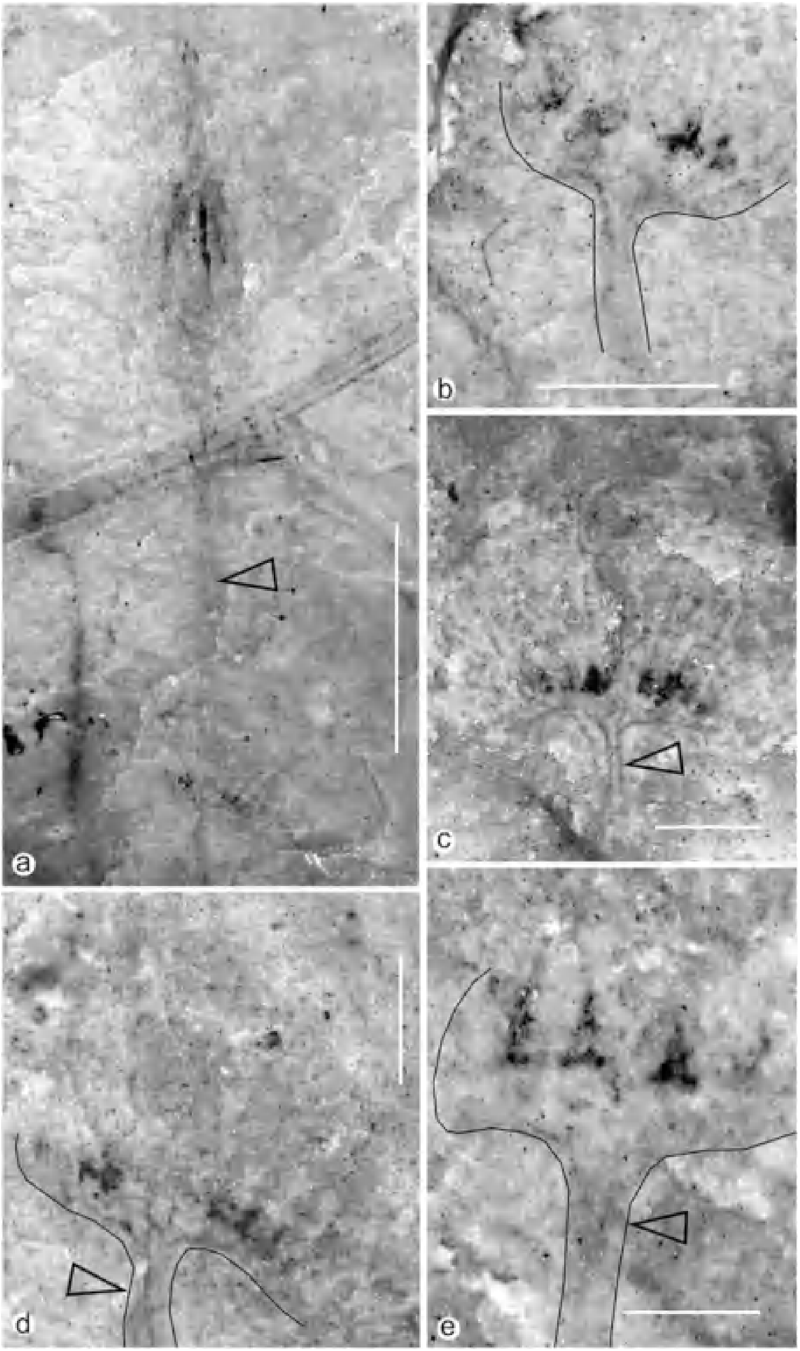

Fig. 5.6 Male flowers and its connection to female flower. (a) Female flower f in Fig. 5.2a (top) and its connection to its male flower (bottom). Bar = 5 mm. (b) Another male flower. Note its outline and relationship to the branch. Bar = 1 mm. (c) Side view of two male parts oppositely attached to a branch. Note the vertical branch (bottom), two opposite male parts, rigid upward

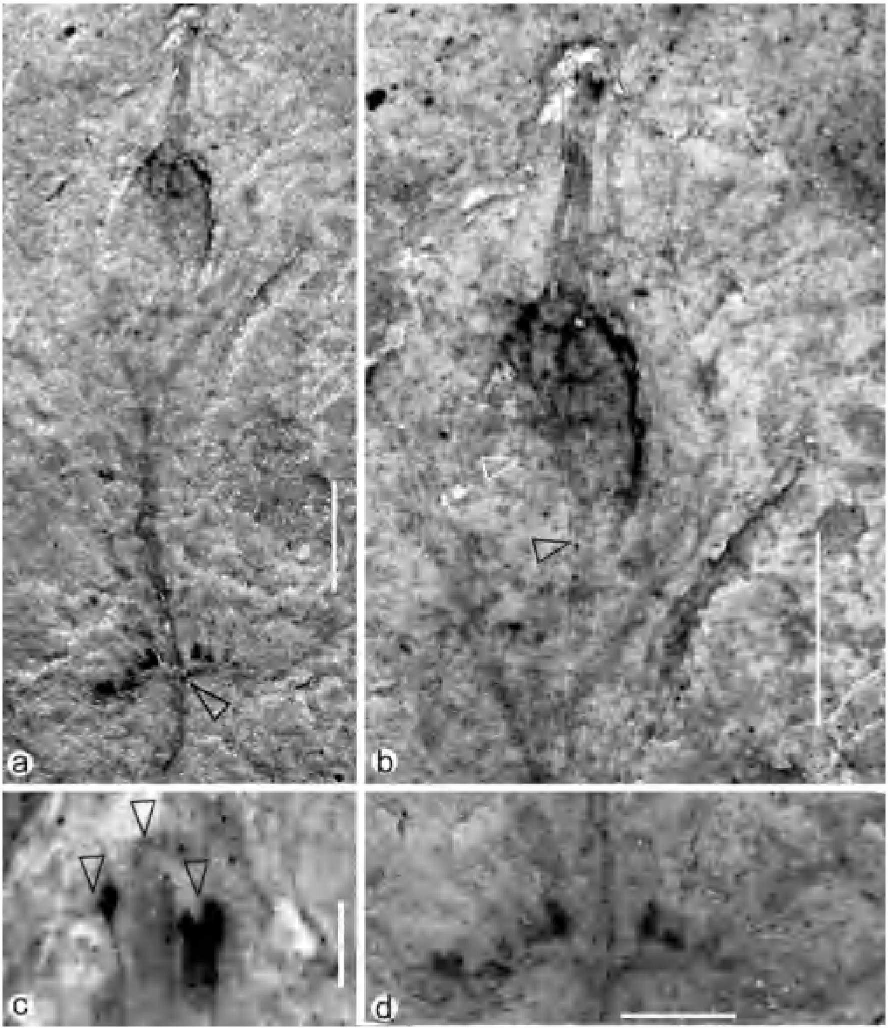

Fig. 5.7 Connected female flower and male flower. (a) Whole flower. Note the physical connection between the female flower (top) and male flower (bottom). Bar = 2 mm. (b) Detailed view of the female flower. Note the styles on the top, hairs (white arrow) on the surface, and a ribbed branch (black arrow) 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

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Fig. 5.6 (continued) 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 (arrow). Bar = 1 mm. (e) Tangential view of a male part. Note the branch (bottom), outline of the male part (outline), and three or four triangular pollen sacs (dark regions). Bar = 0.5 mm

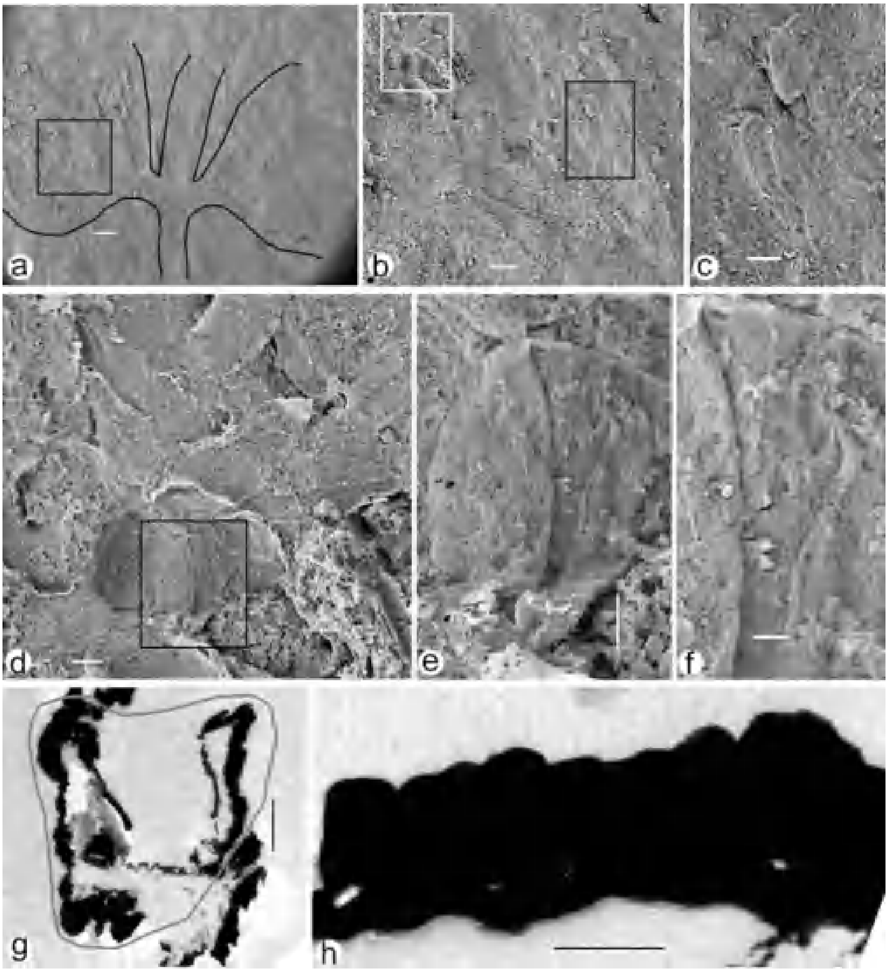

Fig. 5.8 In situ monocolpate pollen grains. (a) SEM view of the male flower shown in Fig. 5.7d. Note the outline of the flower and branch. Bar = 0.2 mm. (b) Detailed view of the rectangular region in (a). Bar = 50 μm. (c) In situ pollen grains in the black rectangle in (b). Bar = 20 μm. (d) In situ pollen 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 varying 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

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 of Chaoyangia in detail although she documented more mature female

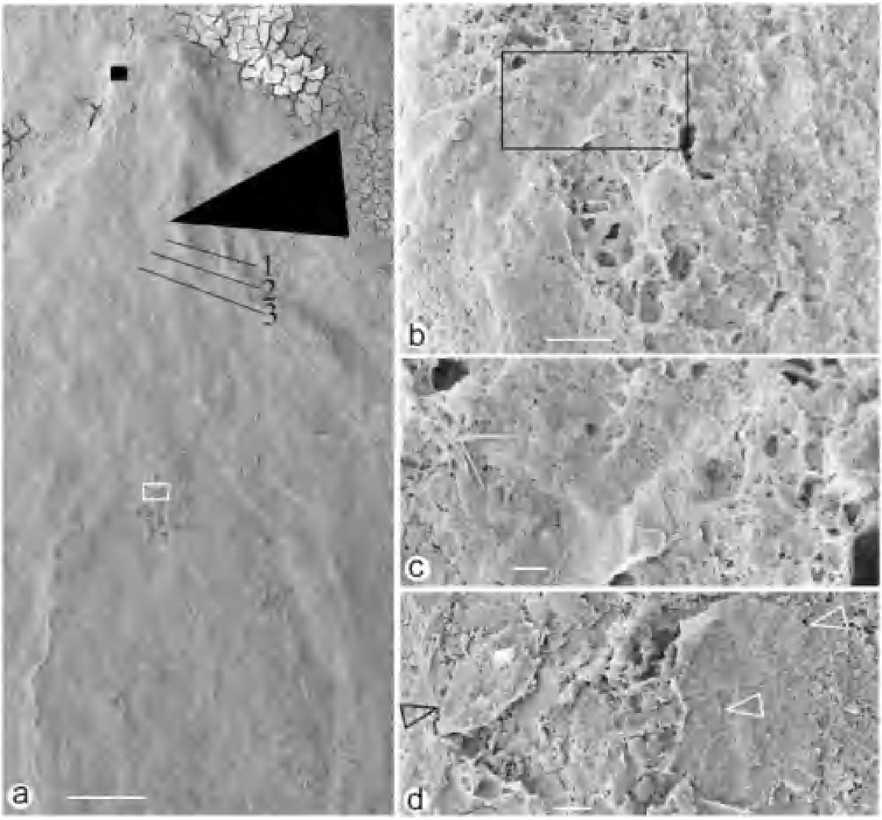

Fig. 5.9 Details of the female flower shown in Fig. 5.7b. (a) Top half of the female flower. Note the elliptic outline of the ovary portion (bottom) and elongate styles (top). Bar = 0.5 mm. (b) Detail of the stigma in the black rectangle in (a). Bar = 10 μm. (c) Detail of the rectangle in (b). Note the 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

flowers that had conspicuous styles and hairs. These more mature female flowers are very similar to the subsequently found isolated fructifications 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 different in several aspects: (1) when 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, suggestive of being receptive, 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.

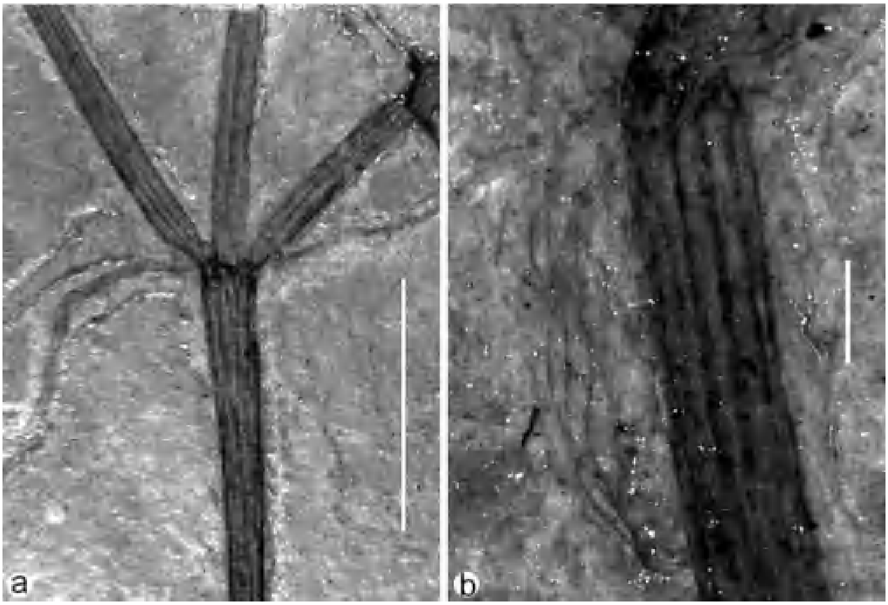

Fig. 5.10 Branches and leaves. (a) Typical opposite branching pattern. Note the subtending leaves and longitudinal ribs on the branch. Bar = 1 cm. (b) Details of leaf venation. Note the near-parallel veins with rare interconnections, as well as longitudinal ribs on the branch. Bar = 1 mm

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 fructifications (Fig. 5.11a–f) represent a continuous morphological 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 to styles (Chamberlain 1957; Bierhorst 1971; Biswas and Johri 1997; Yang 2007; Friis et al. 2009; Crane and Herendeen 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 and Herendeen 2009; Rothwell et al. 2009), as in Chaoyangia. Therefore these groups can be excluded from further consideration hereafter. Micropylar tubes in Ephedra

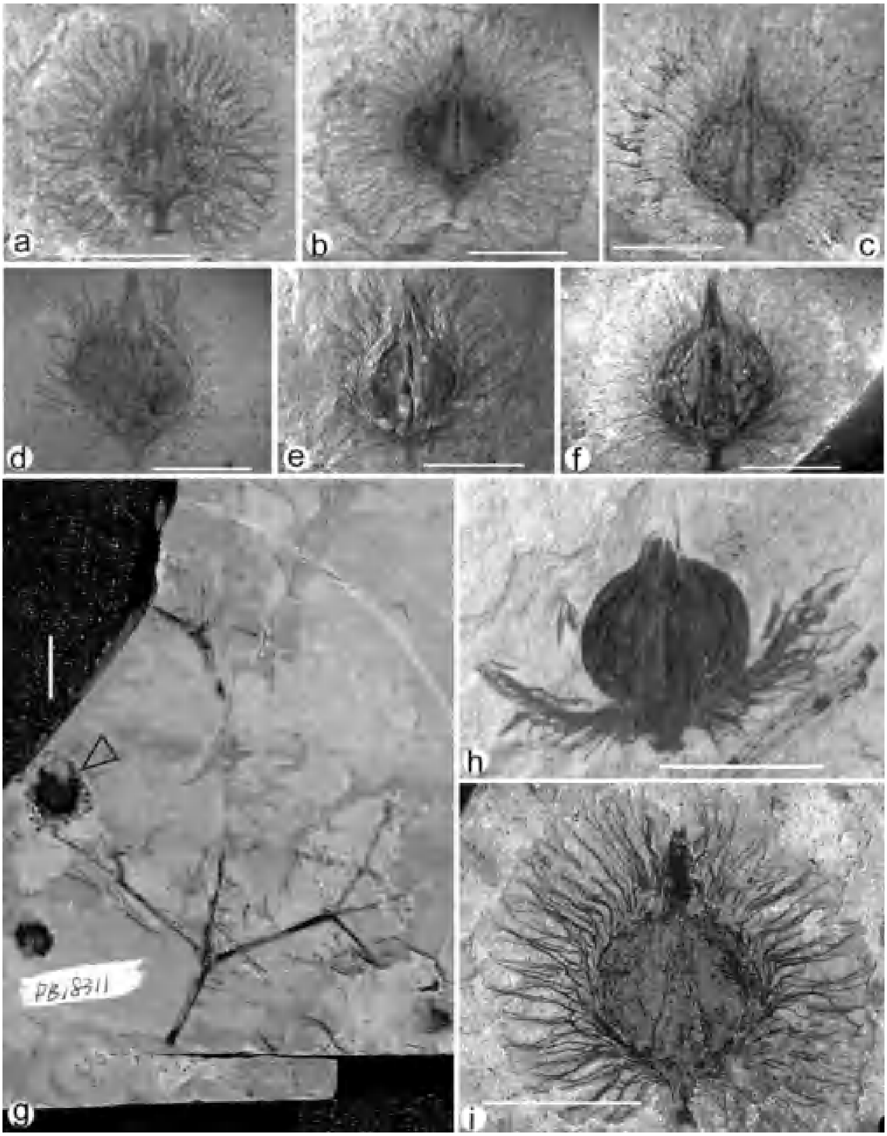

Fig. 5.11 Isolated fructifications and those connected by branches. Note that the styles are eclipsed by the surrounded by hairs, and the dense hairs on the surface of the fructification. (a) Isolated fructification. PB18178. Bar = 5 mm. (b) Isolated fructification with hairs around. PB18176. Bar = 5 mm. (c) Isolated fructification. PB18310. Bar = 5 mm. (d) Isolated fructification. Note the relatively sparse hairs around the fructification. PB18183. Bar = 5 mm. (e) Isolated fructification. Note the rigid coating layer around the fructification. PB18181. Bar = 5 mm. (f) Isolated fructification. PB18180. Bar = 5 mm. (g) Branch connected with fructifications. Note the opposite branching pattern. Bar = 1 cm. (h) Isolated fructification. Note the hairs in the upper portion of the fructification have fallen off. PB21389. Bar = 5 mm. (i) Isolated fructification. CNU-Plant-2008-001a. Bar = 5 mm

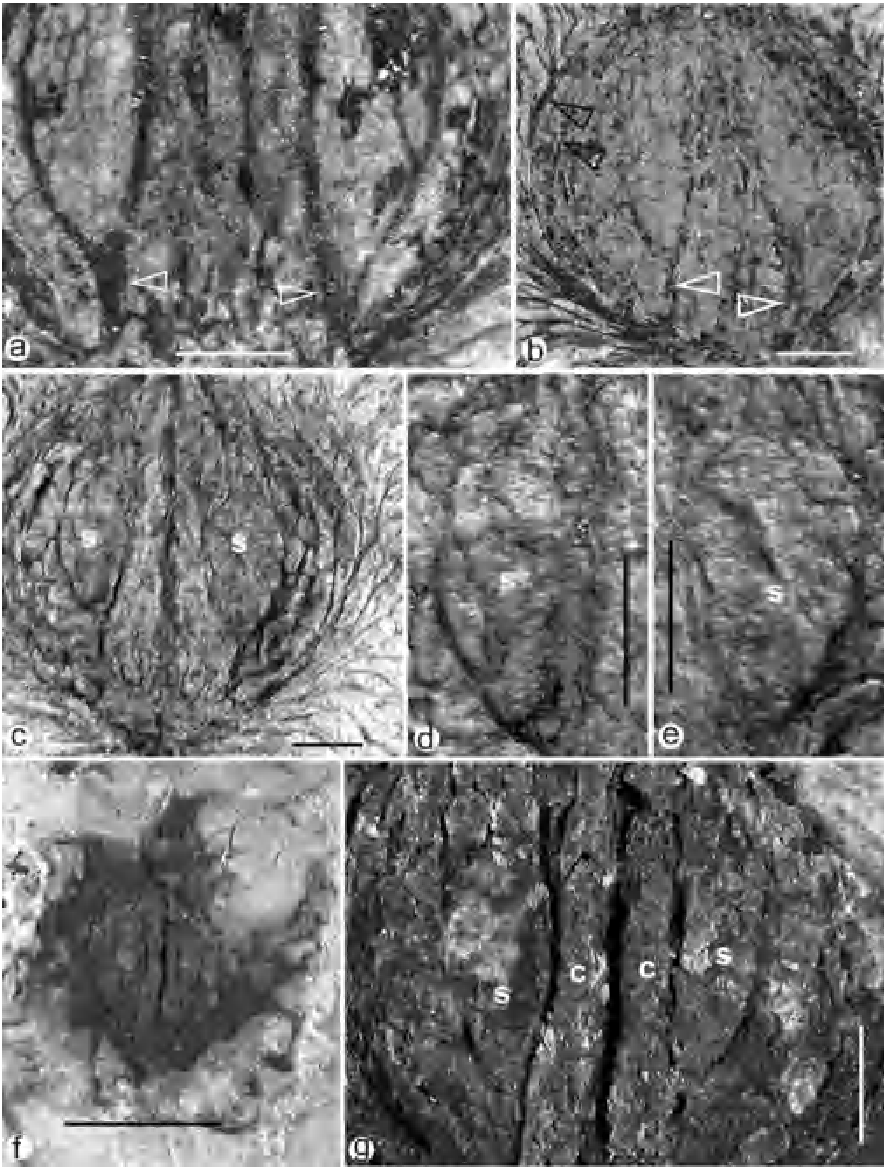

Fig. 5.12 Details within the fructifications. (a) Detailed view of the fructification in Fig. 5.11f. Note the vascular bundles (arrows) corresponding to ovule/seed in other fructifications. Bar = 1 mm. (b) Detailed view of the fructification in Fig. 5.11i. Note the coating layer (between black arrows) and vascular bundles (white arrows) corresponding to ovule/seed in other fructifications. Bar = 1 mm. (c) Detailed view of the fructification in Fig. 5.11c. Note the seeds (S) and the vascular bundles at their bases. Bar = 1 mm. (d and e) Detailed views of two seeds in (c). (f) Fructification (black arrow in Fig. 5.11g) with in situ seeds. Bar = 5 mm. (g) Details in the fructification shown in (f). Note the separated ovary walls (C) and seeds (S) inside ovary, borders between the seeds and ovarian wall, ovary wall covering the seed in the upper-left region, and gap between two ovaries. Bar = 1 mm

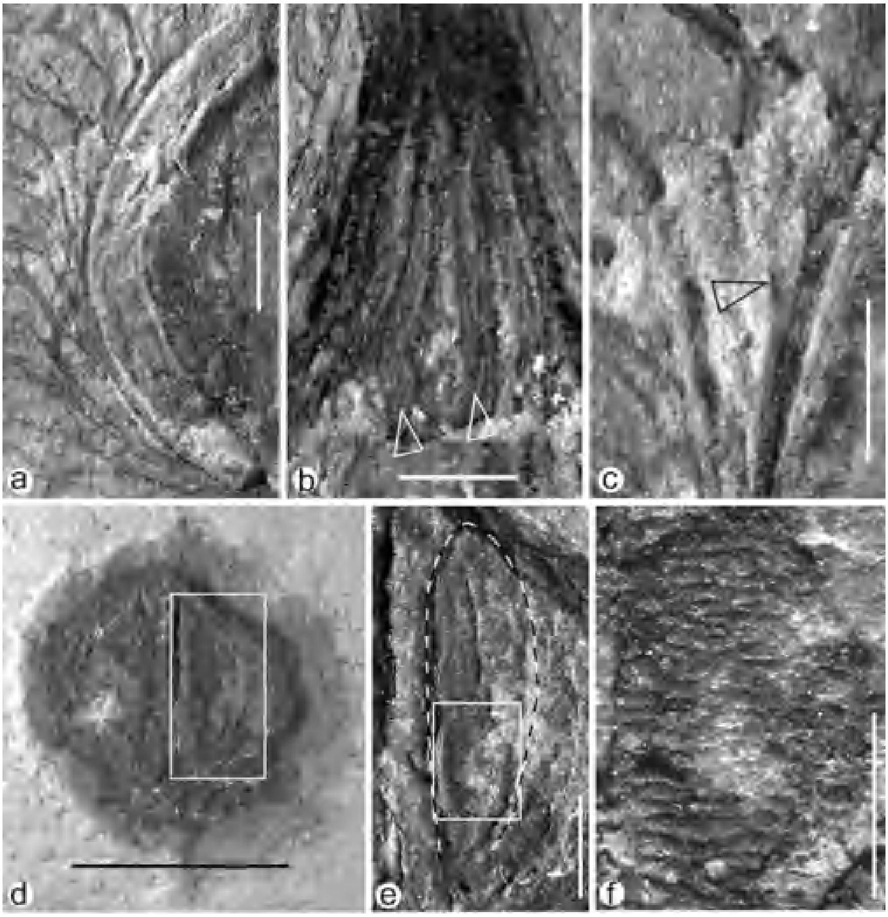

Fig. 5.13 Fructification and in situ seed. (a) Details of the fructification shown in Fig. 5.11e. Note the coating layer (between arrows) of uniform thickness and bearing hairs on its surface. Bar = 1 mm. (b) Hairs (arrows) surrounding the style, visible after removing the styles. Bar = 0.5 mm. (c) Detailed view of the hairs on the coating layer surface. Note the rigid outer surface of the coating layer, a hair (black arrow) just arising from the coating layer, adjacent hairs on different planes (out of focus). Bar = 0.5 mm. (d) Another fructification 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

(Ephedraceae) may be in group of more than one (Yang 2007) and thus easier to be confused with styles of Chaoyangia. However, micropylar tubes in Ephedra are relatively shorter, with pointed tips, sometimes entangled while the styles in Chaoyangia are very elongated, more or less expanded and capitate with some sticky material, and always distinct in the flower. Chaoyangia is further alienated from Ephedra by its linear leaves, hairy fructifications, male flower, and in situ

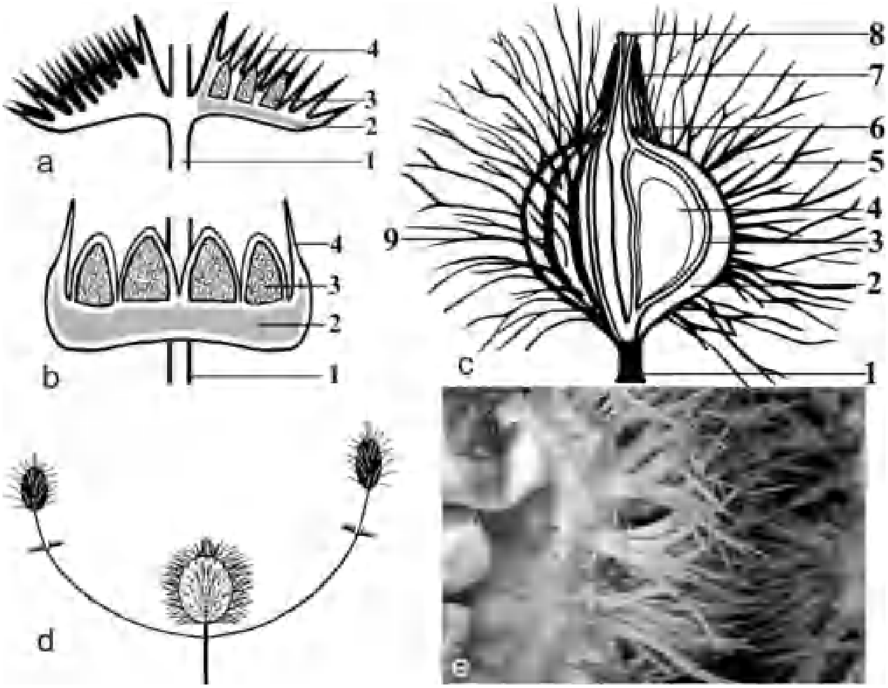

Fig. 5.14 Idealized diagrams of male flower, fructification, and inflorescence. (a) Side view of two stamens, right one partially dissected to show inner details. Note the opposite arrangement of male floral parts along the branch (1), foliar structure (2) supporting pollen sacs (3) on its adaxial surface, 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) Fructification with the front-right quarter removed to show the inner details. Note the stalk (1), coating layer (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 coating layer. (d) The arrangement of the male and female flowers in the inflorescence. (e) Branched hairs on the fructifications of Castanea

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 (Figs. 5.4a, 5.5a, 5.6a, 5.7a–b, 5.9a–c). This feature may be related to pollination in Chaoyangia as is true in other angiosperms.

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; 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, specimens of Chaoyangia had been treated without hesitation as female structures. Recent 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 in Chaoyangia are usually below 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 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 structures and compositions in aperturate and non-aperturate region (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 before pollination (see Chap. 3 for details). Seeds in Chaoyangia were rarely considered until recently. New investigation indicates that there are three seeds/ovules in the three ovaries that are surrounded by a coating layer. This is especially evident in isolated fructifications split through the middle (Figs. 5.11, 5.12, and 5.13d–f), which are more mature than the female flowers in the holotype. Each of these seeds is situated in an ovary and has horizontal ripples on its surface. These seeds are enclosed by ovary walls, which are connected to the styles and in turn surrounded by the coating layer. The positions and outlines of these seeds correspond well to and are suggested by the vascular bundles on the base of the ovaries. 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. 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 could not pass through the styles even if the latter had internal canals. Considering all features of the styles and pollen grains, there is no chance for pollen to be transferred as in Gnetales in the styles of Chaoyangia, and the seeds are completely enclosed 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 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. 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 coating layer bearing forked hairs on its surface and enclosing three ovaries. Three ovaries inserted on central bottom of coating layer, each with a straight slender style and a terminal stigma. A single ovule inserted to ovary bottom. Fructification indehiscent. Seed single, enclosed in a fruit, attached to the base of the fruit. Hairs likely shed in fructifications.

5.1.5 Description

Chaoyangia liangii Duan emend. Wang

(Figs. 5.2, 5.3, 5.4, 5.5, 5.6, 5.7, 5.8, 5.9, 5.10, 5.11, 5.12, 5.13, and 5.14)

Synonyms: **Chaoyangia liangii** Duan, Duan 1998, P14–20, Figs. 1–4

Chaoyangia liangii Duan, Wu 1999, P22, Pl. XIV, Figs. 1,1a, 2,2a, 4,4a, Pl. XV, Figs. 2,2a

Gurvanella exquisita Sun, Zheng et Dilcher, Sun et al. 2001, P107-108, 207-208, Pl. 24, Figs. 7–8, Pl. 25, Fig. 5, Pl. 65, Figs. 2–11

Gurvanella sp. Zhou et al. 2003, P812, Fig. 6b–d

Gurvanella dictyoptera Krassilov, Krassilov et al. 2004, P705, Fig. 10B

Gurvanella dictyoptera Krassilov, Krassilov 2009, P1273, Fig. 6

Diagnosis: the 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 maturities, preserved on two facing slabs of sandstone (Fig. 5.2). Another physically connected specimen including branch and fructifications is approximately 8 cm long and 7 cm wide (Fig. 5.11g). All other specimens are isolated fructifications that are 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 obvious 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, oval 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 three closed carpels and an urceolate coating layer covered with forked hairs (Fig. 5.3n–r, 5.4c, 5.5a, 5.11a–f, h–i, 5.12, 5.13, and 5.14c, d). The hairs are 40–180 μm wide and up to 3 mm long, forked, tapering to the tip, and scattered over the fructification surface (Figs. 5.3j–r, 5.4a, b, 5.5a, 5.6a, 5.7a, b, 5.11a–f, i, 5.12c, 5.13a, c, 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 as the flower grows mature (Figs. 5.11a–f, i, 5.12c, 5.13a, c, and 5.14c, d). Some hairs may be shed from mature fructifications (Figs. 5.11h and 5.13d). The mature coating layers are almost uniformly 0.6 mm thick in mature fructifications (Figs. 5.12b, 5.13a, and 5.14c). Each carpel base is fixed to the base of the coating layer (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 (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 carpels in the coating layer (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 (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 when preserved, 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-Aptian, 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 and fall off after pollination. 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 good form, their pricks are straight and pointing upward.

Female flowers demonstrate changes in several aspects, including size, amount of hair, coating layer, styles, and hairy envelope around styles. The female flowers are much smaller and elongated 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 fructification. 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 latters. In mature fructifications, the hairs may be shed. Coating layer is barely visible in young female flowers, but in fructifications becomes a rigid spherical covering of uniform thickness surrounding the ovaries. The most constant 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 forming a strong contrast against the poorly preserved styles. The stigmas in mature female flowers are less conspicuous because styles in mature female flowers and fructifications are better preserved, 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 fossils of different developmental stages.

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 grains 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 Additional Points

5.1.8.1 Spiny Fructification

One of the most conspicuous features of Chaoyangia is its hairs or spines on the surface of the fructification, which make Chaoyangia distinct among all known seed plants from the Mesozoic. This feature is hitherto never seen in any gymnosperms. Conversely, such spines on fructifications are frequently seen in some angiosperms. For example, spines similar to those of Chaoyangia fructifications have been seen Castanea (Melchoir 1964). Such spines may play some role in the interaction between Chaoyangia and contemporaneous animals. In the meantime, structures similar to the coating layers of Chaoyangia fructifications have been seen Monimia (Lorence 1985), and Siparuna (Endress 1980b), besides Castanea (Fig. 5.14e; Melchoir 1964). It appears that such additional protection for seeds in fruits may have given some edge to Chaoyangia in its competition against peers. Such more or less advanced strategy adopted by Chaoyangia and Callianthus implies that the origin time of angiosperms is much older than the Early Cretaceous, in agreement with the molecular clock studies and fossil evidence in next Chapter.

5.1.9 Affinity

5.1.9.1 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/fructification (Figs. 5.3j–r, 5.7b, 5.13a, c, and 5.14c), and coating layer 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 fertilization since many bigger flowers are 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 and observed in fossils (Wang and Zheng 2010; Wang et al. 2010a, b). They are indistinguishable from those in angiosperms, and are unlike the three usually pointed, sometimes entangled, micropylar tubes in Ephedra (Fig. 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 coating layer). Therefore these characters, especially seed enclosed in an ovary and carpel closed before fertilization, 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, coating layer form and appendages, position of carpels, and slender exserted style are comparable to those in Monimiaceae, e.g. Atherosperma moschatum (P89, Fig. 20.5, Takhtajan 1969) and Monimia rotundifolia (P34, 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 columellae 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 a 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, Callianthus, Liaoningfructus, and Baicarpus, Nothodichocarpum (Sun et al. 1998, 2001, 2002; Leng and Friis 2003, 2006; Ji et al. 2004; Wang and Zheng 2009; Wang and Han 2011; Han et al. 2013, 2017)] demonstrate diversified angiospermous reproductive strategies, suggesting that angiosperms already had undergone a certain period of evolution before and 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 the Barremian.

Table 5.1 Comparison among Chaoyangia and other seed plants

	Chaoyangia	Castanea	Atherosperma moschatum	Monimia rotundifolia	Gurvanella	Ephedra	Welwitschia
Leaf	Linear	Oblong	Elliptical	Orbicular	?	Triangular	Strap-like
Leaf venation	Parallel	Pinnate	Pinnate	Pinnate	?	Parallel?	Parallel
Phyllotaxy	Opposite	Helical, 2-raked	Decussate	Decussate	?	3 in a whorl	Decussate
Joint/ internode	+	–	–	–	?	+	+?
Sexuality	Bisexual?	Unisexual	Unisexual	Unisexual	Unisexual?	Unisexual?	Unisexual?
Flowering branch	Compound dichasium	Catkin	Decussate	Compound dichasium	?	Compound strobilus	Compound strobilus
Pollen organ	Below female one, sessile pollen sacs	Independent of the female, anther on fil-ament	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	6–12 in a whorl	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	Tricolpate	Colpate	Inaperturate	?	Inaperturate, polyplicate	Monoaperturate, polyplicate
Female flower position	Terminal	Axillary	Axillary?	Terminal	?	Axillary in compound cone?	Axillary in compound cone
Female flower form	Globular	Globlar	Globular	Globular	Flattened	Triangular in cross section	Flattened

(continued)

Table 5.1 (continued)

	Chaoyangia	Castanea	Atherosperma moschatum	Monimia rotundifolia	Gurvanella	Ephedra	Welwitschia
Female flower symmetry	Radial	Radial	Radial	Radial	Bilateral	Bilateral	Bilateral
Receptacle	Urceolate	Urceolate	Urceolate	Urceolate	N/A	N/A	N/A
Female flower appendage	Forked hairs	Forked hairs	Hairs	Hairs	Lateral wing?	N/A	Lateral wing
Female flower stalk	Short with an enlarged base	Short	Long	Long	?	N/A	Short with an enlarged base
“Carpels”	3 in a whorl, free	3, 6	Numerous, free	Numerous, free	2?	1(−3) ovuliferous unit in a whorl	1 ovuliferous unit
“Carpel” position	In receptacle	In receptacle	In receptacle	In receptacle	?	In bract axil	In bract axil
Ovulate part tip	3 long styles	3, 6 long styles	∞ long styles	∞ long styles	1 style	1 micropylar tube	1 micropylar tube
“Stigma”	Lobed, expanded, secretory	Dry, papillate	?	?	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
? Unknown

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, 2013; Wang et al. 2007a, b; 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.

5.1.9.2 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): eleven 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. Next, 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 atpB, 18S, and rbcL 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 4654 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 Paup4.0 beta10 with heuristic search of 1000 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 (Trithuria, 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, produced by heuristic search of 1000 replications, indicate that Archaefructus

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

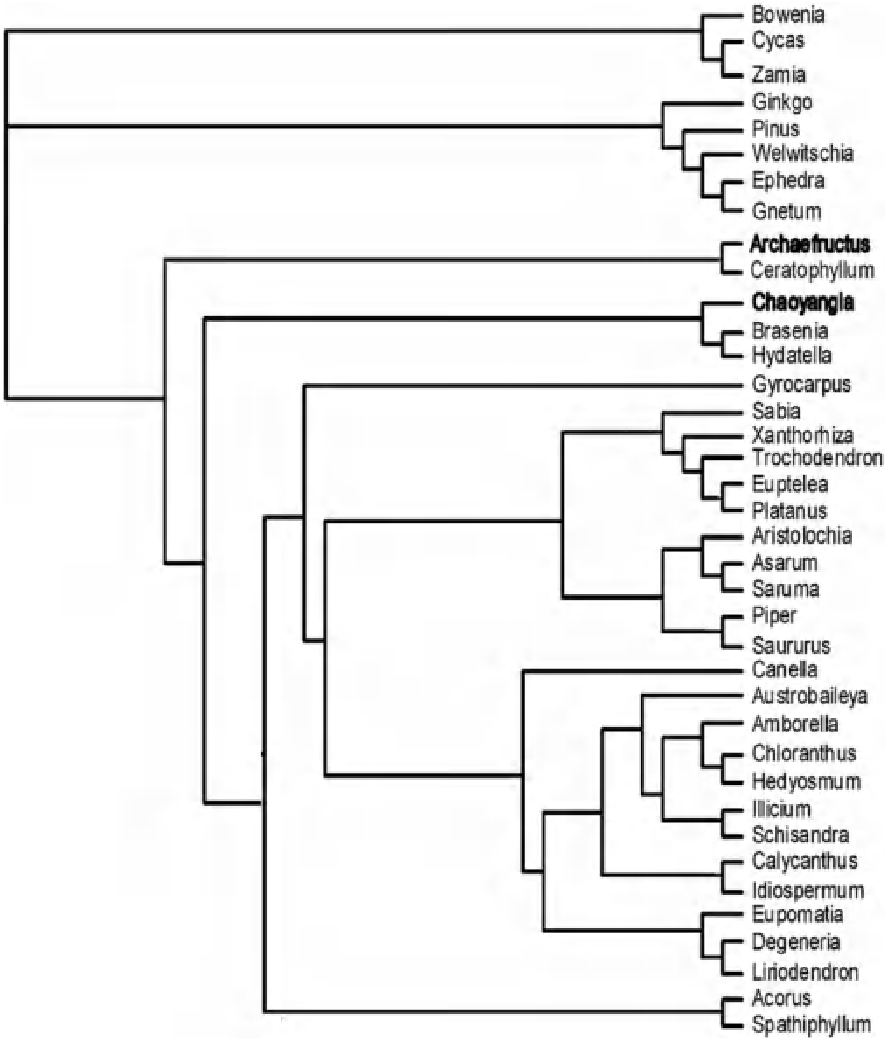

Fig. 5.15 Possible phylogenetic relationship among Chaoyangia, Archaefructus, and other seed plants, inferred based on morphological data. The relationships among living plants are fixed according to APG (2003)

plus Ceratophyllum is the first branch followed by a lineage of Brasenia together with Trithuria. Chaoyangia becomes the third branch in six of the nine trees, and in the other three trees, [Chaoyangia, (Brasenia, Trithuria)] 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, Trithuria) in all 12 trees. Furthermore, if Trithuria is excluded from the analysis by the same constraint, only one MP tree is produced from 1000 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 Trithuria 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, Trithuria)) 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, (Trithuria, Chaoyangia)).

The analyses (especially the constrained ones) based on morphological data strongly support a close affinity between Chaoyangia and Trithuria, 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 Trithuria from the analysis, even though Brasenia is attracted toward eudicots under this condition.

Above all, in all the analyses, Chaoyangia is closely related to Trithuria while Archaefructus is frequently placed basalmost in angiosperms (Fig. 5.15). Considering the well-supported phylogenetic framework given by APG, (Brasenia, (Chaoyangia, Trithuria)) 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.

5.1.10 Problems Unsolved

Although its holotype is quite big, 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 in the past decades. 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 in police academy, interpreted the discovery of *Archaefructus* from their own perspectives. It is thus not surprising that *Archaefructus* also 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 puzzle 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 (Friis et al. 2003; Dilcher et al. 2007). Whether or not *Archaefructus* is a Jurassic angiosperm now appears settled. According to present 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 at odds with recent research on angiosperm phyolgeny (Qiu et al. 1999; Soltis et al. 2004, 2008), restudies of *Archaefructus* (Ji et al. 2004; Wang and Zheng 2012), and fossil plants from the Jurassic (*Xingxueanthus*, *Schmeissneria*, *Euanthus*, *Juraherba*, and *Yuhania*) (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 row of ovules/seeds (Sun et al. 1998, 2002; Ji et al. 2004; Wang and Zheng 2012).

Archaefructus liaoningensis, the first species, was found near Huangbanjigou, Beipiao, China, and the specimen is incomplete (Fig. 5.16). 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

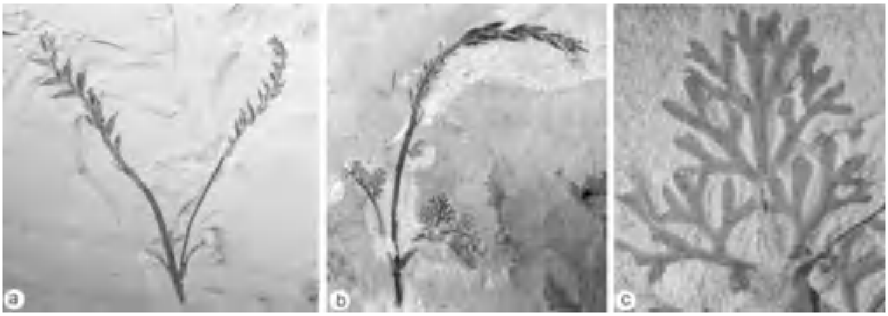

Fig. 5.16 *Archaefructus liaoningensis*. (a) Holotype, preserved with only female parts. (b) Specimen including female part (distal), male part (middle), and dissected leaf (basal). (c) Detailed view of a dissected leaf

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 carpels with laminar placentation. Both main and lateral shoots terminate in numerous fruits. Fruits are crowded oppositely or in whorl 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. 10 to 12 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 and Wang and Zheng 2012).

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 to 12 seeds. A stamen consists of a short fine filament and a broad long anthers ending with a prominent connective. No petals, sepals, or bracts are seen. (After Sun et al. 2002, and modified according to Ji et al. 2004).

Archaefructus eoflora (Fig. 5.17), the third species in the genus, is based on a specimen of a whole plant. It is excavated from Sihetun, Beipiao, Liaoning, China.

Fig. 5.17 Reconstruction of **Archaefructus eoflora**. From Ji et al. (2004), with permission from Dr. Qiang Ji and Acta Geologica Sinica

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 congeneric species. 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 also 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 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* 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 several papers documenting *Archaefructus*, controversies arose around 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; (3) is their status (leaf, carpel) primitive or derived, (4) which placentation do they have.

Since it was 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; Swisher et al. 1998). 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 *Archaefructus*-yielding layer in 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 of time, but rather a range in time. Recent study dated the overlying Jiufotang Formation to 120.3 Ma (He et al. 2004a, b), 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. 2009), 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 could not place what later called seed ferns into either ferns or seed plants convincingly. 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, Trithuriaceae, 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, suggestive of 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). If angiosperms are not seen until the Early Cretaceous, then the former is more likely and the evolutionary roadmap is similar to what depicted by Dilcher (2010). However, if angiosperms have a pre-Cretaceous history, then the latter scenario is favored. Current knowledge seems to favor the latter, if several interesting Jurassic angiosperms in next Chapter are taken into consideration.

The carpel of Archaefructus was initially claimed as conduplicate and thus 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 Magnolia is not the basal-most angiosperm, implying that a conduplicate carpel is not 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 (Endress and Doyle 2015). 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 favored by an unexpected great diversity of angiosperms in the Yixian Formation (Duan 1998; Sun et al. 1998, 2002; Leng and Friis 2003, 2006; Ji et al. 2004; Wang and Han 2011; Han et al. 2013, 2016, 2017) and early angiosperms from the Jurassic documented in Chap. 6.

According to the Magnolia-primitive theories, the early carpels in angiosperms should have marginal placentation. This conception is widely accepted and very influential as the precursor of carpels is supposed to be a leaf bearing ovules along its margin. Initially Sun et al. (1998) interpreted the carpels of Archaefructus as conduplicate with marginal placentation. However, this sound interpretation is never evidenced by their figures. Ji et al. (2004) first challenged this interpretation based on their observation of Archaefructus eoflora, in which the ovules are shown inserted to the supposed dorsal vein of the carpel. This observation is confirmed later by observation on further fossil materials as well as the holotype of Archaefructus (Wang and Zheng 2012). The later more careful observations evidenced by figures reject the presence of marginal placentation in Archaefructus. This conclusion further undermines the previous assumption of precursor of carpels. Now it seems more likely that the formerly called carpel is actually a composite organ derived from two parts of plants in gymnosperms. For details, please refer to Chap. 8.

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 (Fig. 5.15), 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 model 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).

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; Wang and Zheng 2012). This brings its diagnosis more accurate and closer to completion. The following is based on the latest knowledge on *Archaefructus* (Ji et al. 2004; Wang and Zheng 2012): Herbaceous, aquatic plants with branching stems. Main axis often bearing axillary infructescence axes terminating in fruits, and infructescence axes organized alternately. Poorly developed sparsely branched roots. Leaves helically arranged, petiole bases slightly enlarged, petioles of various lengths. Blades pinnately dissected two to six times into linear to slightly spatulate lobes, stipules absent. Reproductive axes forming a lateral branching system or a pseudo-indeterminate system associated with a main inflorescent axis in a cymose pattern. Infructescence axis long, unisexual/bisexual, occasionally branching, bearing stamens at the proximal and fruits at the distal. Stamens 2–3 per cluster, linear, with connectives. Pollen monosulcate, exine reticulate to verriform. Carpel and stamen rarely in the same cluster. Two or more fruits in groups or pairs, oppositely or whorled arranged along the infructescence axis. Fruit with a pedicel, 3–26 mm long, with 1–12 seeds per fruit. Ovules/seeds inserted on the midrib on the abaxial side of the carpel/fruit. Seeds with straight or slightly twisting texture.

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 original 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, but 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 specimen to Dr. Ge Sun who was a research professor at the Institute. Dr. Sun received it and did not pay immediate attention before putting it 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 Kunming 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 a scientific publication. To ascertain the stratigraphy related to this fossil plant, Dr. Sun asked for help from Dr. Shaolin Zheng. Dr. Zheng was a palaeobotanist 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 one 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 soon spread all over the world.

5.3 Sinocarpus

Sinocarpus decussatus was uncovered at the Yixian Formation (Early Cretaceous) outcrops 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).

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 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). This makes the comparison with Sinocarpus far from convincing. Apparently, how to weigh the above similarities and differences is a challenge. The Dilcher et al. (2007) paper contained an error: on the page 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 has 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′ academic attitude (Fig. 5.18).

Leng and Friis (2003, 2006) interpreted the ovules of Sinocarpus as anatropous. Such anatropous ovules are at home among the assumed basal angiosperms, especially Magnoliaceae (Eames 1961; Cronquist 1988). However, this interpretation is not supported by any figure. Examining Figs. 18–20 of Leng and Friis (2006) indicates that the so-called “chalazal region” is actually micropyle, because the breaking scar expected for chalaza is completely missing. It is apparent that the lower-right corner of Fig. 19 of (Leng and Friis 2006) is the funiculus of the ovule and it is where the chalaza is. The lack of trace of funiculus near the micropyle and the antihilar position of the micropyle indicate that the ovules in Sinocarpus are orthotropous rather than anatropous. Thus Leng and Friis′ interpretation of

Fig. 5.18 Fructification of Sinocarpus. (a) Holotype including fructifications and decussately arranged branches. Bar = 1 cm. (b) Two basally fused fruits with seeds borne along the adaxial. Bar = 5 mm

anatropous ovules in Sinocarpus is not favored by their own figures. Rejection of such interpretation further undermines the Magnolia-primitive theory.

Although Dilcher et al. (2007) interpreted the perianth as free, this claim is still tentative as it is never confirmed by any actual observation and figures. Therefore I put perianth of Sinocarpus as unknown in the following paragraph. The real status of perianth awaits further observations to elucidate.

The following diagnosis of Sinocarpus is a combination from Leng and Friis (2006), Dilcher et al. (2007), and my personal observation (Fig. 5.18): 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 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 fruits long and slender. Receptacle of flower small, probably slightly dome- to cone-shaped. Perianth unknown. 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 orthotropous 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 fructification 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 fructification 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, Plate 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 hairy 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 fruits examined) and Erenia suggest that they belong to two distinct fossil plants. Therefore the fossil formerly described as “Erenia stenoptera Krassilov” by Wu (shown in Fig. 5.27a, b) should be assigned to Callianthus dilae because it shares, besides the same locality, almost exactly the same gynoecium and fructification 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 a typical angiospermous flower. 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. 5.19a, b as two carpels, for the following reasons. (1) Two hairy 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 in angiosperms; (3) They are physically connected to stamens, perianth, and pedicel; (4) The stamens, which are missing when mature (Figs. 5.27 and 5.28), are positioned peripheral to the carpels, an arrangement typical of angiosperms; (5) Their positions and morphology correspond closely to two fruits in other fossil fructifications (Figs. 5.27 and 5.28); (6) If the fleshy envelope is compared to the outer integument, there would be two rather than one ovuliferous unit/seed per outer integument, a feature unexpected in Gnetum and Welwitschia (Gnetales); (7) Although sometimes there are two seeds surrounded by fleshy tissues in Ephedra, the tepals in Callianthus are distinct from the triangular bracts Ephedra.

Dégaging does not show any trace of a third style. The smooth connection (Figs. 5.20a, 5.27, and 5.28) 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 fructifications.

There is a vertical mark in Fig. 5.28a, which appears narrower than the gap between carpels, much more inconspicuous and different from the gap. In addition, the dark line on the dorsal of the carpel in Fig. 5.19b may represent a dorsal vascular bundle, therefore the mark in Fig. 5.28a is interpreted as a dorsal ridge on the fruit.

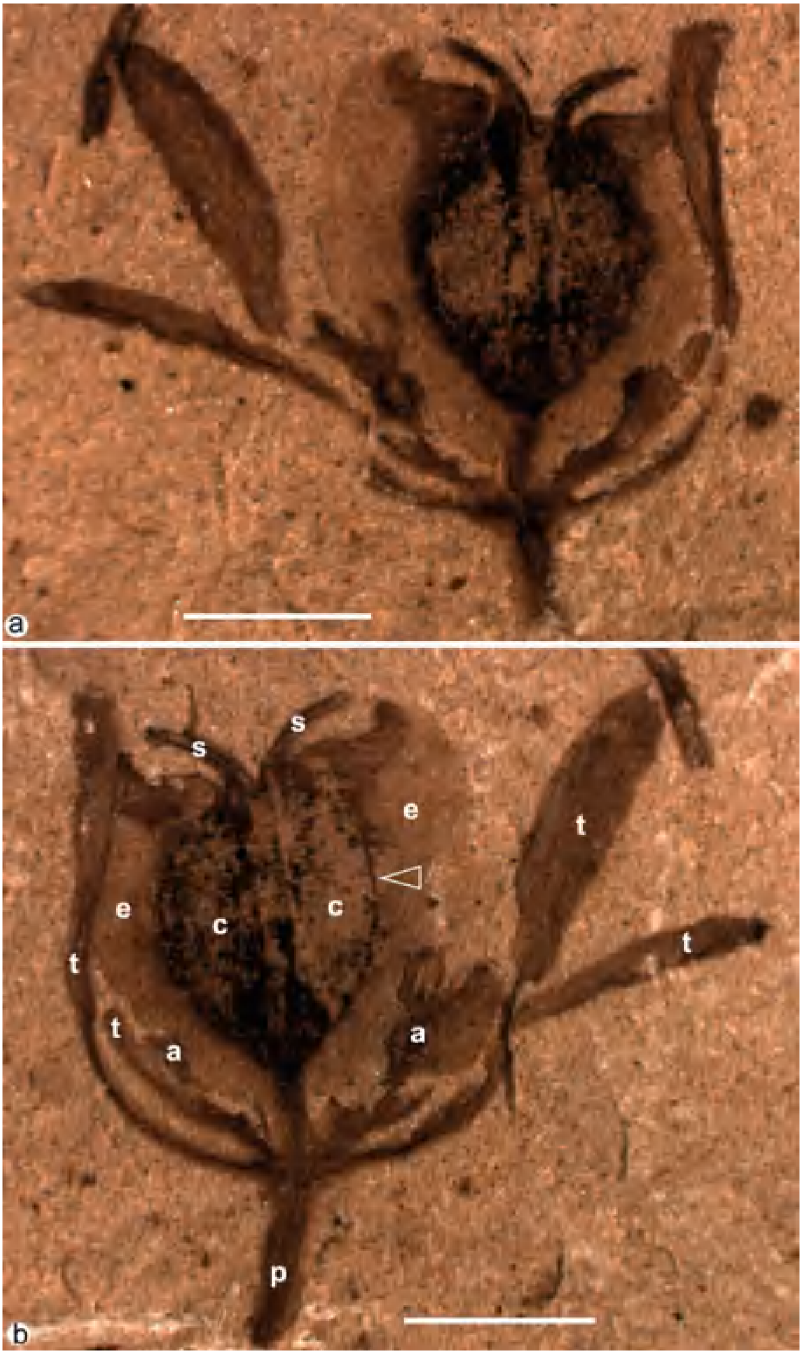

Fig. 5.19 Two facing parts of the same flower of Callianthus. Note the pedicel (p), tepals (t), stamens and anthers (a), fleshy envelope (e), carpels (c), their styles (s), and the abaxial vascular bundle of the carpel (arrow). Figures 5.19–5.26 are about the holotype (PB21047, NIGPAS). Bar = 2 mm. Courtesy of Journal of Integrative Plant Sciences

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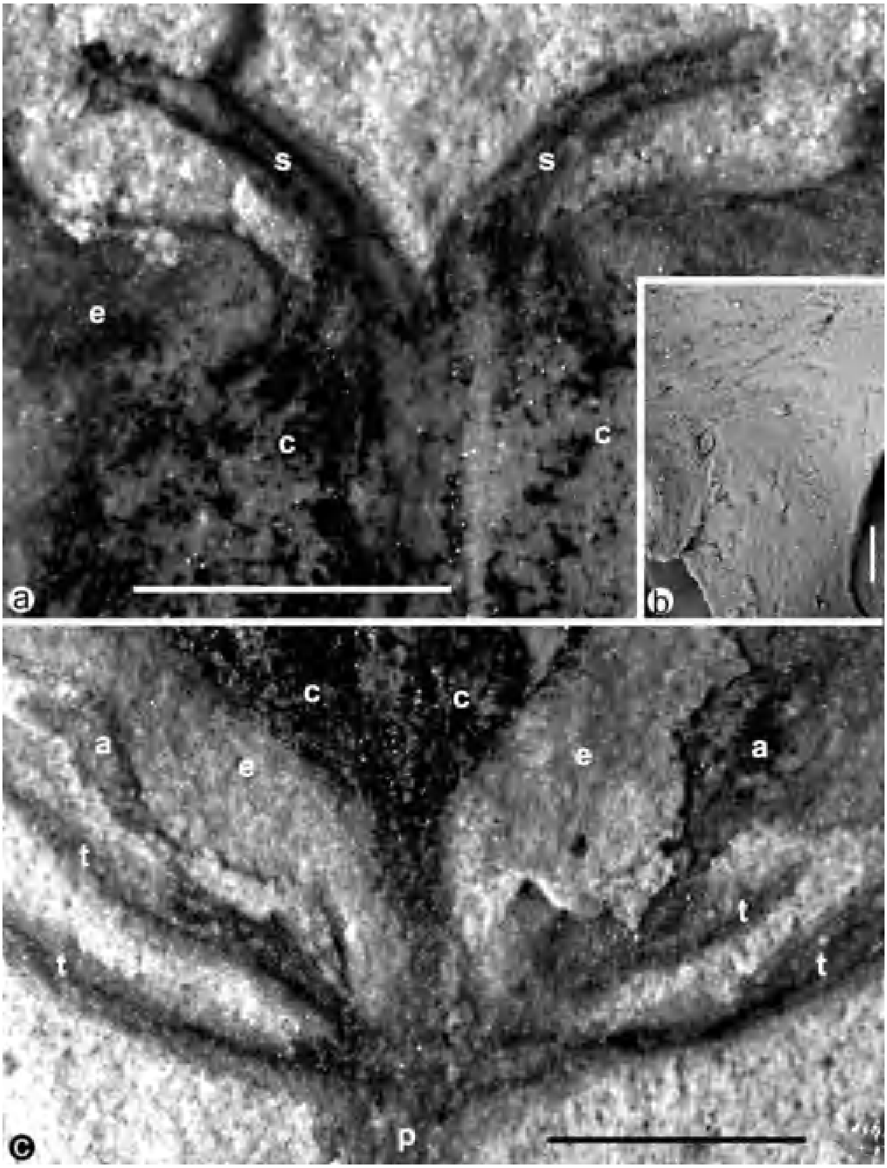

Fig. 5.20 Styles and arrangement of floral parts. (a) The divergent styles. Note the relationship between the fleshy envelope (e), carpels (c) and styles (s). Bar = 1 mm. (b) Style surface covered with hairs scars of variable sizes. Bar = 10 μm. (c) The arrangement of the pedicel (p), tepals (t) in two cycles, stamens (a), fleshy envelope (e), and carpels (c). Bar = 1 mm. Courtesy of Journal of Integrative Plant Sciences

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/fructification. No similar feature has been seen in gymnosperms, with the exception of some Ephedra. Also, micropylar tubes in Ephedra are glabrous rather than hairy (Yang 2007). In Callianthus it is hard to differentiate the style and stigma. Hairs cover the whole style. Most likely the whole style functions as a stigma in this plant.

The dimensions of the hairs on the styles are very variable even in the same SEM picture (Fig. 5.20b). This is unlikely due to preservation or other artifacts. It is more plausible to interpret the hairs as being conical in form. The different appearances of similar hairs may be interpreted as the result of the hairs being cut in 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. 5.23, 5.24, and 5.25). The repeated occurrence of the same kind 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 on 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. 5.20b), 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 Fruits

Fruits 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 fruits and flower suggests that the male parts and perianth of Callianthus dilae tend to fall from the pedicel when mature.

The subtle differences among Figs. 5.19, 5.27, and 5.28 suggest that these fructifications are preserved in different orientations. In Figs. 5.19 and 5.27a, b the bedding plane appears parallel to the plane of the styles, therefore there is a wide space between the two divergent styles. The fructification in Figs. 5.27c and 5.28b 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 fructification in Fig. 5.28a appears to be rotated about 90° from that in Fig. 5.19a, b since the figure shows a ridge in the center of the fruit that is only seen at the margin in Fig. 5.19b. There are more than four horns at its top (Fig. 5.28). The constant presence of a fleshy envelope in all flowers and fructifications preserved at various orientations (Figs. 5.19, 5.27, and 5.28) suggests that the gynoecium/fruit is more or less of radial symmetry and that the gynoecium is 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 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. 5.25a–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. 5.23c and 5.24c), 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. 5.23c and 5.24c 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. 5.24c). 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 differentiation is seen in the perianth. Currently only four tepals are visible in the specimens (Fig. 5.19a, b), but the actual number of tepals is assumed to be more.

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 surrounding two separate carpels. Each carpel composed of a hemi-globular ovary and a hairy style. Fructification 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 certain 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). 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

Synonyms:
Erenia stenoptera Krassilov, Wu, 1999, Plate XVI, Figs. 5,5a
Erenia stenoptera Krassilov, Wu, 2003, Fig. 243
Callianthus dilae Wang and Zheng, Wang and Zheng 2012, 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. 5.19a, b). The pedicel is up to 1.8 mm long and 0.35 mm wide (Fig. 5.19a, b). Four tepals and two stamens are seen attached to the pedicel (Figs. 5.19a, b and 5.20c). 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. 5.19a, b, 5.20c, 5.21c, and 5.22a). Each tepal has two major parallel veins in the distal portion (Figs. 5.19c and 5.26d). A stoma is seen on a tepal, with stomatal aperture 1–2 × 7–8 μm (Fig. 5.26c). A stamen is 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. 5.19a, b, 5.20c, 5.21a, and 5.22b). Another 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. 5.19a, b, 5.22b, and 5.26). Pollen grains in situ are compressed into various shapes, but two of them appear round-triangular, 28–32 μm in diameter (Figs. 5.23, 5.24, and 5.25, 5.26a). Similar pollen grains have been seen three times in the anther region on the replicas (Fig. 5.25f, g). Two stylate carpels are base-fixed in a cup-shaped fleshy envelope, which has a rough surface (Figs. 5.19a, b and 5.20a–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 0.4 mm-high horns along the upper margin (Figs. 5.19a, b and 5.20a). Each carpel is separated from the facing one almost to its base by a gap about 0.3 mm wide (Figs. 5.19a, b, 5.20a, and 5.21b). Each carpel includes an apical style and a basal ovary (Fig. 5.19a, b). The ovary is hemi-globular, about 3.1 mm high and 1.4 mm thick (Fig. 5.19a, b). The style is short, slightly curved, hairy, more than 1 mm long, and about 0.2 mm wide (Figs. 5.19a, b and 5.20a, b). The hairs on the style are probably conical-shaped, tapering distally, at least 5 μm long, covering the whole length of the style (Fig. 5.20b).

Additional specimens: In morphology and dimensions, the fructifications look like the gynoecium (Figs. 5.27 and 5.28). The fructification includes two facing fruits and a fleshy envelope, about 4–5.8 mm high and 4–5.5 mm wide (Figs. 5.27 and 5.28). The fleshy envelope surrounds two facing fruits, and has raised horns at the top (Figs. 5.27a, c, 5.28b, and 5.29a, b). Each fruit is hemi-globular, with a persistent style more than 1 mm long and about 0.2 mm wide (Figs. 5.27a–c and 5.28b). Stamens and tepals are missing in the fructifications (Figs. 5.27a–c and 5.28a, b). There are traces of vascular bundles entering the fruits and envelope, respectively, in the proximal (Fig. 5.27c). 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. 5.27a–c and 5.28b).

Holotype: PB21047a&b.

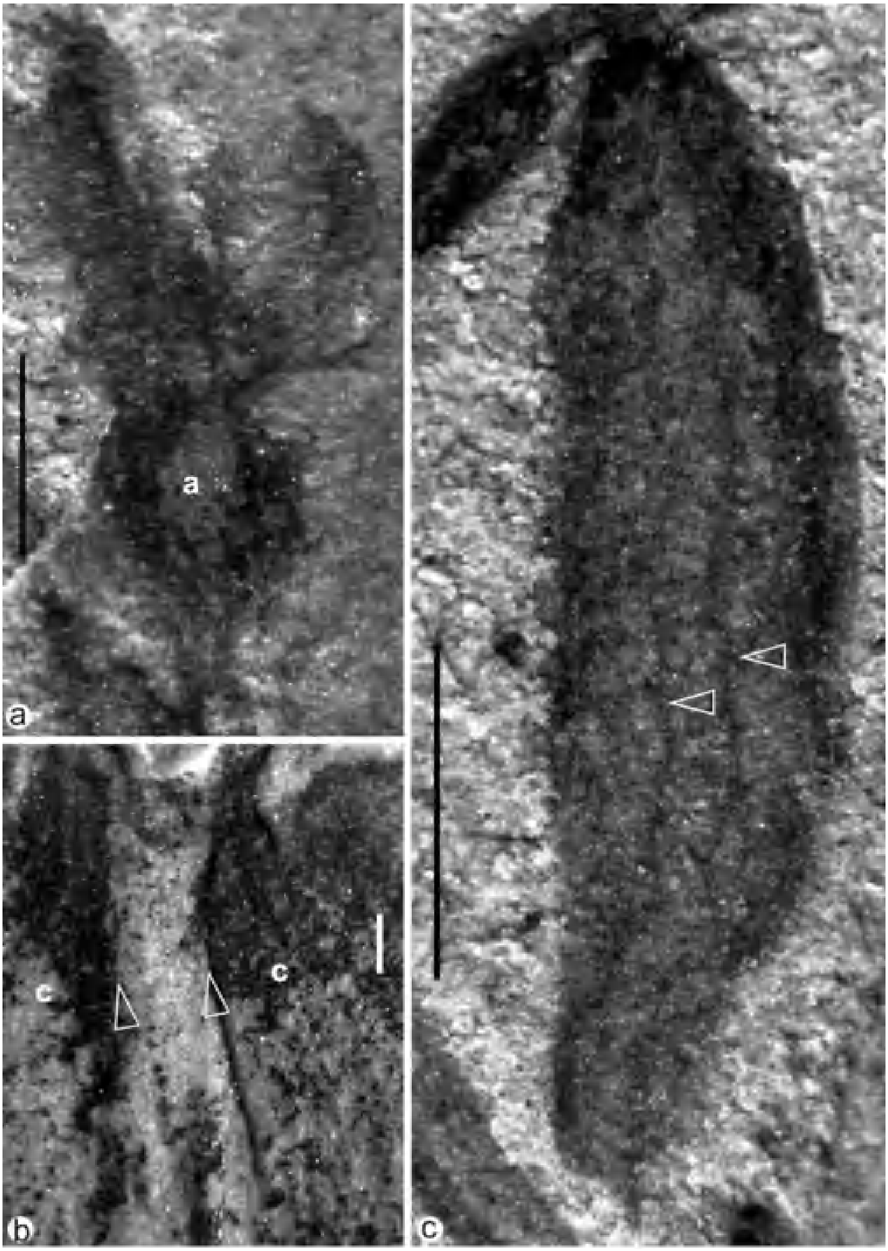

Fig. 5.21 Stamen, tepal, and gap between carpels. (a) One of the anthers enlarged from Fig. 5.19a. Note the globular anther (a), and bristles at the apex. Bar = 0.5 mm. (b) A detailed view of the gap (arrows) between the carpels (c) in the flower shown in Fig. 5.19a. Bar = 0.2 mm. (c) The top portion of a tepal in Fig. 5.19a, with two parallel veins (white arrows). Bar = 1 mm. Courtesy of Journal of Integrative Plant Sciences

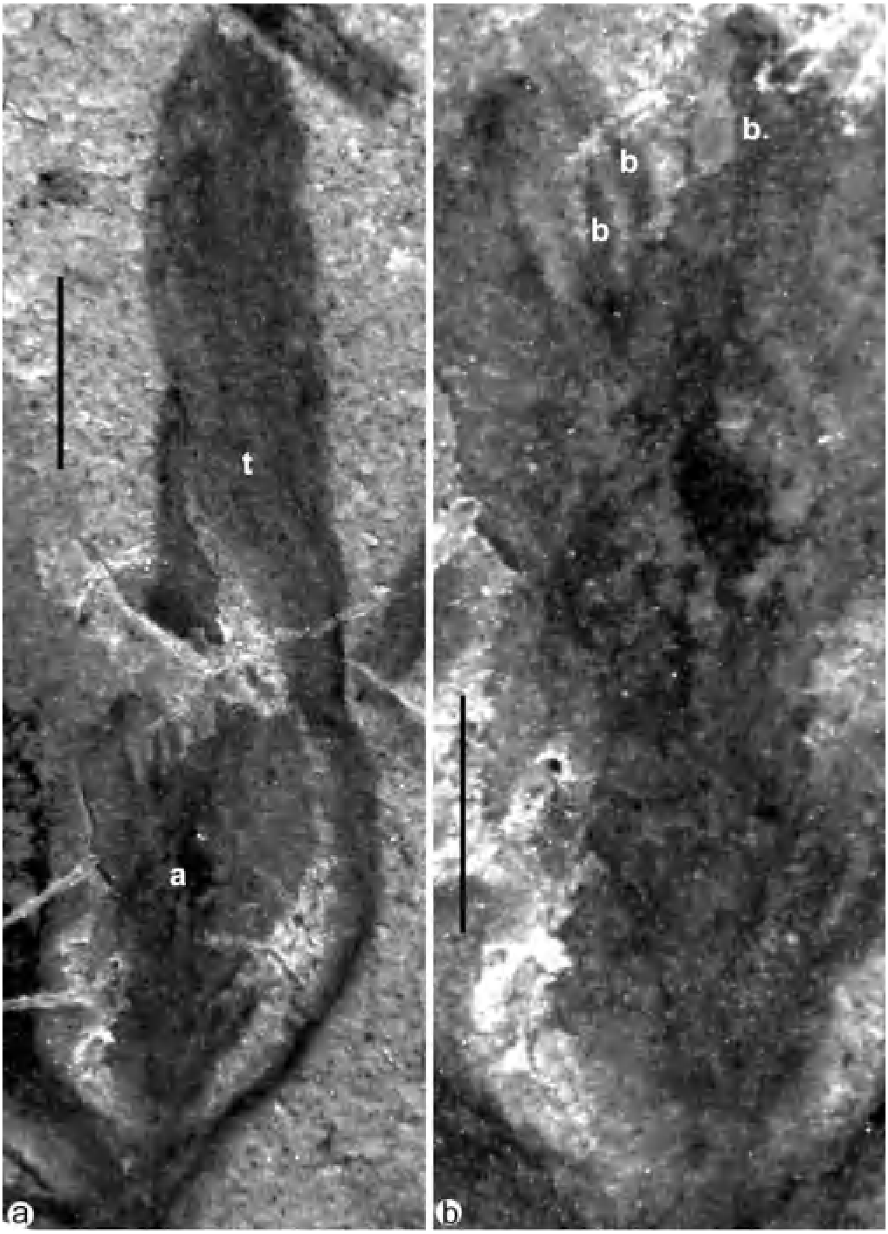

Fig. 5.22 Whole tepals and stamen. (a) Complete tepal (t) exposed after degaging. Note the spatulate shape, long claw, round tip, and its relationship to the stamen (a). Bar = 1 mm. (b) Stamen shown in Figs. 5.19b and 5.22a. Note its globular anther and bristles (b) at the apex. Bar = 0.5 mm. Courtesy of Journal of Integrative Plant Sciences

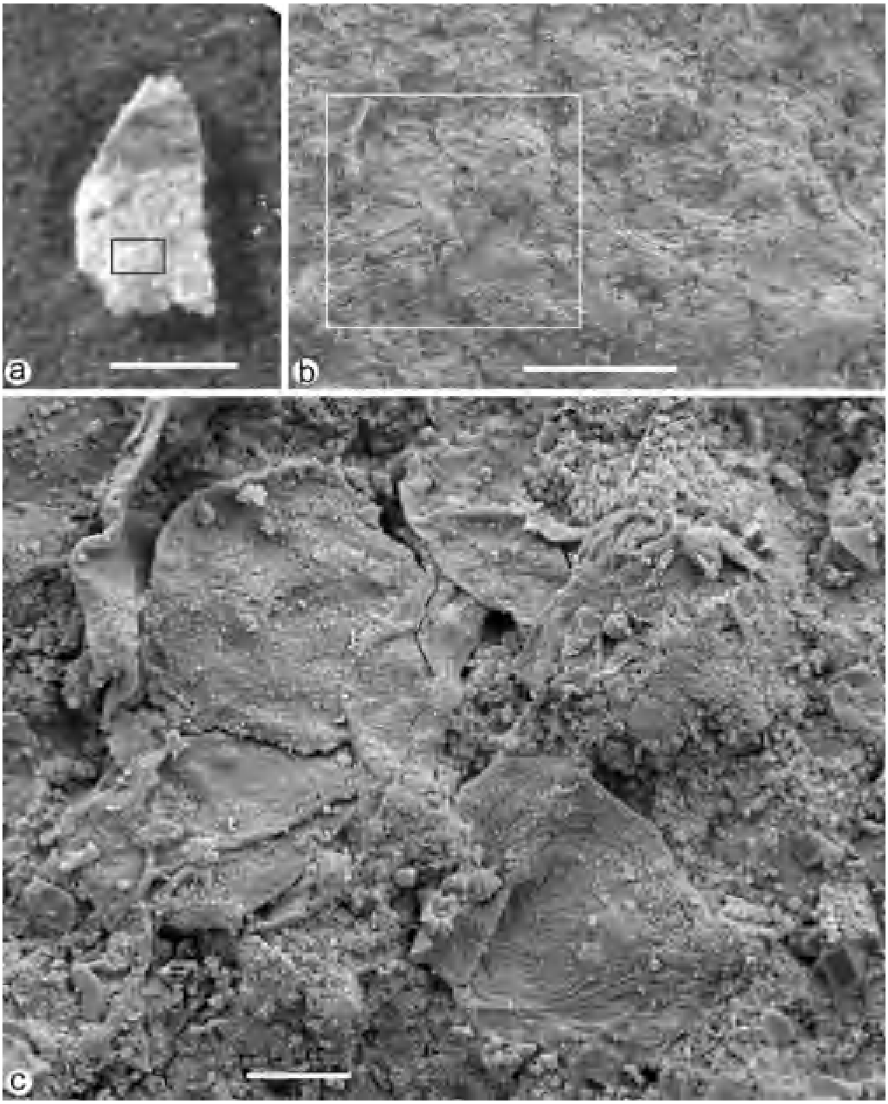

Fig. 5.23 In situ pollen grains. (a) Piece of rock removed from the anther region. Bar = 0.5 mm. (b) Clusters of pollen grains visible on the surface of the rock, without chemical processing. Enlarged form the rectangle in (a). Bar = 50 μm. (c) Pollen grains in the rectangle in (b). Bar = 10 μm. Courtesy of Journal of Integrative Plant Sciences

Additional 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.

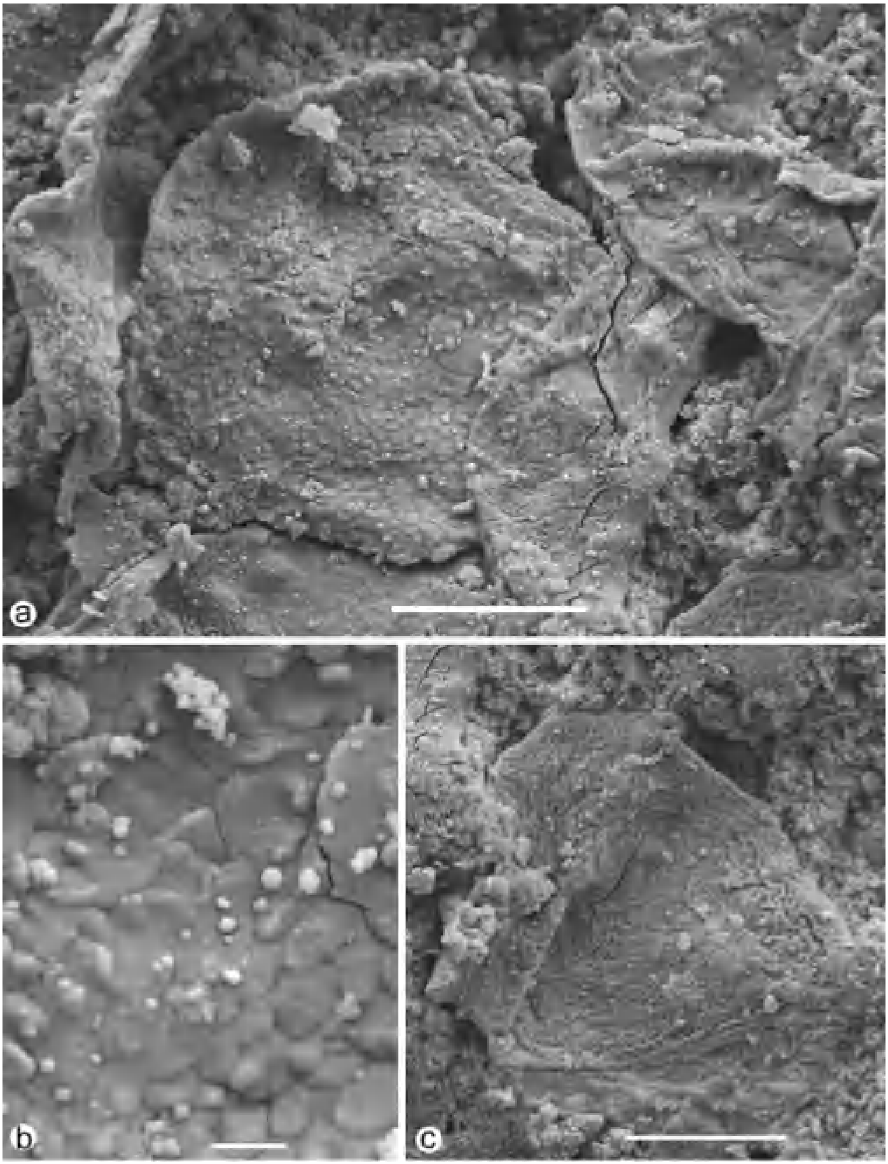

Fig. 5.24 Details of Callianthus pollen grains. (a) Pollen grains enlarged from Fig. 5.23c. Note the round shape of the central one. Bar = 10 μm. (b) Sculpture of the pollen grain in (a). Bar = 1 μm. (c) Triangular pollen grain from Fig. 5.23c. Bar = 10 μm. Courtesy of Journal of Integrative Plant Sciences

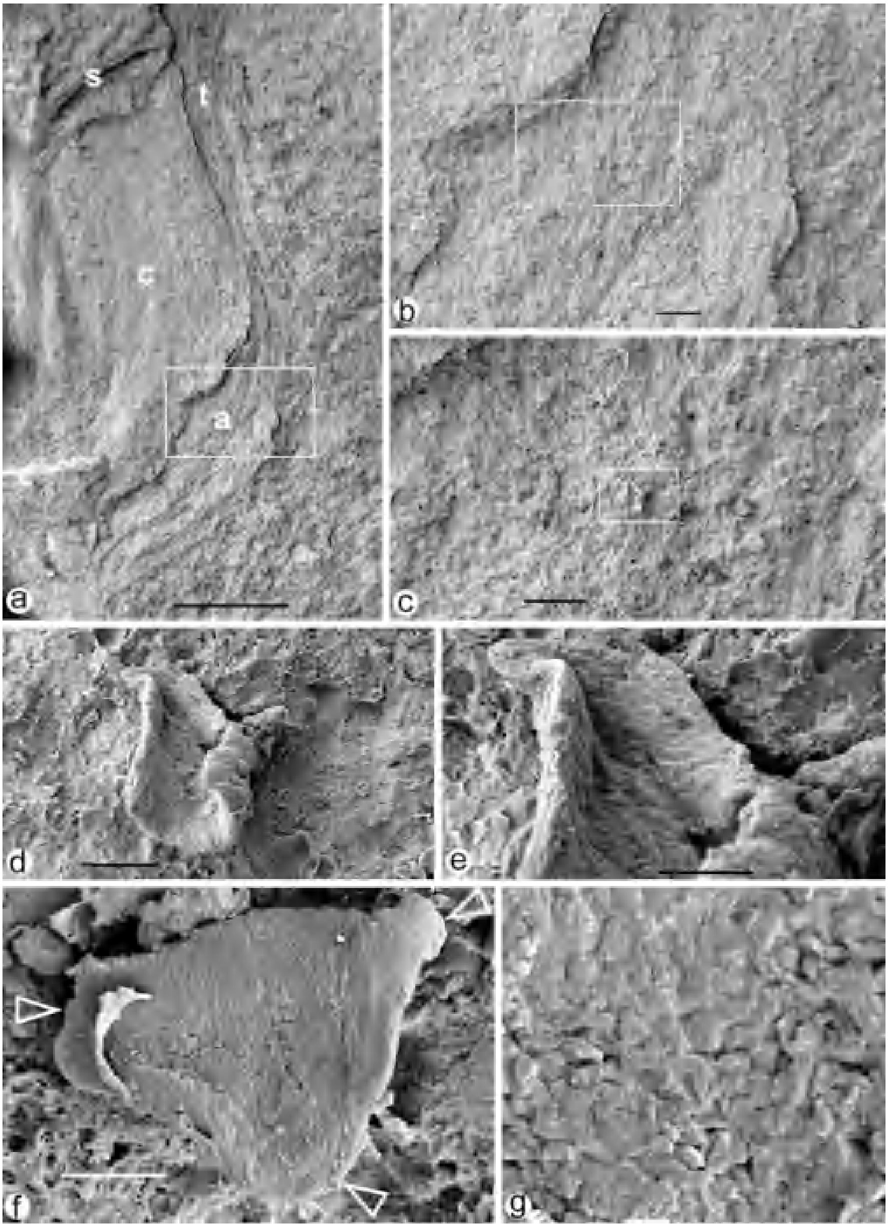

Fig. 5.25 In situ pollen grains seen on replicas. (a) Portion of the flower including anther (a), carpel (c), tepal (t), and style (s). Bar = 1 mm. (b) Details in the rectangle in (a). Bar = 0.1 mm. (c) Details in the rectangle in (b). Bar = 50 μm. (d) In situ pollen grain. Bar = 10 μm. (e) Sculpture on the pollen grain in (d). Bar = 5 μm. (f) Round-triangular pollen grain in the anther. Bar = 10 μm. (g) The sculpture of the pollen grain in (f). Bar = 1 μm. Courtesy of Journal of Integrative Plant Sciences

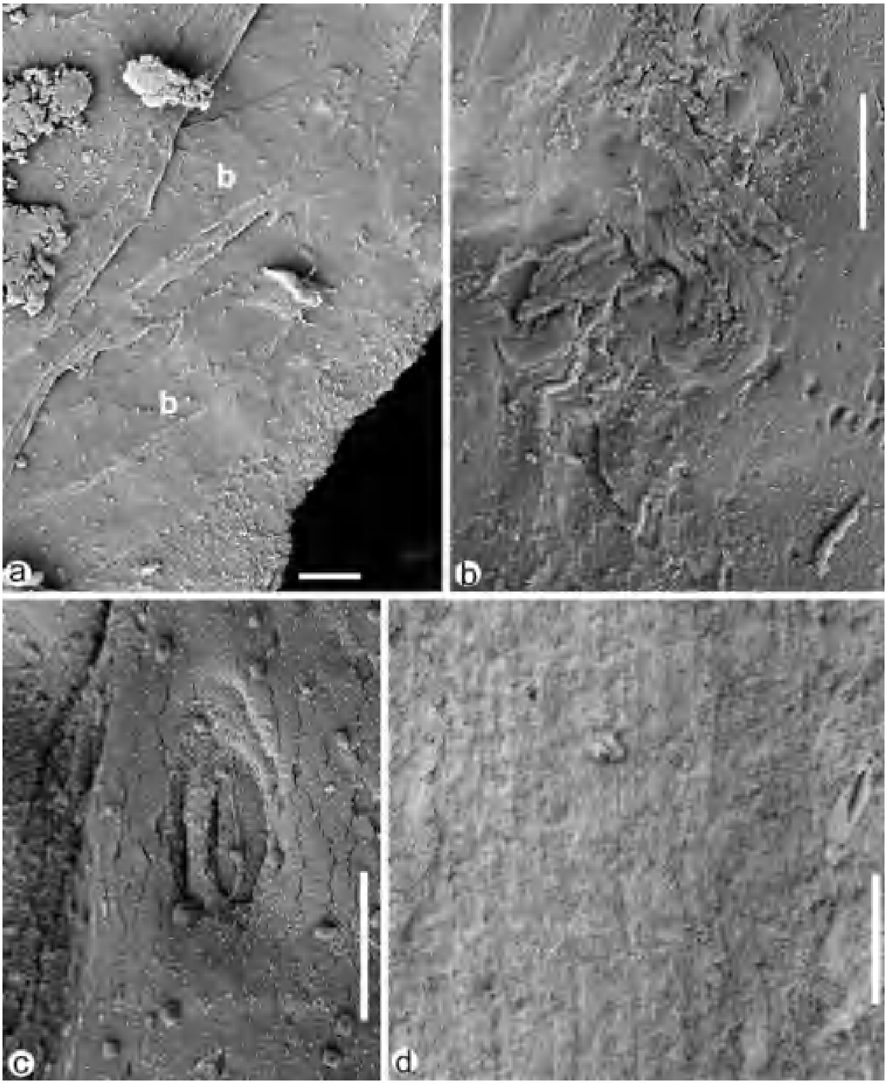

Fig. 5.26 Details of bristles, stomata, fructification surface, and tepal veins. (a) Two bristles (b) at anther apex. Bar = 10 μm. (b) Clusters of trichomes on the surface of the fleshy envelope. The outside of the fleshy envelope is toward the left. Bar = 10 μm. (c) Stoma on a tepal. Bar = 10 μm. (d) Parallel veins in a tepal. Bar = 0.1 mm. Courtesy of Journal of Integrative Plant Sciences

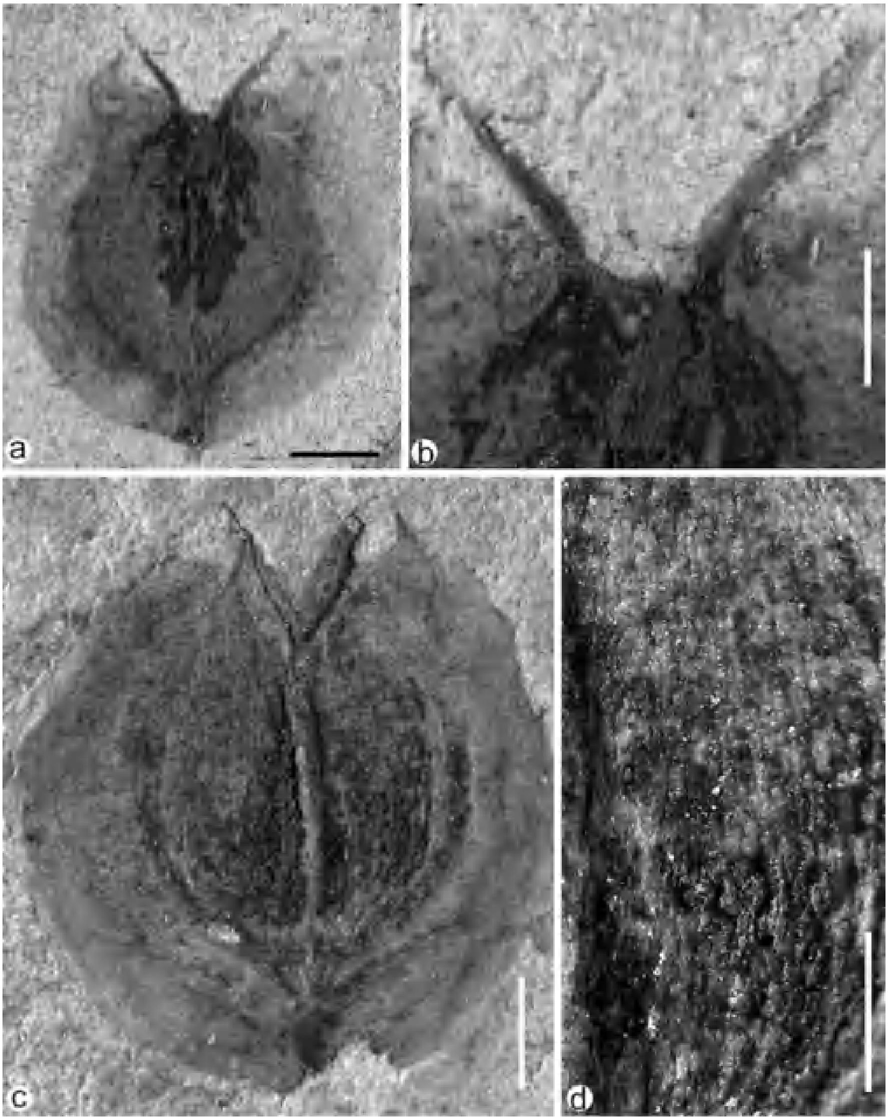

FIg. 5.27 Fructifications and their details. (a) Fructification including two fruits with persistent styles surrounded by a fleshy envelope. PB18320, NIGPAS. Bar = 1 mm. (b) Two persistent divergent styles in (a). Note the wide space between the styles. Bar = 0.5 mm. (c) Another fructification including two fruits surrounded by a fleshy envelope and persistent styles. Note the space between two styles narrower than in Figs. 5.19a, b and 5.27a, b. PB21092, NIGPAS. Bar = 1 mm. (d) Longitudinal striations on the cuticular relics of the seed in (c). Bar = 0.5 mm. Courtesy of Journal of Integrative Plant Sciences

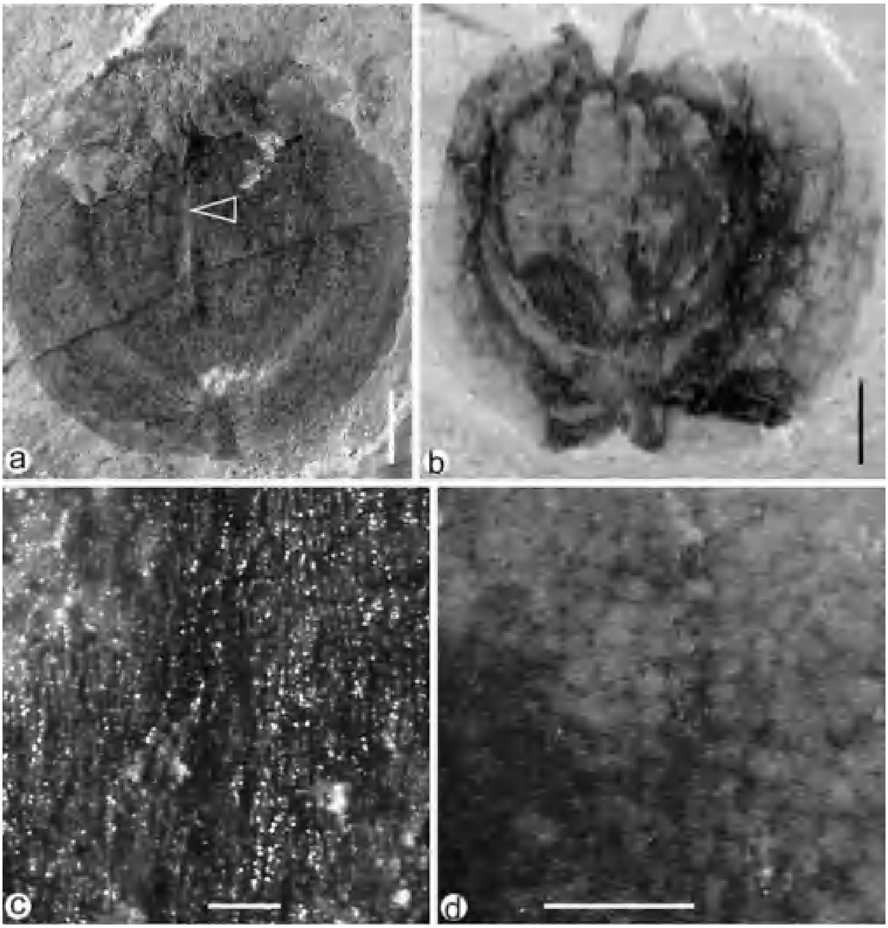

Fig. 5.28 *Callianthus* fructifications and details. (a) Fructification with its top portion of the envelope preserved. Note the dorsal ridge in the fruit (*arrow*), and a vascular bundle at the bottom. PB21091b, NIGPAS. Bar = 1 mm. (b) fructification with its styles partially preserved. PB21390, NIGPAS. 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 Journal of Integrative Plant Sciences

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

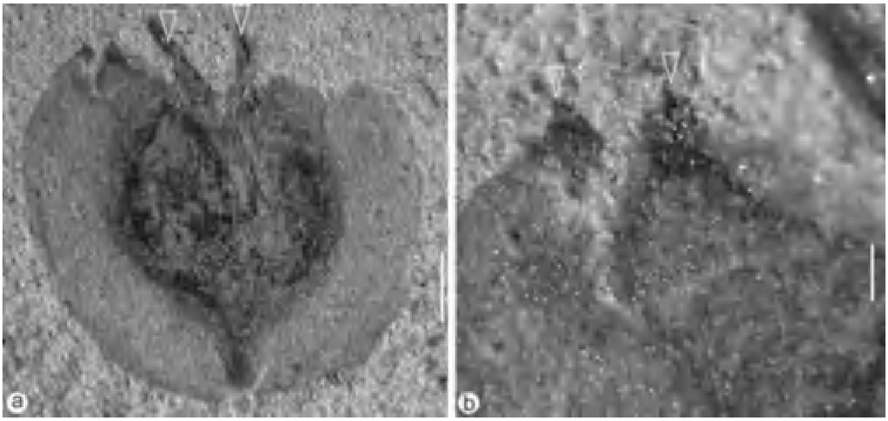

Fig. 5.29 Details of the fructification. (a) Fructification with two fruits bearing persistent distal styles surrounded by fleshy layer. Bar = 1 mm. (b) Two horns on the upper margin of the fleshy receptacle. Bar = 0.2 mm

Comparison among different specimens that reflect different aspects and 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 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 (Wheeler and Pennak 2013). 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 that 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 (the reason is presumed to be in its post-pollination stage) and surrounded by the fleshy envelope. Its styles are divergent and have hairs on its surface. However, when the fruits 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 fructifications, including the fleshy envelope and carpel-derived tissue, fall off the plant when mature. Future specimens will shed more light on other aspects of Callianthus.

5.4.7 Pollination and Dispersal

Currently, there is no evidence to indicate how *Callianthus* is pollinated. On one hand, the hairs 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 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 pollination. Otherwise the function of the bristles on the anthers would be hard to explain.

What is the function of the fleshy envelope in fructifications of *Callianthus*? This is a difficult question, but common sense and statistics on living plants can help. Most fleshy fruits 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 challenges 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 infructescence associated 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 proposed by Friis et al. (2006). It is not surprising that *Callianthus* was taken as the earliest typical flower (Wheeler and Pennak 2013).

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 hairy 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 bracts (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 within angiosperms with certainty.

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; Wang and Han 2011; Han et al. 2013, 2017) and early record of eudicots (Brenner 1976; Drinnan et al. 1994; Pedersen et al. 2007; Wilf et al. 2017), which is regarded more derived than the basal clades, 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. 2007a, b; Wang 2009; Wang and Wang 2010; Zheng and Wang 2010; Han et al. 2016, 2017) as well as molecular analyses (Soltis et al. 2004).

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; 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). 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). 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, 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. The only thing comparable to this is the coating layer in Chaoyangia from the Yixian Formation. But the latter is distinct from Callianthus in its surface spines. Otherwise there is no comparable part in the previous Cretaceous fossil record (Dilcher 1979; Friis et al. 2006), and 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 1980a, b) 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 1980a, b), unlike the situation in Callianthus where the stamens and tepals are distinct and arranged below the fleshy envelope (Figs. 5.19a, b, 5.20c, 5.21a, and 5.22b). 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 at this time.

The seeds of Callianthus are poorly preserved and only relics of cuticle is preserved (Figs. 5.27d and 5.28c), although they can be safely interpreted as seeds. The outlines of seeds in Fig. 5.27c, 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 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), Sinocarpus (Leng and Friis 2003, 2006; Hyrcantha, Dilcher et al. 2007), Liaoningfructus (Wang and Han 2011), and Baicarpus (Han et al. 2013), is among the earliest widely-accepted angiosperms and thus shed new light on the early radiation of angiosperms. In addition, Callianthus is a 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 be diminished. Rather it would be the monotype of a new, isolated class of seed plants, and thus could provide raw material for the study of seed plant evolution, diversity, and phylogeny (Fig. 5.30).

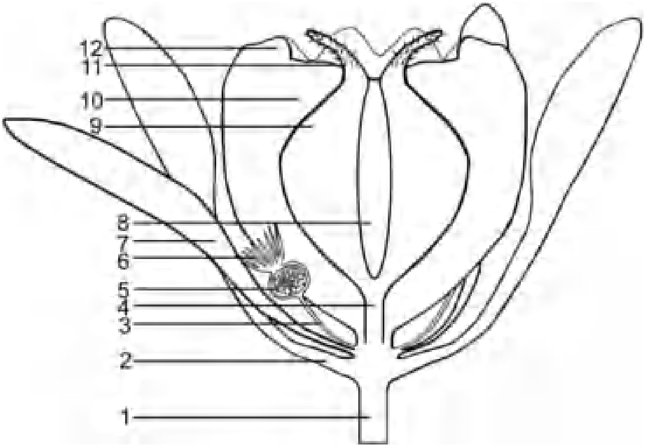

Fig. 5.30 Sketch of the flower. Note the pedicel (1), outer tepal (2), inner tepal (7), filament (3), bristles (6) at the apex of the anther (5), vascular bundle (4) to the carpels, gap (8) between two carpels (9), fleshy envelope (10) around the carpels, hairy style (11), and a horn on the fleshy envelope (12). Modified from Wang and Zheng (2009) in Journal of Integrative Plant Sciences

5.5 Liaoningfructus

5.5.1 General Background

The specimens of *Liaoningfructus* was collected from the outcrop of the Yixian Formation near Huangbanjigou, Beipiao, Liaoning, China. Various pioneer angiosperms have been documented from the Formation, some even from exactly the same locality (Duan 1998; Sun et al. 1998, 2001, 2002; Leng and Friis 2003, 2006; Ji et al. 2004; Dilcher et al. 2007; Wang and Zheng 2012). The specimen was preserved as a compression embedded in yellowish, muddy siltstone.

5.5.2 Generic Diagnosis

Fruit more or less lanceolate in shape, of three portions. Upper portion tapering distally. Middle portion enclosing two seeds, one above the other. Lower portion constricting slightly to the base. At least nine longitudinal, smoothly curving vascular bundles in the fruit wall. Vascular bundles serving seeds slightly sinuous, arising from the central bottom of the fruit.

Etymology: *Liaoning-* for Liaoning Province, *-fructus* for fruit, *ascidiatus* for ascidiate form of the fruit.

5.5.3 Liaoningfructus ascidiatus

Generic diagnosis: The same as the genus.

Description: The fruit is more or less lanceolate and slightly asymmetrical in shape, about 25 mm long, and 8.5 mm wide (Fig. 5.31a). The fruit comprises three portions (Fig. 5.31a). The middle portion encloses two seeds, one above the other (Fig. 5.31a). The upper seed is slightly bigger, 3.8 × 4.4 mm, and the lower one smaller, 2.2 × 2.5 mm (Fig. 5.31a, d). The upper portion of the fruit tapers gradually into the tip, which is 2.1 mm wide, convex and with several tooth-like protrusions (Fig. 5.31a, b). The lower portion constricts slightly to the base, with a truncated and partially broken base (Fig. 5.31a, c). There are about nine longitudinal vascular bundles running through the fruit wall, terminating at the fruit tip and may be eclipsed by the seeds (Fig. 5.31a–c, f). The vascular bundles are 125–175 μm in width, with an interval 80–202 μm in between (Fig. 5.31a, b). The vascular bundles serving the seeds are slightly different from others in being sinuous (Fig. 5.31a, c). They arise from the central bottom of the fruit (Fig. 5.31c). One of them is smoothly connected to the lower seed (Fig. 5.31c). There is a protrusion of sediment in the depression left by the

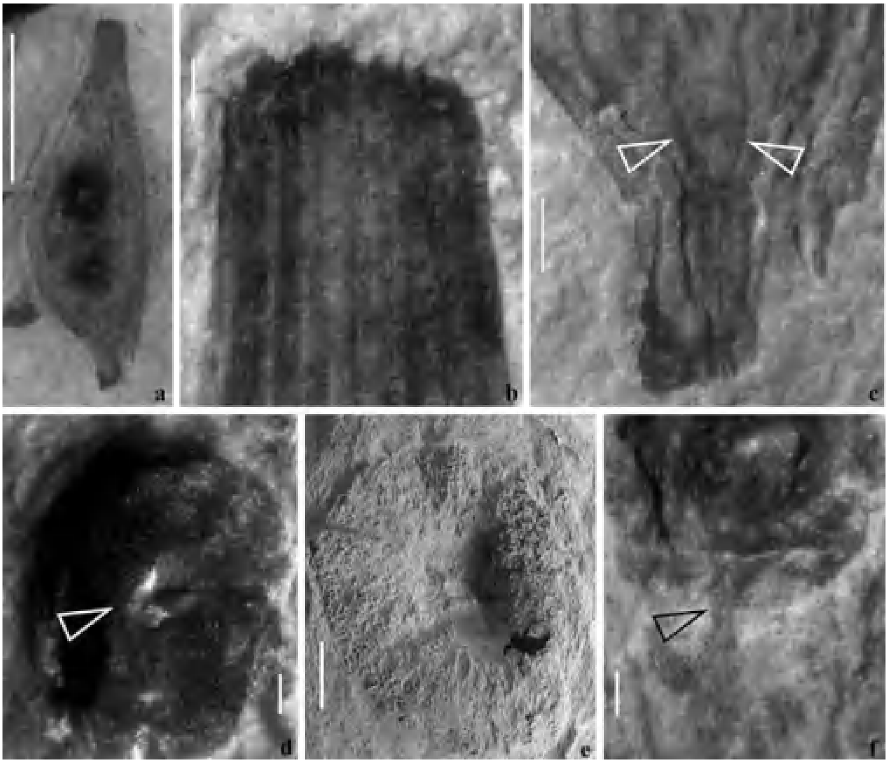

Fig. 5.31 General morphology and details of Liaoningfructus ascidiatus. (a) The general morphology. Note two seeds one above the other in the fruit. Bar = 10 mm. (b) The convex terminal of the fruit, with about nine parallel veins and tooth-like protrusions. Bar = 0.5 mm. (c) The base of the fruit. Note the two sinuous vascular bundles (arrows) connected to seeds arising in the center, and the broken base. Bar = 1 mm. (d) Details of the upper seed. Note its round shape, dark material of the seed, a protrusion (arrow) of sediment. Bar = 0.5 mm. (e) Replica of the seed in (d), under SEM. Note the micropyle (central depression) in the seed. Bar = 0.5 mm. (f) Details of the lower seed. Note the coherent connection (arrow) of the vascular bundle to the seed. Bar = 0.5 mm. Courtesy of Acta Geologica Sinica

seed (Fig. 5.31d, e), which becomes obvious cavity on the replica made of the seed when observed using SEM (Fig. 5.31e).

Holotype: PB21405.

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

Horizon: the Yixian Formation, Lower Cretaceous (125 Ma).

Depository: Nanjing Institute of Geology and Palaeontology, CAS, Nanjing, China.

5.5.4 Discussions

5.5.4.1 Eliminating Alternatives

Galls are frequently seen on leaves of plants. A gall on a leaf with parallel venation may appear similar to Liaoningfructus to certain extent. However, a gall is never a coherent portion of a leaf, therefore the spatial relationship between it and the leaf is random rather than coherent (LeBlanc and Lacroix 2001). When compressed onto a leaf, a gall may eclipse certain veins and the veins are continued across the gall (LeBlanc and Lacroix 2001). The vascular bundle serving the seed in Liaoningfructus is apparently coherently connected to the seed, widens near the seed on one side, and missing completely on the opposite side of the seed (Fig. 5.31a, f). Furthermore, Liaoningfructus with such an asymmetrical shape, blunt tip, and venation does not look like any known leaf in nature. Therefore this alternative is dropped hereafter.

Another alternative interpretation would require reversing the above proposed orientation of Liaoningfructus. However, this alternative appears less believable than our above interpretation because: (1) if the above proposed tip of Liaoningfructus were actually its base, then its new tip would appear broken and split (Fig. 5.31a, c), a situation never seen in any plants; (2) its new tip would be bigger than its base, a configuration rarely seen in vegetative parts of plants (Fig. 5.31a); (3) the convex tip with tooth-like protrusions in above interpretation, is natural and could not be attributed to truncation; (4) the basal ovule in the above interpretation would turn to be pendulous in the newer interpretation. A pendulous ovule usually is served by a vascular bundle rising first and then turning down before finally entering the ovule. However, such an expected vein pathway is apparently missing in Liaoningfructus. Taking all together, this up-side-down alternative is dropped hereafter.

5.5.4.2 Affinity

With two seeds inside, Liaoningfructus satisfies the typological definition of angiosperms. Although it is still an open question whether its ovules are enclosed before the pollination, a strict criterion adopted in this book for angiosperms, angiospermy and fruit morphology of Liaoningfructus distinct from any known gymnosperms suggest that placing Liaoningfructus is a decent treatment. However, as information on the mother plant is still lacking, currently available information is not enough to resolve the exact position of Liaoningfructus in angiosperms.

5.5.4.3 Evolutionary Implications

The deployment of the vascular bundles in the fruit usually is strongly correlated to the carpel form, from which the fruit is derived. The vascular bundles run almost parallel from the bottom to the tip of the fruit in Liaoningfructus, at least in the portion not eclipsed by the seeds, suggesting that all vascular bundles in the fruit wall may be radially symmetrically deployed. This has little to do with plicate carpel since its pinnate venation in plicate carpels would have not produced the venation pattern seen in Liaoningfructus. Since many plicate carpels may initially be ascidiate in form during their early development (Van Heel 1981; Taylor 1991; Friis et al. 2003; Endress 2005) and there is no example of a mature ascidiate carpel that is plicate initially, the carpel that gives rise to Liaoningfructus fruit is very likely ascidiate in form.

Ascidiate carpel is proposed ancestral based on various evidence, including morphology, molecular data, development, and cladistic analysis (Van Heel 1981; Taylor 1991; Endress and Doyle 2009). However, without supporting fossil evidence, substituting plicate carpels with ascidiate ones as the archetype is not easy to win a wide acceptance. Although the Yixian Formation has yielded widely accepted megafossil angiosperms (Duan 1998; Sun et al. 1998, 2001, 2002; Leng and Friis 2003, 2006; Ji et al. 2004; Dilcher et al. 2007; Wang and Zheng 2012), the previous lack of ascidiate carpels or fruits appeared not favoring the ascidiate-carpel-primitive hypothesis, leaving the above on-going shift in thinking on the angiosperm evolution at least tentative. Apparently, Liaoningfructus with a typical ascidiate carpel in the Yixian Formation (the Barremian, Early Cretaceous) provides a convincing and long-needed support for the above shift in thinking.

Wang (2010a) proposed that a carpel with a basal placenta, like in some Caryophyllales, should be among the most primitive forms based on analysis of living and fossil plants. This conflicts with the classic thinking on angiosperm evolution, and is still in need of fossil evidence support. The vascular bundles supplying the seeds in Liaoningfructus arise from the central bottom of the fruit and are independent of those in the ovary wall, implying possible presence of basal placentation in this fossil plant, loaning support for Wang′s new hypothesis.

5.6 Baicarpus

The specimens described here were collected from the Jianshangou Beds of the Yixian Formation near Huangbanjigou, Beipiao, Liaoning, China. The age of the Yixian Formation is about 125 Ma (Dilcher et al. 2007). Early angiosperms, including Chaoyangia (Duan 1998), Archaefructus (Sun et al. 1998, 2001, 2002; Ji et al. 2004; Wang and Zheng 2012), Callianthus (Wang and Zheng 2009), and Liaoningfructus (Wang and Han 2011), have been recovered from the Formation near Huangbanjigou Village. The specimens of Baicarpus from this locality are preserved on slabs of light yellowish siltstone, including 11 fructifications preserved in similar rocks (Fig. 5.32a–j).

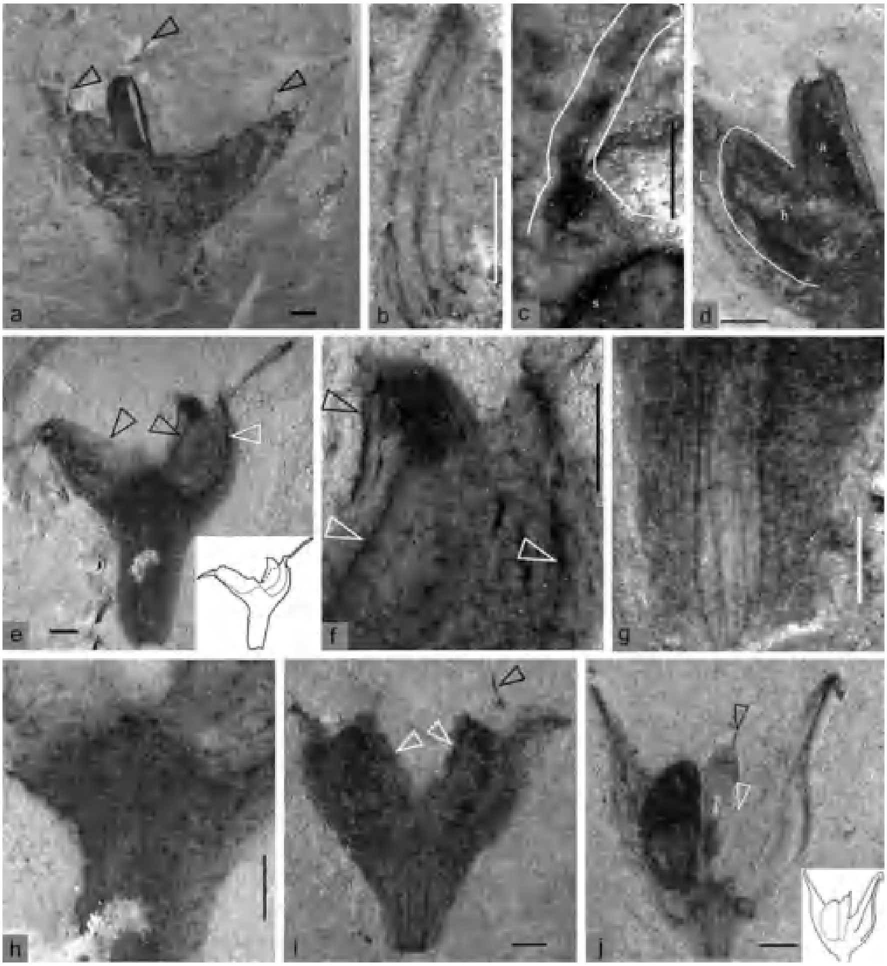

Fig. 5.32 Details of Baicarpus huangbanjigouensis. Stereomicroscopy. (a) Fructification with three fruits (white arrows). Note the projections, and styles (black arrows) partially embedded in the sedimentary matrix. Bar = 1 mm. (b) Longitudinal vascular bundles in one of the projections in a. Bar = 1 mm. (c) Detailed view of fruit (b) in d. Note the seed(s) with smooth outline, the style (outlined) attached to the conical ovary tip that was still embedded. Bar = 0.5 mm. (d) Details of two fruits in a, before trimming off the sediment. Note the spatial relationship among the fruits (a, b), style (arrow), and gynobase (f). Bar = 1 mm. (e) Fructification with two projections and a fruit. Note the gynobase (black arrows) extended between the fruits, and mark (white arrow) left by a fall-off fruit. Bar = 1 mm. (f) Detailed view of the fruit in e. Note the fruit (black arrow), inner margin of the gynobase (left white arrow), and the mark (right white arrow) left by a fall-off fruit. Bar = 1 mm. (g) Peduncle of the fructification in a. Note the longitudinal vascular bundles. Bar = 1 mm. (h) Convex center of the fructification/flower in e. Bar = 1 mm. (i) Fructification with two fruits (white arrows). Note the projections and style (black arrow) on a fruit. Bar = 1 mm. (j) Fructification with two fruits/carpels and a persistent style (black arrow), straight projections. Note the edge of the inner margin (white arrow) of the gynobase. Bar = 1 mm. Courtesy of Acta Geologica Sinica

5.6.1 Diagnosis

Pedunculate fructification. Peduncle with longitudinal vascular bundles and spirally arranged scars of floral parts. Gynobase urn-formed, with projections along the rim and fruits surrounded by the gynobase. Projections straight or curving, with vascular bundles. Fruits deeply sunken in the gynobase, each with an elongated ovary and an apical persistent style. Style attached to the adaxial side of the ovary tip. Seed fused with the abaxial pericarp, separated from the adaxial pericarp, with a terminal beak and smooth seed coat.

Type species: Baicarpus huangbanjigouensis.
Etymology: Bai- for Mr. Xuedong Bai, who donated the first specimens for this study; -carpus meaning ′fruit′ in Latin.
Horizon: Jianshangou Beds, Yixian Formation, Lower Cretaceous.
Locality: Huangbanjigou Village, Beipiao, Liaoning, China (41°12′N, 119°22′E).

5.6.2 Baicarpus huangbanjigouensis (Figs. 5.32 and 5.33)

Specific diagnosis: Fructification 6–10 mm long, 6–13 mm wide. Peduncle short and stout. Projections short, straight or slightly curved.

Description: Eight specimens of Baicarpus are studied (Fig. 5.32a–j). The fructifications are preserved as compressions embedded in yellowish siltstones (Fig. 5.32a–j). The fructifications are 6–10 mm long, 6–13 mm wide (Fig. 5.32a–j). The peduncles are 0.7–5.5 mm long and 1.2–2 mm wide, with longitudinal vascular bundles, gradually intergrading to the gynobase (Fig. 5.32a, g–j). The gynobase is urn-formed, well-developed, with a convex center on which the fruits are attached (Fig. 5.32e, h–i). The basal floral parts are abscised, leaving a spirally arranged series of scars on the peduncle (Fig. 5.33j). Reflexed or straight projections are 2–4.5 mm long, and with longitudinal, straight or curved vascular bundles (Fig. 5.32a, b, j). Each fruit includes an apical style and a basal ovary sunken into the gynobase (Fig. 5.32a, d, i–j). The styles are 100–170 μm wide and 0.5–1.5 mm long, straight, uniform in width, smoothly attached to the adaxial of the conical ovary tip (Fig. 5.32a, c, d, j). The ovary is 3.1–3.5 mm long, 1.3–2 mm thick (between adaxial and abaxial sides) (Figs. 5.32a, d–f, j and 5.33a–c, h–i). The pericarp is composed of approximately ten layers of cells, not well stratified, about 0.12 mm thick and separated from the seed on the adaxial side, about 0.16 mm thick and fused with the seed on the abaxial side (Fig. 5.33a–e, h–i). The seed is about 2.5 mm long and 1.4 mm wide, with a smooth outline and/or a beak on its tip (Fig. 5.33a–e). The seed coat is composed of sclerenchymatous cells 6–21 × 14–70 μm (Fig. 5.33k). These cells are subdivided into various patches by a wall up to 45 μm thick, and are surrounded by a cell wall about 1 μm thick (Fig. 5.33k). Cell walls are straight

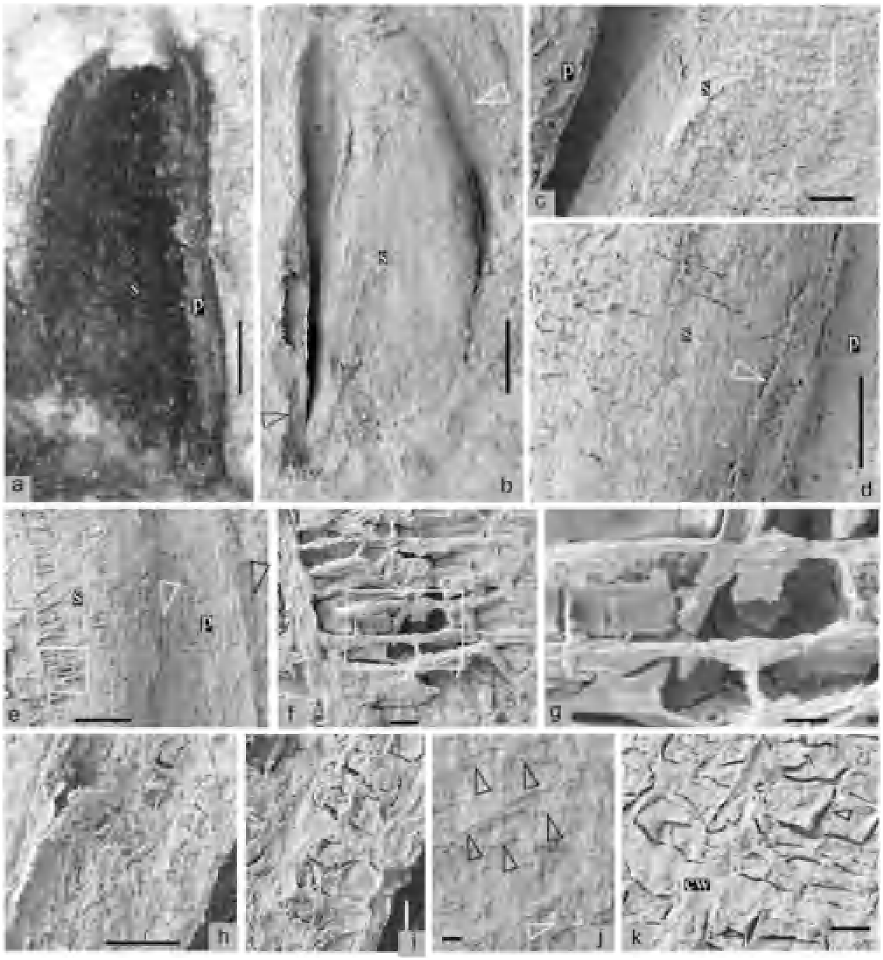

Fig. 5.33 Details of the fructification in Fig. 5.32a. All SEM, except Fig. 5.33a. (a) View of whole fruit (a in Fig. 5.32d). Note the pericarp (p) enclosing the seed (s). Bar = 0.5 mm. (b) View of the fruit in a. Note the abaxial pericarp (white arrow) fused with the seed (s) and the adaxial pericarp (black arrow) separated from the seed by a gap (dark color). Bar = 0.5 mm. (c) Detailed view of middle left of the fruit in b. Note the gap (dark area) between the seed (s) and pericarp (p). The rectangular region is detailed in Fig. 5.33k. Stereomicroscopy. Bar = 0.1 mm. (d) Detailed view of the middle right (abaxial) portion of the fruit in b. Note the pericarp (p) enclosing the smooth-surfaced seed (s). Bar = 0.1 mm. (e) Detailed view of the fruit, enlarged from the region pointed by white arrow in b. Note the outer (black arrow) and inner (white arrow) surfaces of the pericarp (p), and adnate seed (s). Bar = 0.1 mm. (f) Detailed view of the rectangular region in e. Note the straight cell walls of varied thickness, and cell lumina on seed surface. Bar = 10 μm. (g) Detailed view of the rectangular region in f. Note the cell lumina framed by straight cell walls. Bar = 5 μm. (h) Adaxial pericarp separated from the seed, enlarged from the region pointed by black arrow in b. Note the layers of cells, and gap (lower right) separating the pericarp from the seed. Bar = 50 μm. (i) Detailed view of right portion of h, showing cell outlines. Bar = 10 μm. (j) Detailed view of peduncle of the fructification in Fig. 5.32a, with scars left by the abscised floral parts (black arrows). Note vertical striations (white arrows). Bar = 0.1 mm. (k) Sclerenchymatous cells on the

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(Fig. 5.33k). Sometimes cell content remains can be seen in the cell lumina (Fig. 5.33k).

Etymology: huangbanjigouensis for village name of the fossil locality.

Holotype: PB21404 (Figs. 5.32a–d and 5.33a–k).

Additional materials: PB21401-21403, PB21628, PB21632, Z.J.Liu5419, 2012052955.

Depository: PB21401-21404, PB21628, and PB21632 in Nanjing Institute of Geology and Palaeontology, CAS, Nanjing, China; Z.J.Liu5419 and 2012052955 in the National Orchid Conservation Center of China, Shenzhen, China.

5.6.3 Baicarpus gracilis (Fig. 5.34a–e)

Specific Diagnosis: Fructification 12–18 mm long, 12–18 mm wide. Peduncle long and elegant. Projections long, curved.

Description: Two specimens of this species are studied (Fig. 5.34a, e). The fructifications are preserved as compressions embedded in yellowish siltstones (Fig. 5.34a, e). The fructifications are 12–18 mm long, 12–18 mm wide, each with a long peduncle (Fig. 5.34a, e). The peduncles are 7–12 mm long and 1.5–1.6 mm wide, with longitudinal vascular bundles, gradually intergrading to the gynobase (Fig. 5.34a, e). Gynobase is well-developed, 8–9 mm wide, with a convex center on which the fruits are attached (Fig. 5.34a, e). The projections are curved either outward or inward, 5.3–6.3 mm long, and with longitudinal curved vascular bundles (Fig. 5.34a, d). Each fruit includes a basal ovary and an apical style (Fig. 5.34a, c, e). The style is about 100 μm wide and 0.8 mm long, uniform in width, smoothly attached to the conical ovary tip (Fig. 5.34c). The ovary is 2.5–3.3 mm long, 1–1.6 mm thick (between adaxial and abaxial sides) (Fig. 5.34a, c, e). The remains of the pericarp is still attached to the seed (Fig. 5.34b).

Etymology: Gracilis for slenderness of the peduncle and projections.

Remarks: This species is different from the preceding species in slenderness of peduncle and projections

Holotype: PB21630 (Fig. 5.34a).

Additional specimen: PB21629 (Fig. 5.34e).

Depository: the Nanjing Institute of Geology and Palaeontology, CAS, Nanjing, China.

Fig. 5.33 (continued) seed surface, enlarged from the rectangle in (c). Note the different wall thickness, thin walls (arrows), and thick wall (cw) between patches of cells. Bar = 20 μm. Courtesy of Acta Geologica Sinica

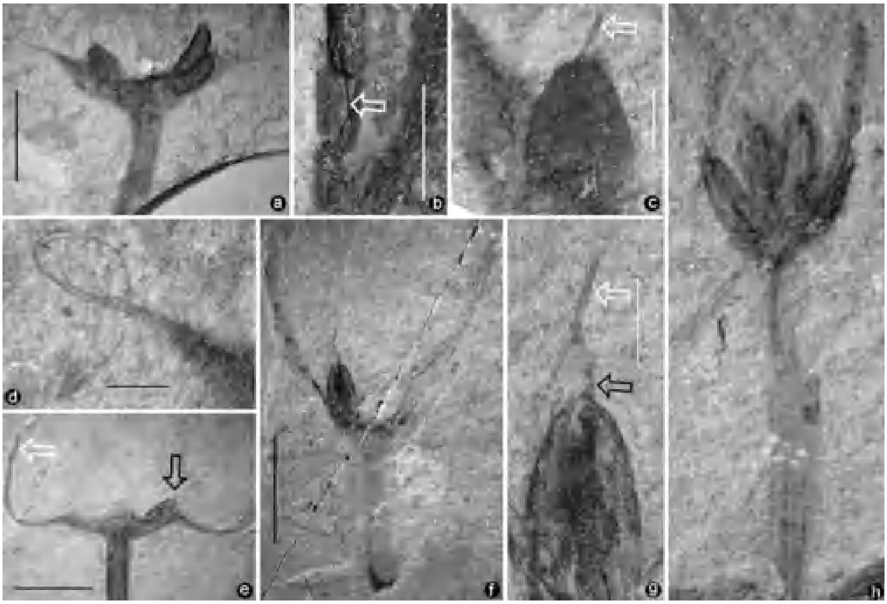

Fig. 5.34 Further details of Baicarpus. (a–e) B. gracilis; (f–h), B. robusta. (a) A mature fructification with attached fruits. Bar = 5 mm. (b) Detailed view of fruit arrowed in a. Note the pericarp covering the seed (s). Bar = 1 mm. (c) Detailed view of the left fruit in a, with persistent style (arrow). Bar = 1 mm. (d) Tendril-like terminal of the left projection in a. Note the curving vascular bundles. Bar = 1 mm. (e) A mature fructification with only one fruit (black arrow) attached and curved projection (white arrow). Bar = 5 mm. (f) A mature fructification with only one attached fruit. Note the robust projections (arrows). Bar = 5 mm. (g) Detailed view of the fruit in f. Note the persistent style (white arrow) and a seed with a terminal peak (black arrow) in fruit. Bar = 1 mm. (h) A mature fructification with attached fruits and only one projection (arrow). Bar = 2 mm. Courtesy of Acta Geologica Sinica

5.6.4 Baicarpus robusta (Fig. 5.34f–h)

Specific Diagnosis: Fructification 11–18 mm long, 3.5–11 mm wide. Peduncle long and elegant. Gynobase poorly developed. Projections long and robust, slightly curved.

Description: Two specimens are collected for this species (Fig. 5.34f, h). The fructifications are preserved as compressions embedded in yellowish siltstones (Fig. 5.34f, h). The fructifications are 11–18 mm long, 3.5–11 mm wide (Fig. 5.34f, h). The peduncles are about 7 mm long and 0.9–1.2 mm wide, with longitudinal vascular bundles (Fig. 5.34f, h). Gynobase is not obviously expanded (Fig. 5.34f, h). The projections are strong and straight, 3.4–10 mm long, and with longitudinal curved vascular bundles (Fig. 5.34f, h). The number of fruits may vary from one to three due to preservation (Fig. 5.34f, h). Each fruit includes a basal ovary and an apical style, attached on the gynobase (Fig. 5.34f, h). The style is about 130 μm wide and 1 mm long, smoothly attached to the conical ovary tip (Fig. 5.34g). The ovary is 1.8–4 mm long, 0.7–1.5 mm thick (between adaxial and abaxial sides) (Fig. 5.34f–h). There is a beak on the seed terminal (Fig. 5.34g).

Etymology: robust- for strong projections.

Remarks: This species is different from the preceding species in strong and straight projections, and weakly developed gynobase.

Holotype: PB21633 (Fig. 5.34f).

Additional specimen: PB21631 (Fig. 5.34h).

Depository: the Nanjing Institute of Geology and Palaeontology, CAS, Nanjing, China.

5.6.5 General Remarks

The number of fruits per fructification may be three or more. Those with fewer fruits attached are probably due to poor preservation. The spatial relationship among the three fruits seen in Fig. 5.32a suggests that at least one fruit is missing in this fossil. Future studies may shed on more light on actual number of fruits per fructification.

The number of ovules per carpel is very likely to be one since, except some ovules might have been aborted, which is not a rare case (Stevens 2008), normally, the number of ovules corresponds to that of the seeds. This conclusion is open to further confirming.

Yang and Wang (2013) published a new species, Ephedra carnosa, from the Huangbanjigou Village, Beipiao, Liaoning, based on two specimens. In their documentation there was no evidence showing the claimed key ephedraceous features, including outer envelope, outer envelope opening, and micropylar tube in their specimens. Considering that the outer integument has been documented in various fossil materials preserved in different status (Rydin et al. 2006a; Rydin and Friis 2010; Wang and Zheng 2010a), lack of such information in Ephedra carnosa makes their treatment dubious. Their specimens share several features, including general organization, fruit with style, projection, and seed beak, with Baicarpus. The conspicuous projections shared between their and our specimens have no counterpart in extant Ephedra. Further investigation is needed to test the actual affinity of Ephedra carnosa, and whether Ephedra carnosa has anything to do with Baicarpus is still an open question.

5.6.6 Affinity

Several features point to the angiospermous affinity for Baicarpus.

1. Its general organization is angiosperm-like. The parts appear to be arranged radially and concentrated on the receptacle, and thus different from the typical cone structure in Cycadales, Coniferales, Welwitschiaceae, Gnetaceae, Bennettitales, and Pentoxyales (Chamberlain 1957; Bierhorst 1971; Biswas and Johri 1997; Taylor et al. 2009). The non-cone-like structures in Ginkgoales or Ephedraceae (Zhou 2003, 2009; Wang and Zheng 2010a) show no resemblance to Baicarpus, either. Baicarpus show no resemblance to any contemporaneous fossil plants, such as Caytoniales, Corystospermales, and Czekanowskiales (Harris 1933, 1935, 1940; Axsmith et al. 2000; Zan et al. 2008).
2. Reproductive organs with persistent styles are a phenomenon rarely, if ever, seen in gymnosperms, but frequently seen in angiosperms. A style-like projection on the tip of a seed/fruit is a feature restricted to angiosperms (Eames 1961) and the so-called BEG (Bennettitales, Erdtmanithecales, Gnetales) clade in gymnosperms (Rothwell and Stockey 2002; Stockey and Rothwell 2003; Crane and Herendeen 2009; Friis et al. 2009; Rothwell et al. 2009; Wang and Zheng 2010a). Since the reproductive organs in these gymnosperm groups have a general organization different from Baicarpus and no trace of an outer integument or interseminal scales is seen in Baicarpus, it is hard to relate Baicarpus to any known gymnosperm taxon. I have to interpret the apical projection on the fruit as a persistent style rather than a micropylar tube, as this is also in line with analysis of other characters of Baicarpus.
3. Gymnospermous seeds are normally naked, without an additional separated enclosing layer. The seeds in Baicarpus are encapsulated in a separate layer of tissue (Fig. 5.33a–c). Even if this were taken as an equivalent of the outer integument in Gnetales, it would bracket the “style” or “inner integument” (Rydin et al. 2006a; Friis et al. 2007, 2009), a feature not seen in the specimens of Baicarpus. This layer is adnate to the seed on the abaxial side, but separated on the adaxial side in Baicarpus (Fig. 5.3a–c), a phenomenon not expected in Ephedra. This feature is seen and expected angiosperms, in which, by definition, the seeds/ovules are encased in the ovaries.
4. The unique feature of Baicarpus distinguishing itself from all above gymnosperms is the beaked seed in the ovary (Fig. 5.34g). This feature is also clearly seen in Fig. 4e of Yang and Wang (2013). The micropylar tubes of seeds placed in the so-called BEG clade are similar to the seed beak in Baicarpus, however, their micropylar tubes are directly exposed to exterior space whereas the seed beak in Baicarpus is in the ovary. Similar seeds with protruding integument have been seen, for example, Leucosyke, Myriocarpa (Urticaceae), and Sarcandra (Chloranthaceae) (Fagerlind 1944; Meeuse 1963). A similar structure is also seen in one of the fossil plants (Lidgettoniopsis ramulus (Dictyopteridales), Fig. 4b of Ryberg et al. 2012).

5. The spirally arranged scars of the floral parts on the receptacle further strengthen the angiospermous affinity of Baicarpus, although not a defining feature of angiosperms. Such a dense arrangement of appendages is frequently seen in angiosperms but rarely in gymnosperms.

5.6.7 Comparisons

Baicarpus is different from all angiosperms recognized from the Lower Cretaceous Yixian Formation. Chaoyangia, Archaefructus, Sinocarpus, Callianthus, and Liaoningfructus have already been reported from the Formation (Duan 1998; Sun et al. 1998, 2001, 2002; Leng and Friis 2003, 2006; Ji et al. 2004; Dilcher et al. 2007; Wang and Han 2011). Baicarpus is different from Archaefructus in flower-like organization, one-seeded fruit, gynobase, projections, and well-defined styles (Sun et al. 1998, 2001, 2002; Ji et al. 2004; Wang and Zheng 2012). Baicarpus is similar to Sinocarpus (Leng and Friis 2003, 2006; Dilcher et al. 2007) in the star-like arrangement of fruits, but differs in the one-seeded fruit, gynobase, projections, and well-defined styles. It is similar to Chaoyangia (Duan 1998) in its well-defined style, one-seeded fruit, and fruits surrounded by the gynobase, but differs in fruit aggregation, projections, and lack of hairs. Baicarpus differs from Callianthus (Wang and Zheng 2012) in fruit aggregation, style morphology, gynobase, projections, stout peduncle, lack of male part, and lack of fruit-covering fleshy envelope. Baicarpus differs from Liaoningfructus (Wang and Han 2011) in the number of seeds per fruit, fruit aggregation, fruit and style morphology, gynobase, projections, and stout peduncle. Therefore, Baicarpus is a taxon of early angiosperms from the Yixian Formation that has produced various fossil angiosperms.

Among extant angiosperms there are a few apocarpous taxa that show a certain superficial resemblance to Baicarpus, although detailed comparison eliminates any relationship between them and Baicarpus. Magnoliaceae, Illiciaceae, Crassulaceae, Phytolaccaceae, Dilleniaceae, Ranunculaceae, Rosaceae, and Triuridaceae (Judd et al. 1999; Zhang et al. 2004) demonstrate radial symmetry, distinct floral parts, apocarpy, superior ovary, distinct style, and star-like aggregate of fruits. However, detailed comparison of characters, including the arrangement of carpels/fruits, gynobase, projections, ovule attachment, number of ovules per carpel, and style position, distinguish Baicarpus from these families except Spireae in Rosaceae (Judd et al. 1999; Wu et al. 2003; Zhang et al. 2004; Doyle et al. 2008; Stevens 2008). The arrangement of several fruits with elongated styles subtended by a whorl of parts seems to relate Baicarpus to Spireae (Fig. 5.35c). Such potential relationship deserves further testing in the future.

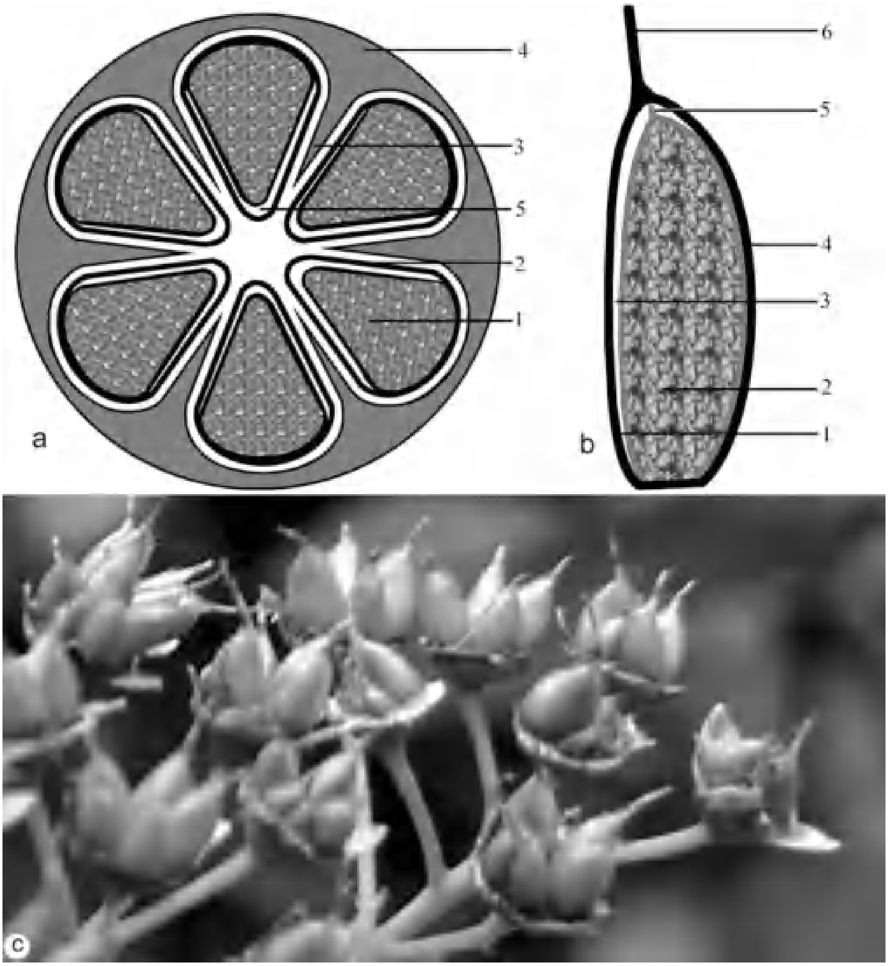

Fig. 5.35 Idealized rendering of *Baicarpus*. (a) Cross view of the fructification. 1, seed; 2, pericarp; 3, gynobase between fruits; 4, gynobase surrounding fruits; 5, ovarian space. (b) Longitudinal section of a fruit: 1, adaxial side of the fruit; 2, seed; 3, ovarian space; 4, abaxial side of the fruit; 5, seed peak; 6, persistent style. (c) Fruits of extant *Spirae*, similar to *Baicarpus*. Courtesy of Acta Geologica Sinica

5.6.8 Implications on Style Evolution

The lack of a style has been seen in some fossil angiosperms, such as *Archaefructus* (Sun et al. 1998, 2001, 2002; Ji et al. 2004; Wang and Zheng 2012) and *Sinocarpus* (Leng and Friis 2003, 2006; Dilcher et al. 2007), from the Yixian Formation. However, some other flowers such as *Chaoyangia* (Duan 1998), *Callianthus* (Wang and Zheng 2012), and *Baicarpus* from the same age have well-defined styles. The styles are smooth in *Chaoyangia* (Duan 1998) and *Baicarpus*, but hairy in Callianthus (Wang and Zheng 2009). Such diversity of styles in the Yixian Formation suggests that these styles are a result of long time evolution that antedates the Early Cretaceous, the age of Yixian Formation.

5.7 Nothodichocarpum

More and more fossils of angiosperms are recovered from the Early Cretaceous, including Chaoyangia, Archaefructus, Sinocarpus, Callianthus, Liaoningfructus, and Baicarpus from the Yixian Formation of Liaoning, China (Duan 1998; Sun et al. 1998, 2002; Leng and Friis 2003, 2006; Ji et al. 2004; Wang and Zheng 2009, 2012; Han et al. 2013). Among them, reproductive organs connected to branches and eudicot-type leaves had been still missing until recently when Nothodichocarpum was recovered from the Yixian Formation (Han et al. 2017).

The specimen of Nothodichocarpum is preserved as compression/impression with some coalified residue, 38 mm long and 21 mm wide, preserved on a slightly yellowish gray siltstone slab. The slab was recovered from the Dawangzhangzi, Lingyuan, Liaoning, China, where Sinocarpus decussatus and Archaefructus sinensis were recovered.

5.7.1 Generic Diagnosis

Distal portion of the plant including branches, leaves, and flowers. Branch slender, straight or slightly curving, with evident nodes. Branches axillary, subtended by leaves. Leaf elongated oboval, petiolate, with pinnate reticulate venation and an attenuated tip. Petiole slender and straight, smoothly transitional to rigid midrib. Leaf margin with distantly spaced teeth. Both female and male parts present, lacking perianth. Male parts opposite or alternate with the carpels/follicles, composed of a slender filament and a long anther. Gynoecium composed of two divergent carpels. Each fruit lacking an obvious style. Fruit follicular, divergent, enclosing two rows of seeds inserted along the dorsal.

Type species: Nothodichocarpum lingyuanensis

Etymology: Notho-, for false in Latin; -dichocarpum, for Dichocarpum, an extant genus in Ranunculaceae similar to this fossil.

5.7.2 Nothodichocarpum lingyuanensis (Figs. 5.36–5.39)

Specific diagnosis: the same as the genus.

Description: The distal portion of the plant is preserved as compression/impression, 38 mm long and 21 mm wide, including branches, leaves, flowers, and "follicles" (Fig. 5.36a). There are two oppositely arranged leaves at the bottom and a branch inserted in one of the leaf axils (Figs. 5.36a and 5.37). Approximately 19 mm above the first node there is another node, which demonstrates the same branching pattern (Fig. 5.36a). The major branch is rigid, with fine longitudinal striations, slightly tapering distally, approximately 0.8 mm wide and wider than all other branches (Figs. 5.36a and 5.37). The leaves at the bottommost node are larger than others in the same fossil, up to 22 mm long, with a strong petiole (Figs. 5.36a and 5.37). The leaf at the node just above the bottommost one is approximately 17 mm long and 3.2 mm wide (Fig. 5.36a). The leaves are symmetrical, narrow obovate, with acute apex, decurrent acute base, and toothed margins (Figs. 5.36a–c and 5.37). The sparse teeth are more concentrated to the distal portion of the leaves (Fig. 5.36b, c). The midrib is moderate, slightly curving (Fig. 5.36b, d). The leaves have pinnate venation (Fig. 5.36d). Male and female parts are concentrated on the termini of the branches (Figs. 5.36a, c, f and 5.37). The branch in the bottommost leaf axil gives rise to a flower, and is terminated by a pair of follicles (Fig. 5.36a, g). Perianth is lacking (Fig. 5.36a, c, f–h). At least two male parts may be preserved in a flower (Fig. 5.36f, g). Some male parts are opposite the carpels, whereas others alternate the carpels (Figs. 5.36f, g and 5.38a). Each male part may be subtended by a strap-shaped bract, including a filament and an anther, both of which are relatively straight in the flowering stage but become curving in the fruiting stage (Figs. 5.36f–g, i and 5.38). When mature, the filament is approximately 3.5 mm long and 0.1 mm wide, and the anther is approximately 2.2 mm long and 0.35 mm wide (Fig. 5.36f, g, i). Some of the male parts are appressed against the carpels initially but well separated from them later (Figs. 5.36g and 5.38). No in situ pollen grains are seen in the anther. The carpels are in pairs, located in the center of the flowers, slightly coalescent basally, divergent at the distal, lacking styles, more or less lanceolate in shape, 4–8 mm long and 0.8–2.8 mm wide (Fig. 5.36f–h, j–k). Numerous ovules are present inside the carpels (Fig. 5.36g, j, k). Each "follicle" has a curving ventral side and more or less straight dorsal side, enclosing multiple seeds (Fig. 5.36g, j, k). The seeds are approximately 1.4 mm long and 1 m wide, and arranged in two rows along the dorsal vein of the fruit (Fig. 5.36g, j, k).

Etymology: lingyuan-, for Lingyuan, the fossil locality.

Holotype: HGP038.

Type locality: Dawangzhangzi, Lingyuan, Liaoning, China (41°15′N, 119°15′E).

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

Depository: the Palaeontological Center, Bohai University, Jinzhou, China.

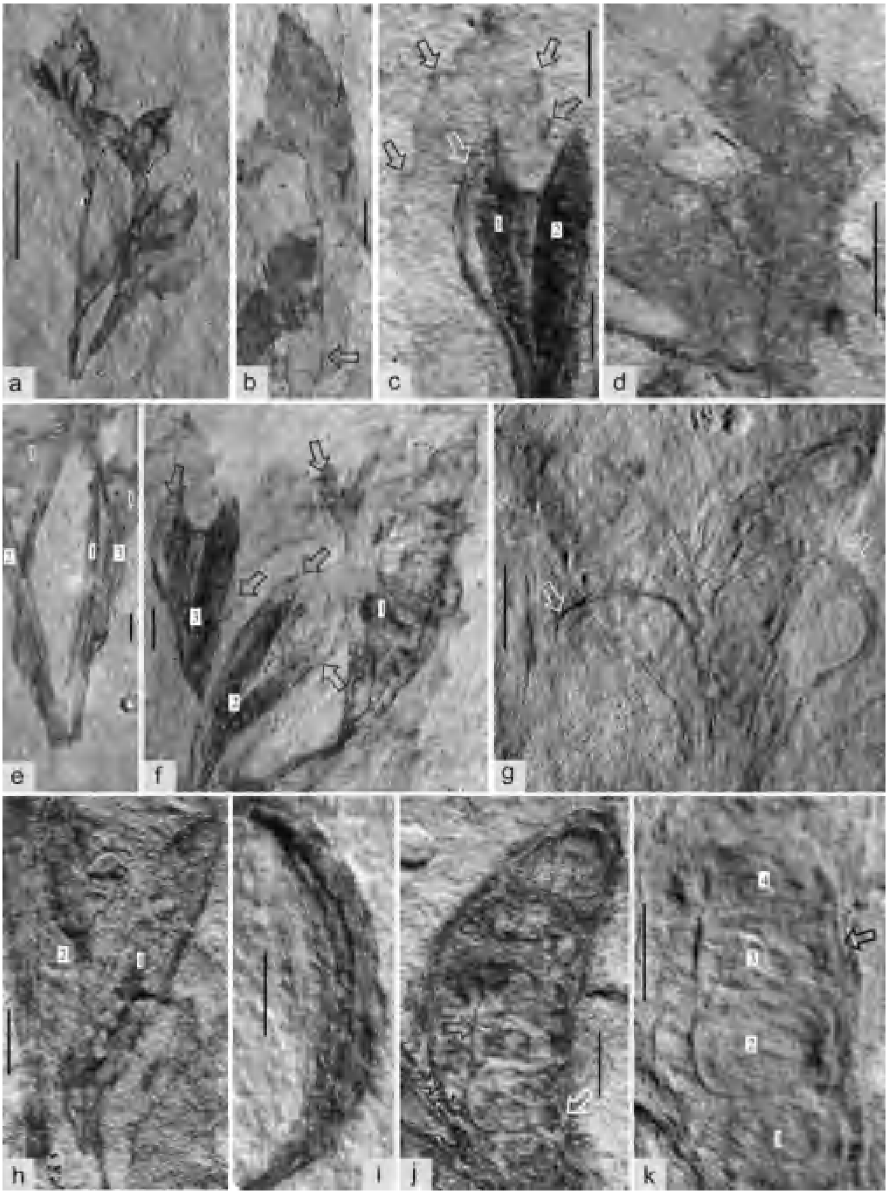

Fig. 5.36 Holotype of Nothodichocarpum and its details. HGP038. (a) Holotype including branches, leaves, and flowers. Refer to Fig. 5.37. Bar = 1 cm. (b) One of the leaves with midrib (arrow). Bar = 1 mm. (c) Another narrow obovate leaf with attenuated tip and several teeth (black arrows), overlapped by a young flower including two carpels (1, 2) and at least one male part (white arrow). Bar = 1 mm. (d) Pinnate venation in one of the leaves. Bar = 0.5 mm. (e) Opposite branching. Note the major branch (2), axillary branch (1), subtending leaf (3), and leaves (l). Bar = 1 mm. (f) Three flowers (1–3) of different developmental stages overlapping leaves. Note several male parts (arrows) beside carpels (dark lanceolate structures). Bar = 1 mm. (g) Two

5.7.3 Remarks

Only two male parts are clearly seen in the mature organs of Nothodichocarpum (Fig. 5.36g), but the total number of male parts may be up to four in Nothodichocarpum. This possibility is suggested by the position of male part relative to the female part (Figs. 5.36g and 5.38), e.g. one male part is opposite a follicle whereas the other is positioned between the two follicles. Furthermore, there are two scars (arrow in Fig. 5.38) left by fallen-off parts, which are arranged at the same level as the other male part and three of them are equal-distanced in Fig. 5.38. Considering presence of two carpels, four male parts can be inferred for each flower of Nothodichocarpum.

The ovules/seeds of Nothodichocarpum have smooth margins on the ventral side, implying that they are not connected to the ventral margin of the "follicles"/carpels (Fig. 5.36g, j, k). This character is in agreement with the near-dorsal position of the seeds in the "follicles" (Fig. 5.36g, j), and the ovule are inserted on the dorsal side of the fruit (Fig. 5.36k).

5.7.4 Affinity and Comparison

Angiosperms are distinguished from other seed plants by the enclosed ovules and seeds. Only enclosed ovules before pollination is a feature sufficient to ensure an angiospermous affinity for a plant (Tomlinson and Takaso 2002). The seeds of Nothodichocarpum are apparently enclosed by the fruit wall, suggesting an angiospermous identity for it. This conclusion is further strengthened by the ovules enclosed in the young carpels, thanks to the preservation of connected flowers and "follicles" in the same fossil. Both of these characters pin down the angiospermous affinity for Nothodichocarpum (Fig. 5.39).

The leaf morphology of Nothodichocarpum also provides additional information for its affinity. The leaves are oppositely arranged (Fig. 5.36a, e), unlike most basal angiosperms and monocots. In addition to angiosperms, reticulate venation has been seen in other plants, including Gigantopteriales, Dipteridaceae, Caytoniales, and some Bennettitales (Harris 1964, 1969; Sun 1981; Li et al. 1994). But these plants do not have enclosed ovules/seeds and thus have little to do with

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Fig. 5.36 (continued) divergent, basally coalescent "follicles" and two male parts (arrows). Note the spatial relationship between the follicles and male parts. Bar = 2 mm. (h) Two young basally coalescent carpels (1–2). Bar = 1 mm. (i) Detailed view of the right male part in g. Bar = 0.5 mm. (j) The right fruit in g, showing abutting seeds (black arrows) inserted along the dorsal vein (white arrow). Bar = 1 mm. (k) Four abutting seeds (1–4) in the fruit shown in g. Note seed 4 is apparently connected to the dorsal of the fruit (black arrow). Bar = 1 mm. Courtesy of Acta Geologica Sinica

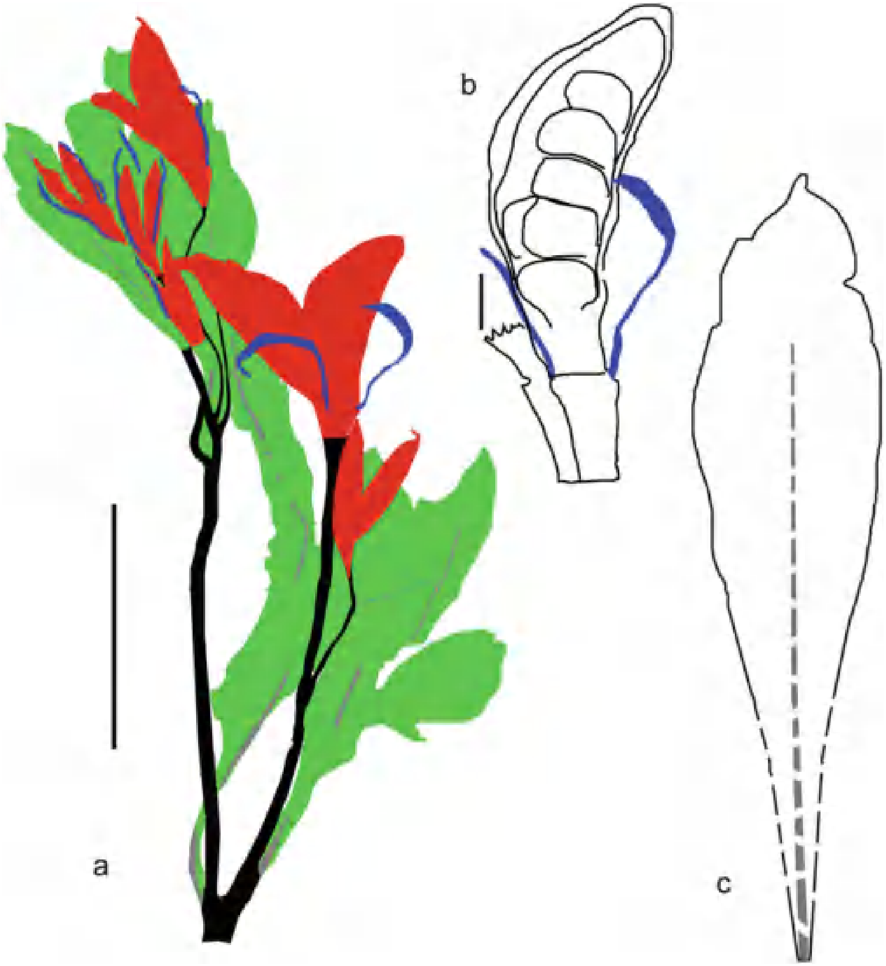

Fig. 5.37 Sketches of Nothodichocarpum. (a) Sketch showing the physical connection among various parts. Green: leaf; gray: leaf vein; red: follicle/carpel; black: branch; blue: male part. Bar = 10 mm. (b) The fruit shown in Fig. 5.36g, j. Note the seeds inserted onto the dorsal vein (right) and male part (blue). Bar = 1 mm. (c) Semi-idealized sketch of the leaf shown in Fig. 5.36c. Courtesy of Acta Geologica Sinica

Nothodichocarpum. Thus the only interpretation left for Nothodichocarpum is angiosperm.

Several fossil and extant plants share similar character assemblage with Nothodichocarpum. The gynoecium of Callianthus is characteristic of its two carpels, but Callianthus can be distinguished by its two characteristic divergent styles and its carpels surrounded by a fleshy layer (Wang and Zheng 2009). Sinocarpus demonstrates great resemblance to Nothodichocarpum in term of fruit morphology (Leng and Friis 2003, 2006). However, the leaves of Sinocarpus

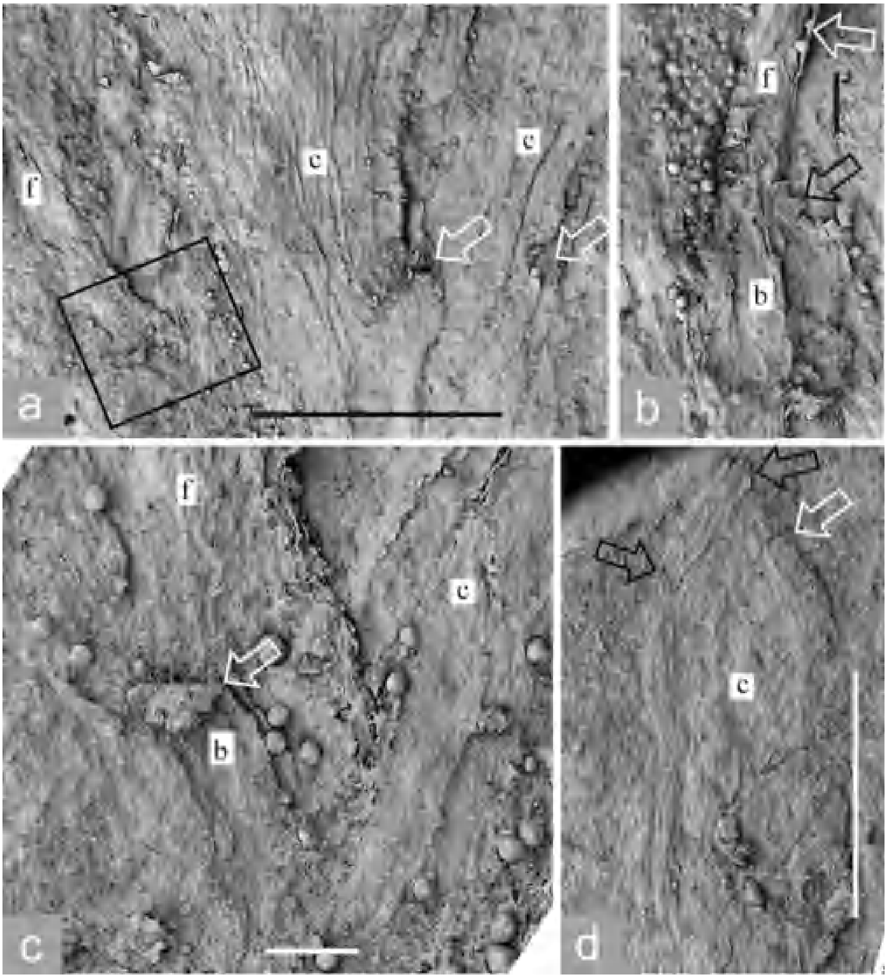

Fig. 5.38 Details of flowers under SEM. (a) Basal portion of the fruit shown in Fig. 5.36g. Note the scars left by fallen off male parts (arrows), and their spatial relationship with the carpel (c) and filament (f). Bar = 1 mm. (b) A filament (f) subtended by a bract (b). This male part corresponds to the one marked by left white arrow in a. Bar = 0.1 mm. (c) Detailed view of rectangle in a. Note spatial relationship among the bract (b), filament (f) in its axil, and carpel (c). Bar = 0.1 mm. (d) Detailed view of the fruit 2 in Fig. 5.36f. Note the relationship between the carpel (c, white arrow) and male part (black arrows). Bar = 1 mm. Courtesy of Acta Geologica Sinica

require further effort to confirm, its male parts are missing, and its seeds are borne on the ventral side of the follicles (Leng and Friis 2003, 2006). These factors prevent us from further comparison between Sinocarpus and Nothodichocarpum. Among the extant plants, Dichocarpum (Ranunculaceae) demonstrates the greatest similarity to Nothodichocarpum, in term of divergent follicles and pinnate leaf venation (Wu et al. 2001). However, the difference between these two genera are

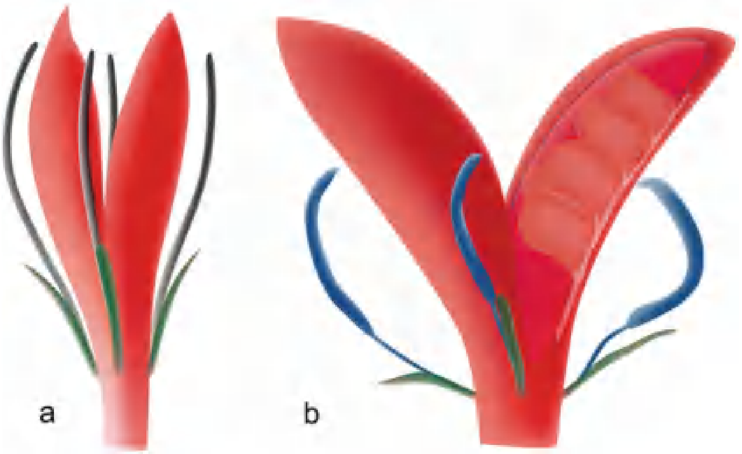

Fig. 5.39 Reconstruction of Nothodichocarpum flower/fruit in its flowering (a) and fruiting (b) stages. Note the dorsal vascular bundle connected with seeds in an opened fruit (b). Courtesy of Acta Geologica Sinica

equally obvious, for examples, the ovules are inserted along the ventral side of the fruit in Dichocarpum but along the dorsal side in Nothodichocarpum, the teeth are far too weak in Nothodichocarpum than in Dichocarpum, and the perianth obvious in Dichocarpum is missing in Nothodichocarpum. These differences make further comparison improper.

5.7.5 Implications on Flower Forming

Among seed plants, angiosperms are characterized by their flowers, in which male and female parts are frequently closely arranged. It appears that the whole male-female complex (flower?) in Nothodichocarpum is the aggregation of male and female shoot systems, namely, the male part and its subtending bract constitute a lateral complex, whereas the female part is the terminal shoot (Fig. 5.39). Although such spatial arrangement of these parts is not completely in accordance with the conception of a flower, it is possible that the aggregation of these two sexual shoots may have given rise to the angiosperm flower. The close arrangement of male and female parts in Nothodichocarpum is especially meaningful for the derivation of the flower. If this aggregation scenario were true for flower-forming, then the assumed distinction between flowers and inflorescences would disappear: both are shoot systems with different degrees of aggregation, fusion, and reduction. This helps to resolve the once-heated debate on whether Archaefructus has flowers or inflorescences.

The dorsal insertion of ovules/seeds in Nothodichocarpum is surprising for many and may shed some otherwise unavailable light on the origin of carpels in angiosperms. Previously, the ovules/seeds have been reported inserted on the dorsal veins of the carpel wall in Archaefructus (Ji et al. 2004; Wang and Zheng 2012). Here Nothodichocarpum once again has its ovules/seeds inserted on the dorsal vein of the carpel wall. Among the living plants, Brasenia (Cabombaceae) bears ovules on the dorsal side of the carpel, forming contrast against many basal angiosperms with ovules along the ventral side of the carpel (Eames 1961; Endress 2005). The latitude of ovule insertion in carpels of both early angiosperms and basal angiosperms suggests that the placenta in angiosperms is a part independent of the carpel wall and may freely fuse with the latter in various ways, as suggested by function gene study (Skinner et al. 2004) and morphological studies (Liu et al. 2014; Zhang et al. 2017). This conclusion is at odds with the Euanthium Theory, in which the ovules are assumed borne along the margins (ventral veins) of the so-called “megasporophylls” (Arber and Parkin 1907). It appears that there are increasing evidence underming the validity of the Euanthium Theory.

5.7.6 Development

Nothodichocarpum has flowers/fruits preserved in different developmental stages (Fig. 5.36a, f–h), allowing us to envision the development of the flowers/fruits. The male parts and carpels occur side by side in their early stage, but later, the male parts become curved and separated from the carpels/“follicles”. The carpels in their early stage are lanceolate or linear, enclosing smaller ovules, and they become more inflated and divergent, convex on the ventral side and straight on the dorsal side, and enclosing bigger seeds in later development. Such changes in the ovule/seed and fruit imply that Nothodichocarpum invests little in its ovules before pollination and that the ovules do not develop until after pollination, a strategy adopted by many angiosperms (Leslie and Boyce 2012).

Nothodichocarpum shares opposite phyllotaxy with basal angiosperms (including Amborella (Buzgo et al. 2004) and Chloranthaceae (Taylor and Hickey 1996)) as well as early angiosperms (including Chaoyangia (Duan 1998), Archaefructus (Wang and Zheng 2012), and Sinocarpus (Leng and Friis 2003, 2006)). Amborella, the basalmost angiosperm (Qiu et al. 1999; APG 2009), has a decussate arrangement in its early development and spiral arrangement when mature (Buzgo et al. 2004). Chaoyangia, a monoecious tricarpous angiosperm producing monocolpate pollen grains (Duan 1998), is frequently wronged as Gnetales due to its decussate branching pattern. Recent re-examinations of Archaefructus indicated that this early angiosperm also has a whorled or at least opposite arrangement of “follicles”/carpels (Sun et al. 2002; Wang and Zheng 2012). Apparently, opposite/decussate branching pattern is a character widespread among early angiosperms (Nothodichocarpum, Chaoyangia, Sinocarpus, and Archaefructus) as well as basalmost angiosperm (Amborella), implying either that such a branching pattern is not idiosyncratic of Gnetales as assumed previously, or that these two groups share a common ancestor in their history.

5.7.7 Summary

Nothodichocarpum is an element of diversified angiosperms in the Yixian Formation. The dorsal ovule insertion in *Nothodichocarpum* and its decussate branching pattern shared with early angiosperms and basalmost extant angiosperm challenge the prevailing Euanthium Theory, prompting botanists to be cautious of the classical botanical theories.

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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 and Southern Germany. *Schmeissneria*, *Xingxueanthus*, *Solaranthus*, *Euanthus*, *Juraherba* and *Yuhania* are female or bisexual organs of plants found in the Middle Jurassic in China and the Early Jurassic in Germany. All of them demonstrate the existence of enclosed ovule in the organ, satisfying the criterion for angiosperms. Among them, *Schmeissneria* is seen in both China and Europe, and thus sheds 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*. 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

X. Wang, *The Dawn Angiosperms*, Springer Geology,
DOI 10.1007/978-3-319-58325-9_6

In arenaceo Keuper dicto ad Reundorf prope Bambergam.

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 Fig. 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. 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 assemblage 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 organ. Although winged seeds were never 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 bear 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. 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 untouched 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. 2007a, b), 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 one day I read the article by Kirchner and Van Konijnenburg-Van Cittert (1994).

Combining the information in the paper and my own, I wrote a paper on Schmeissneria, in which I boldly tried to emend a newly established genus. Rejected in early 1995, the work was suspended until 2005 when I returned to China from the US after I earned my Ph.D degree 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. 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 an angiosperm 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), twenty-six 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. (2007a, b). Furthermore, flowers in anthesis and fruits 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 chimeric plant. A recent error of this sort was a plant reconstructed by Pedersen et al., as pointed out by Rothwell et al. (2009) and Tekleva and Krassilov (2009). The lesson is that we can only have faith in those reconstructions based on connected plant parts. All other reconstructions should be viewed with caution. The sign that

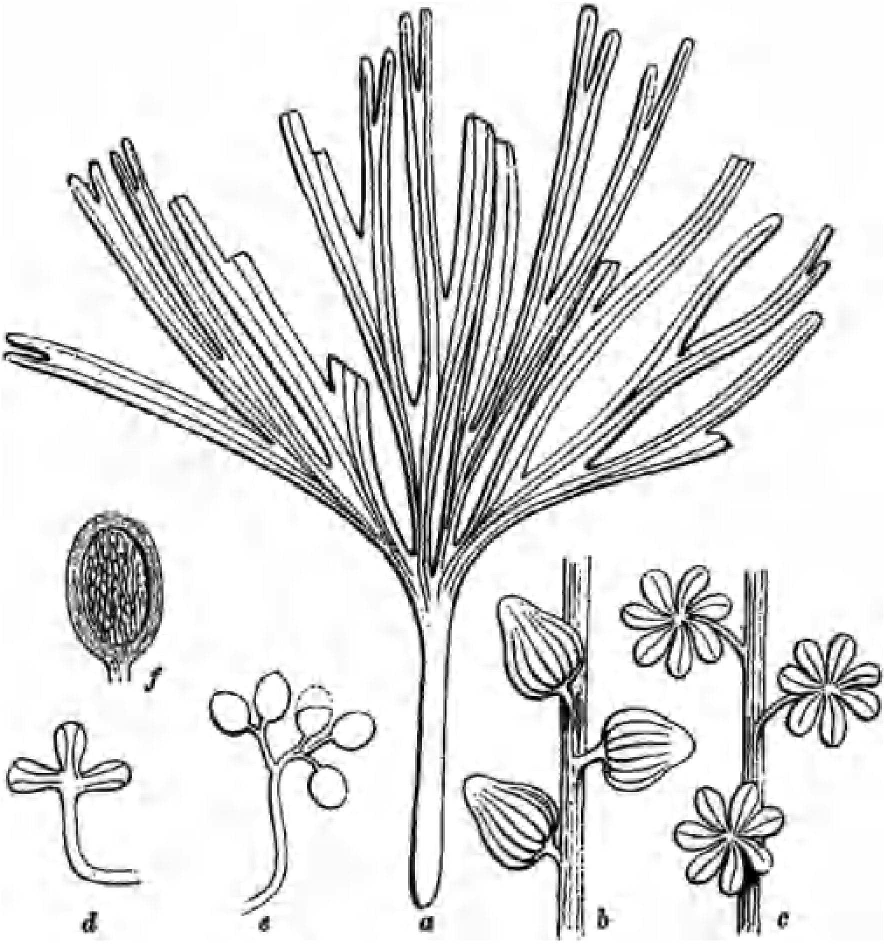

Fig. 6.1 Schmeissneria microstachys (b) was once thought to be a male organ (c) of Baiera (a) in its early development (from Schenk 1890)

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)

Schmeissneria had been erroneously assigned to Ginkgoales started to emerge about the time the new genus Schmeissneria 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 (Fig. 6.2).

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, as seen later in this chapter, the so-called wings in Schmeissneria lack features of a typical seed wing 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 of Schmeissneria, while a normal seed wing usually has well-defined veins. Even if the longitudinal hairs were taken as veins, it would appear that the wing of Schmeissneria 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 junction with a seed. The presence of hairs (according to my interpretation) covering the surface of the so-called seed (Fig. 6.14b, d) conflicts with this

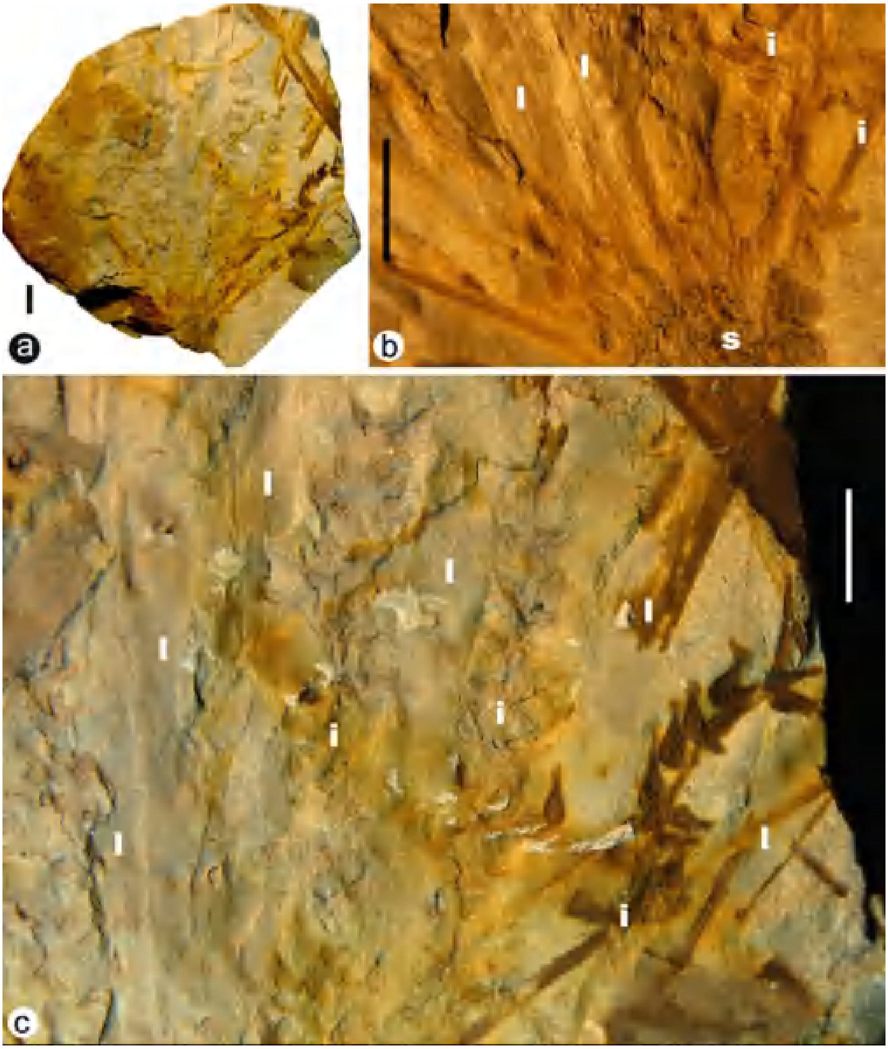

Fig. 6.3 A specimen of *S. microstachys* showing physically connected short shoot, leaves, and female inflorescences in various developmental stages. GDPC 122K04. (a) The specimen in general. Bar = 1 cm. (b) Physical connection among the short shoot (*s*), leaves (*l*), and inflorescences (*i*). Bar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

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

Table 6.1 Comparison of terms used in previous descriptions and this book of Schmeissneria

Kirchner and Van Konijnenburg-Van Cittert (1994)	Wang et al. (2007a)	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

(45 cm × 32 cm) with more than 45 infructescences with more than 1000 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.

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, while the author will not distinguish between them in the following discussion on Schmeissneria, they are distinguished from each other in figure captions.

Recent studies of the German specimens deposited in BSPG, SSPC, and GDPC have yielded more information about Schmeissneria microstachys, including flowers 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 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 on the same plant are less obvious 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 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. 6.3c, 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 mm 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 development. One of these young flowers appears round-triangular in shape in longitudinal profile, with less conspicuous longitudinal ribs (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 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 an imprint on the ovary wall (Fig. 6.12c). It is interesting that

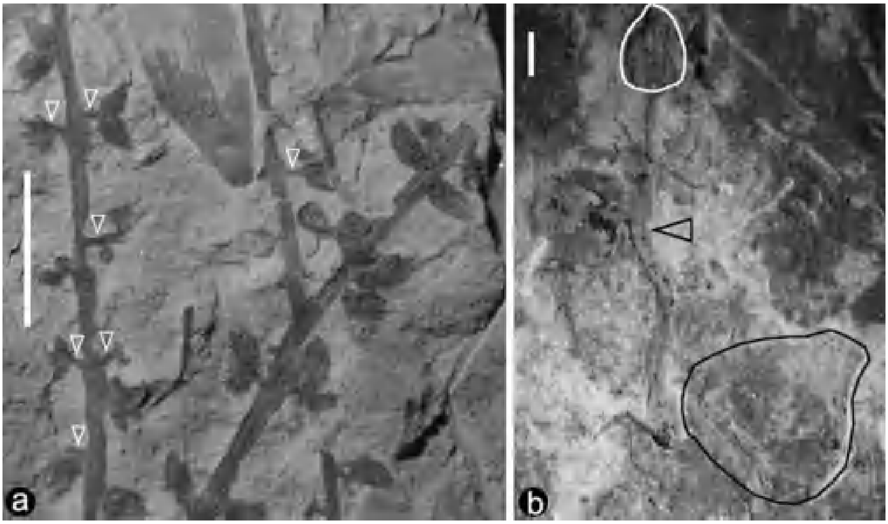

Fig. 6.4 Inflorescences. (a) Three female inflorescence of S. microstachys preserved on the same specimen. GDPC S1K97. Note the common stalk (arrows) shared by two flowers. Bar = 1 cm. (b) Apical portion of a female inflorescence of S. sinensis. Note the inflorescence axis (arrow), and flower size decreasing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

the ovary apex in young flowers is closed and a septum separates the ovary into two locules (Figs. 6.12c and 6.13b–d).

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, the so-called "wing" is highly variable and lacks a consistent morphology (Figs. 6.3c, 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 fanned 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, the distribution of hairs all over the ovary (Fig. 6.14b, d) is hard to conceive. These all contradict the 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. 2007a). 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 to capture pollen grains during pollination. The occurrence of pollen grains on the distal inner surface of the tepals in S. sinensis (Fig. 3j–o, Wang et al. 2007a) is in line with this hypothesis. Interestingly, parallel to this, hairs are also seen on carpels of Urticaceae (Fig. 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 overlooked until recently, although evidence has been available for over a century. The specimen studied by Schenk (Fig. 6.11a) a large slab of sandstone from Veitlahm, about 45 cm by 32 cm. Despite more than 45 infructescences with at least 1000 in situ seeds on this single specimen, they were ignored or downplayed by Schenk, probably because he thought 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 crucial information on fruits of Schmeissneria again was not explored.

Reexamination of the specimen revealed that among the forty-five infructescences, 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. 6.11c, d and 6.17a–d).

6.1.3.5 Enclosed Seeds/Ovules

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 seeds (Fig. 6.18f) and presence of micropyles on the seeds (Fig. 6.18a–c). In short, the oval bodies within the fruits are fossil seeds of Schmeissneria. So in situ seeds have been identified in Schmeissneria.

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 mean that the corresponding ovule is always enclosed. A good example for this is that 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. 2006a, b; Taylor and Taylor 2009). Therefore, to make a convincing case for Schmeissneria′s angiospermous affinity, enclosed seed alone is 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 sinensis. 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 inner 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 or ovules). This interpretation is further strengthened by seeds found in situ in the basal portion of the fruits of S. microstachys (Fig. 6.17a–d). The internal empty space is never seen in ovules or seeds, therefore making Kirchner and Van Konijnenburg-Van Cittert′s (1994) winged seed interpretation less plausible.

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. 2007a, b; Wang 2010a, b), it is safe to say that the immature ovaries of Schmeissneria have two locules and a closed apex, probably before pollination. This is a feature only seen in angiosperms and is also a feature defining angiosperms (Tomlinson and Takaso 2002; Wang et al. 2007a, b; Wang 2009, 2010b).

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 blocked 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; Eriksson 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. (2007a, b). 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. 2007a, b; Wang 2010b). If Schmeissneria 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. (2007a, b).

Re-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) Wang

Type species: *Schmeissneria microstachys* (Kirchner and Van Konijnenburg-Van Cittert) Wang

Additional 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 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, 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.

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 basal openings pointing to the axis (Thomas 1925; Harris 1940, 1964; Reymanowna 1973; Nixon et al. 1994; Barbacka and Boka 2000; Wang

2010a); Leptostrobus has spirally arranged bivalvate multiple-seed-bearing cupules with slit-like openings (Krassilov 1972; Harris and Millington 1974; Liu et al. 2006); 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) Wang (Figs. 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, female inflorescence, and infructescence. 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

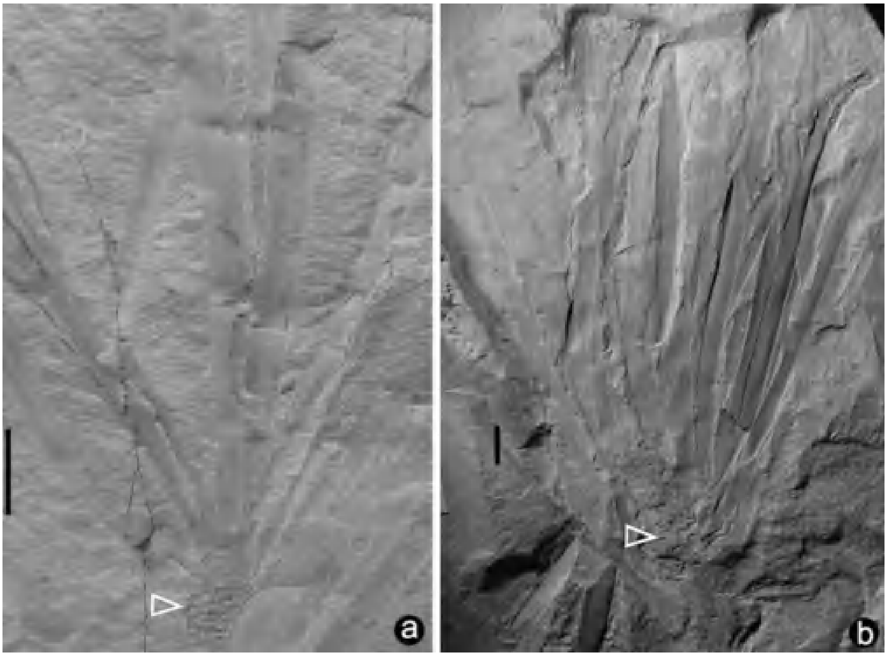

Fig. 6.5 Tufts of leaves attached to the apices of short shoots of S. microstachys. Note the leaf scars on the short shoot (arrow) and variation of the Glossophyllum-like leaves. SSPC G666/97, GDPC 111KI99. Bar = 1 cm

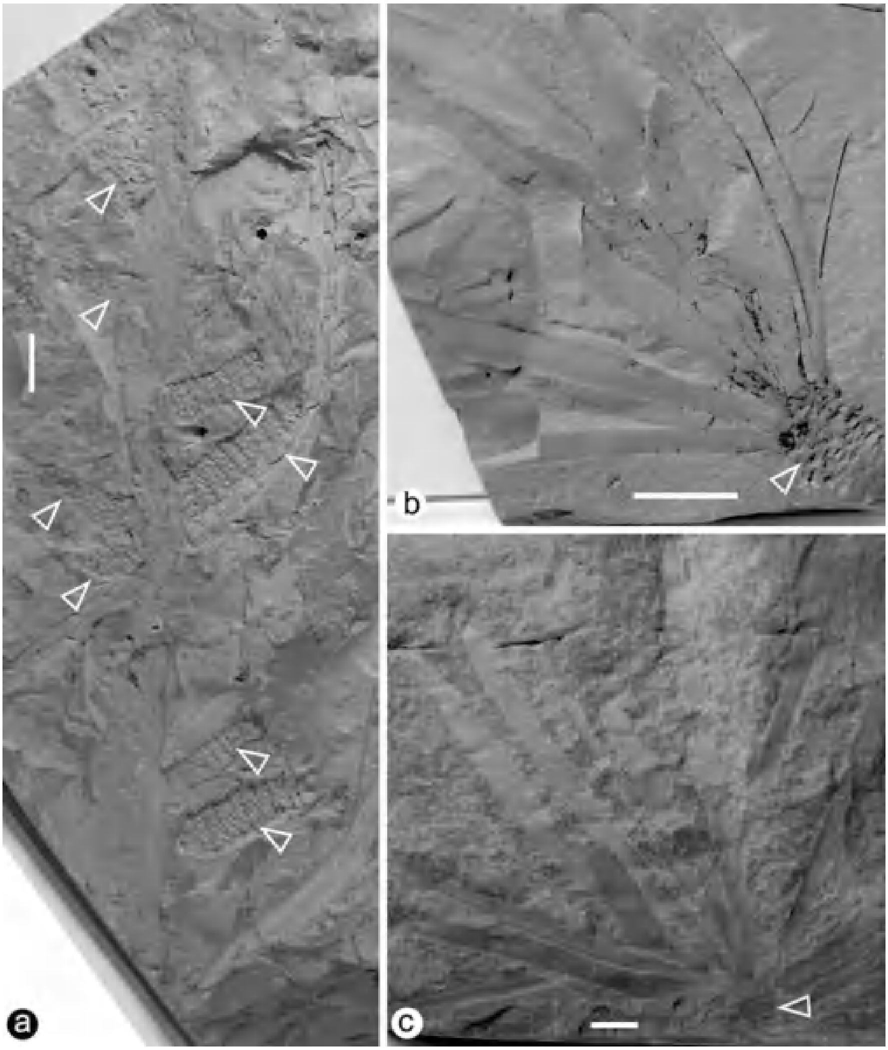

Fig. 6.6 Branches and leaves attached to short shoot of *S. microstachys*. (a) Long shoot with several short shoots (*arrows*) helically arranged. SSPC G254/90. Bar = 1 cm. (b, c) Tufts of leaves attached to the short shoots. Note the leaf scars on the short shoots (*arrow*) and the *Glossophyllum*-like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

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 shoots are at least 17.3 cm long and 6.2 mm wide (Fig. 6.6a–c). Short shoots are up to 8.8 mm in diameter and 2.65 cm long (Fig. 6.6a–c). Leaves are inserted on the apex of a

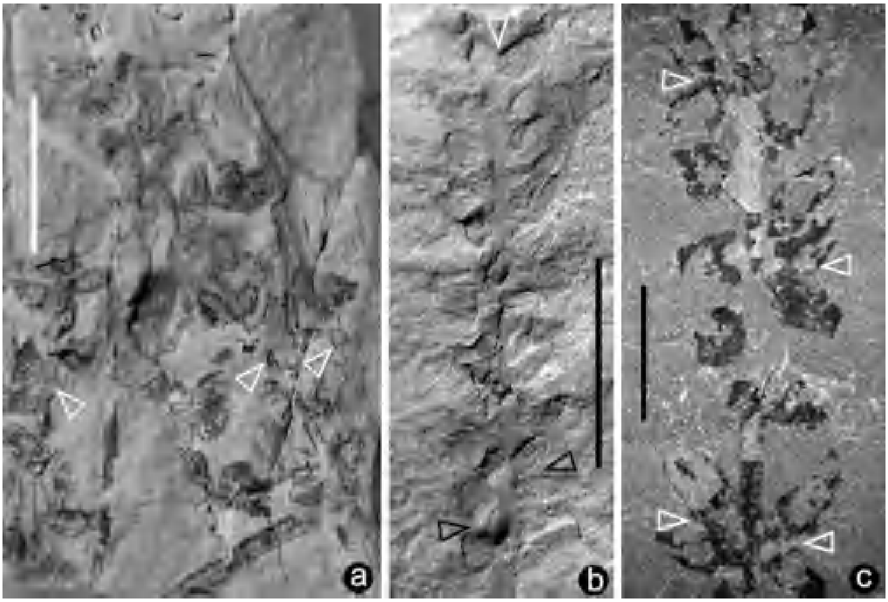

Fig. 6.7 Female inflorescences of *S. microstachys*. (a) Several coalified inflorescences (arrow) preserved in the same specimen. SSPC G111/90. Bar = 1 cm. (b) An inflorescence with several pairs of flowers (arrow). Note the longitudinal ribs on the flower surface. BSPG 2009 1 16. Bar = 1 cm. (c) A coalified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

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 6.7b, 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, and 6.16b–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

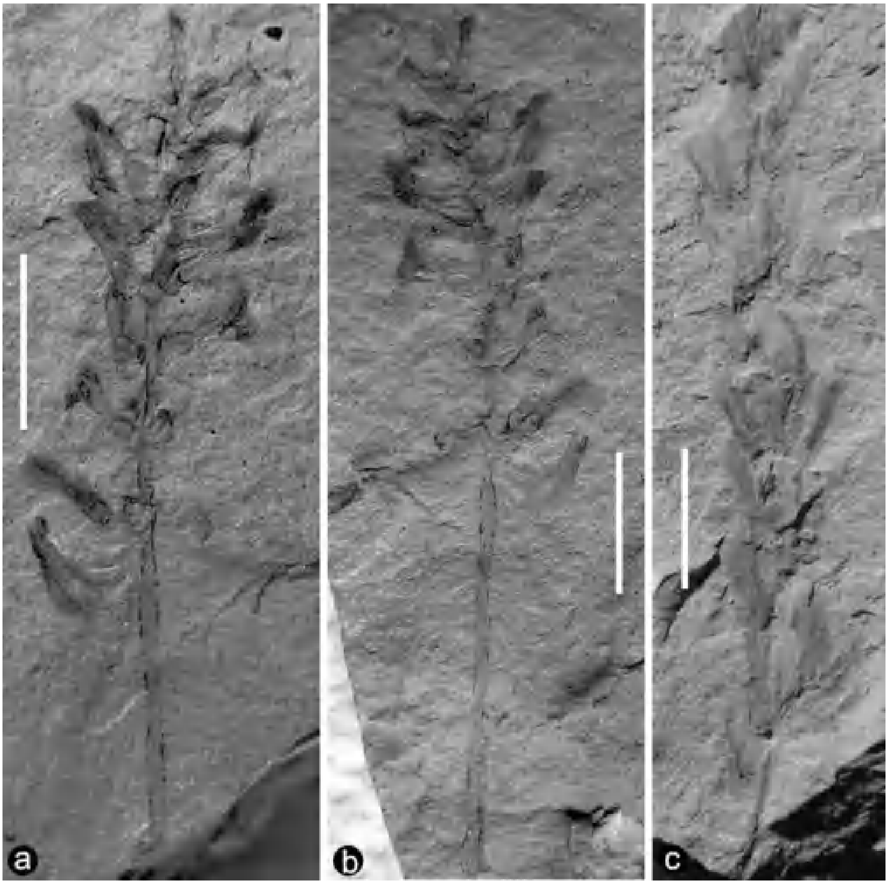

Fig. 6.8 Inflorescences of S. microstachys in anthesis. Note the hairs at the apices of the flowers. (a) Several flowers in the same inflorescence. SSPC G295/91. Bar = 1 cm. (b) The counterpart of the specimen in (a). BSPG 2009 1 19. Bar = 1 cm. (c) Another flowering inflorescence. Note the vertically oriented hairs. GDPC S3K97. Bar = 1 cm. Courtesy of Journal of Systematics and Evolution

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

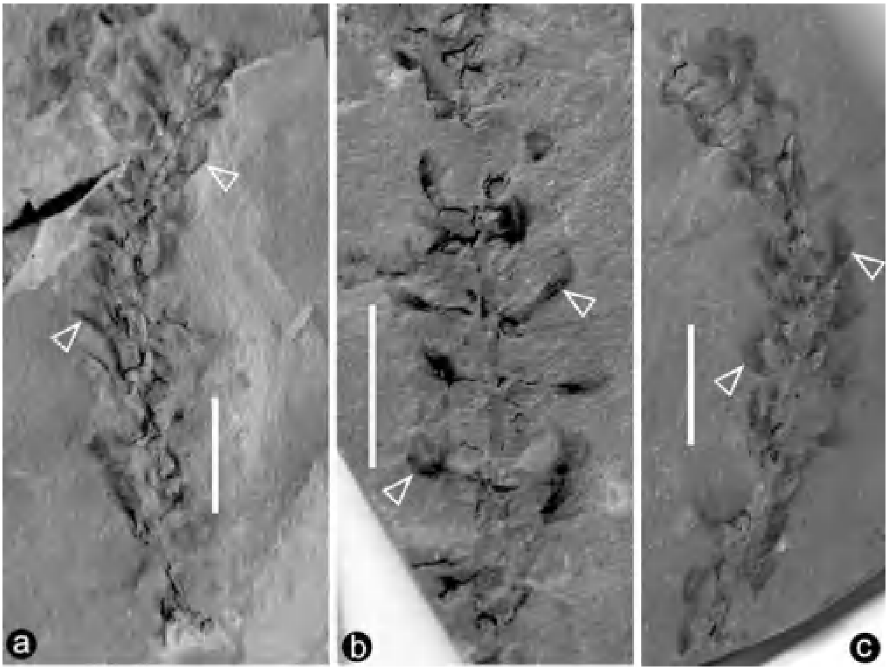

Fig. 6.9 Three inflorescences of *S. microstachys* in anthesis. Note the variable deployment of the hairs (arrow) at the apices of the flowers. (a) SSPC G288/91. (b) SSPC G316/91. (c) SSPC G303/91. Bar = 1 cm

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.

Additional 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.

Additional 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
(Figs. 6.4b, 6.12a–c, and 6.13a–d)

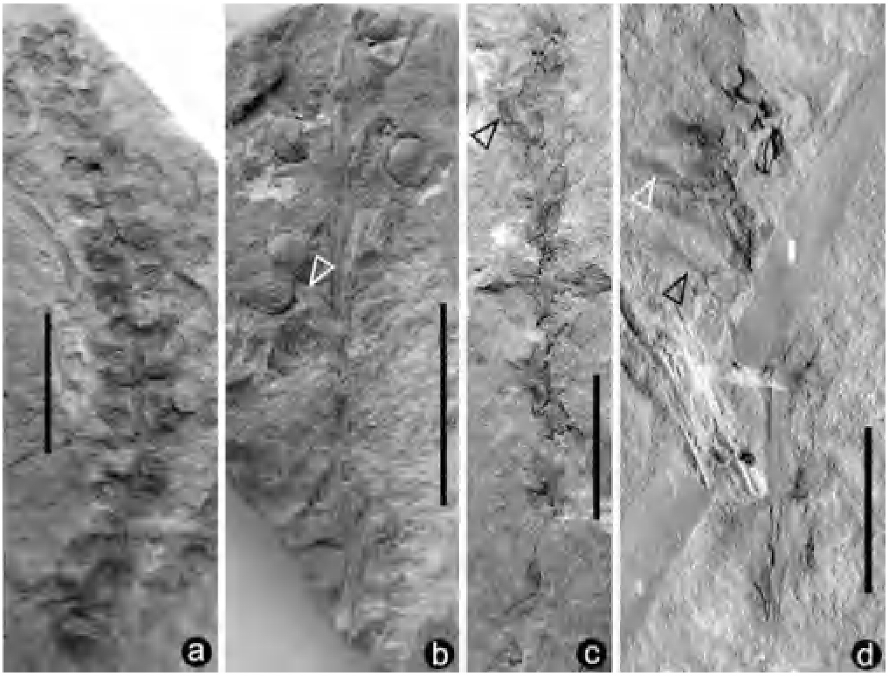

Fig. 6.10 Four female inflorescences of S. microstachys. Note the variable arrangement of the flowers. (a) An inflorescence with densely clustered flowers. Note the longitudinal ribs on the flower surface. BSPG. Bar = 1 cm. (b) The syntype of the genus. Note the long stalk (arrow) supporting the flower 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. Courtesy of Journal of Systematics and Evolution. (d) An inflorescence with blooming flowers (arrow) and associated leaf (l). BSPG 2009 1 18. Bar = 1 cm

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 (Fig. 6.12).

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 axes of the

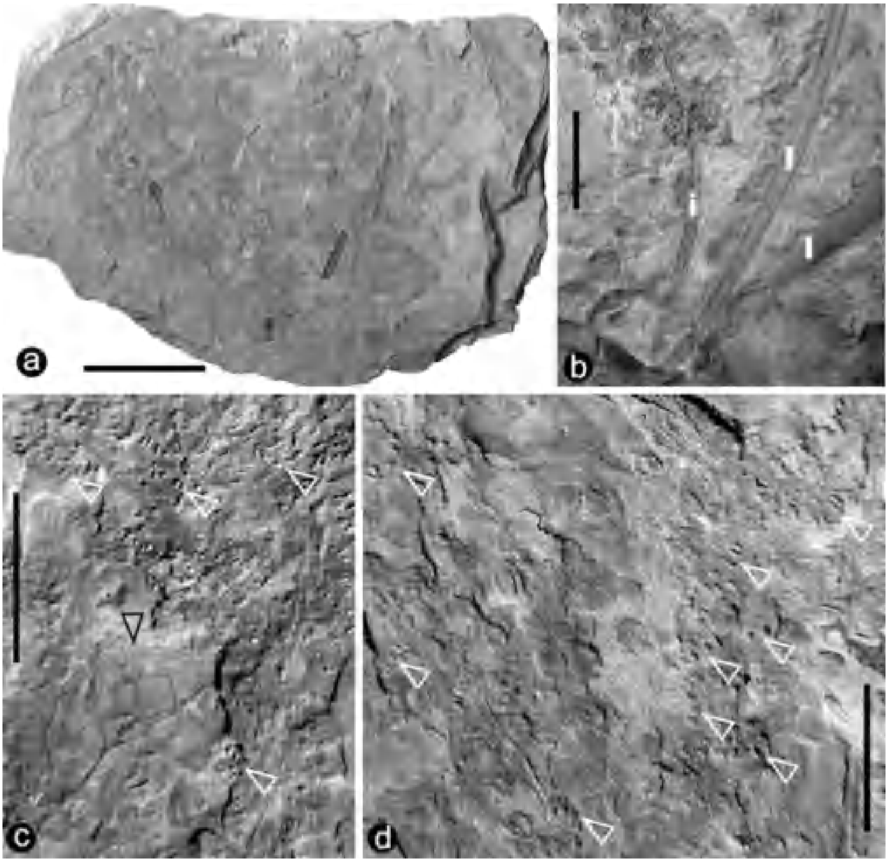

Fig. 6.11 Infructescences, fruits and in situ seeds of S. microstachys. BSPG 4713. (a) Sandstone slab with more than 45 infructescences on it. Bar = 10 cm. (b) Detailed view of the upper-right corner of the specimen in a, showing almost connected leaves (l) and infructescence (i). Bar = 1 cm. (c) A few 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 Journal of Systematics and Evolution

female inflorescences are up to 1.3 mm across basally and only 0.2 mm across apically (Fig. 6.12a). The inflorescence axis 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 (Fig. 6.12b).

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

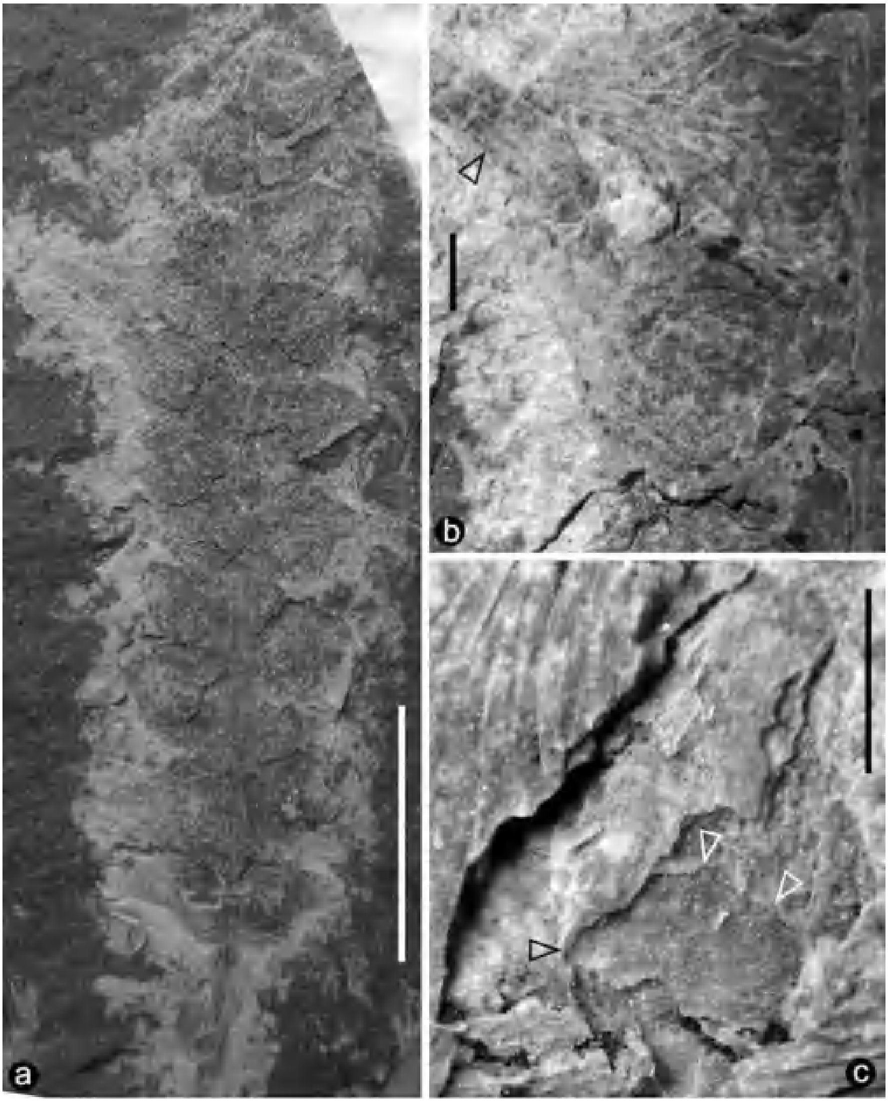

Fig. 6.12 Inflorescences of S. sinensis, and their details. IBCAS 8604. (a) Inflorescence with densely clustered flowers. Bar = 1 cm. (b) Detailed view of two flowers with evident longitudinal ribs from the upper left in a. Note the possible hair bundle (arrow). Bar = 1 mm. (c) Broken flower showing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

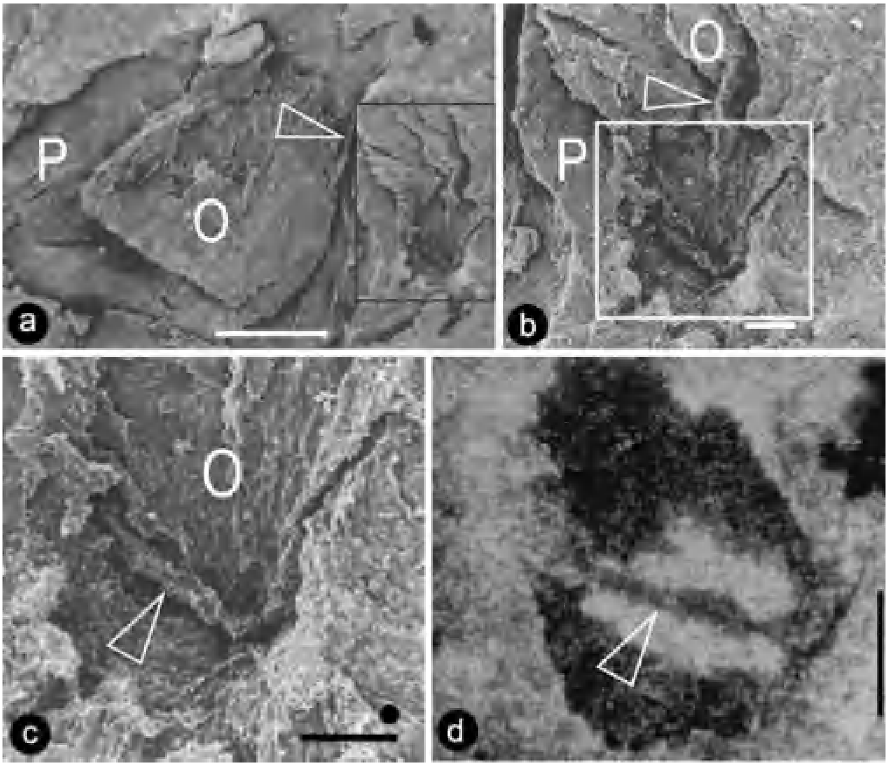

Fig. 6.13 Young flowers of S. sinensis showing closed ovary tip. IBCAS 8604. (a) Two young flowers, one in vertical view and the other (in rectangle) in cross view. Note the ovary (O) surrounded by the perianth (P and arrow). Bar = 0.5 mm. (b) Detailed view of the flower in rectangle in (a). Note the 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 microns 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 BMC Evolutionary Biology

and 6.13a). They 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

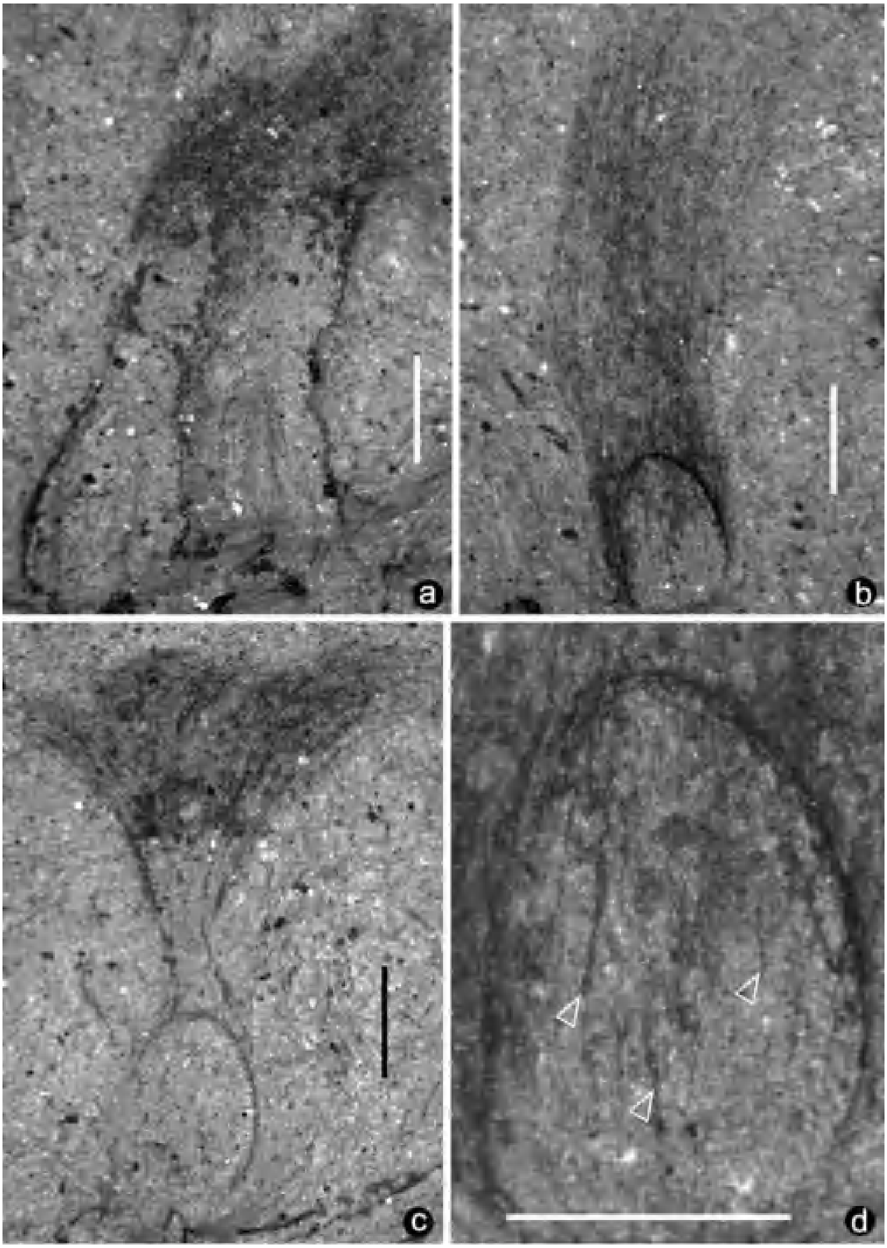

Fig. 6.14 Blooming flowers in a S. microstachys inflorescence, shown in Fig. 6.8b, and their hairs. BSPG 2009 1 19. (a) Two adjacent flowers with brush-like hairs. Bar = 1 mm. (b) Detached ovary with parallel hairs. Bar = 1 mm. (c) Ovary with diverging hairs. Bar = 1 mm. (d) Detailed view of the ovary in b. Note the hairs are emanating from not only the ovary margin, but also the ovary surface (arrows). Bar = 0.5 mm. Courtesy of Journal of Systematics and Evolution

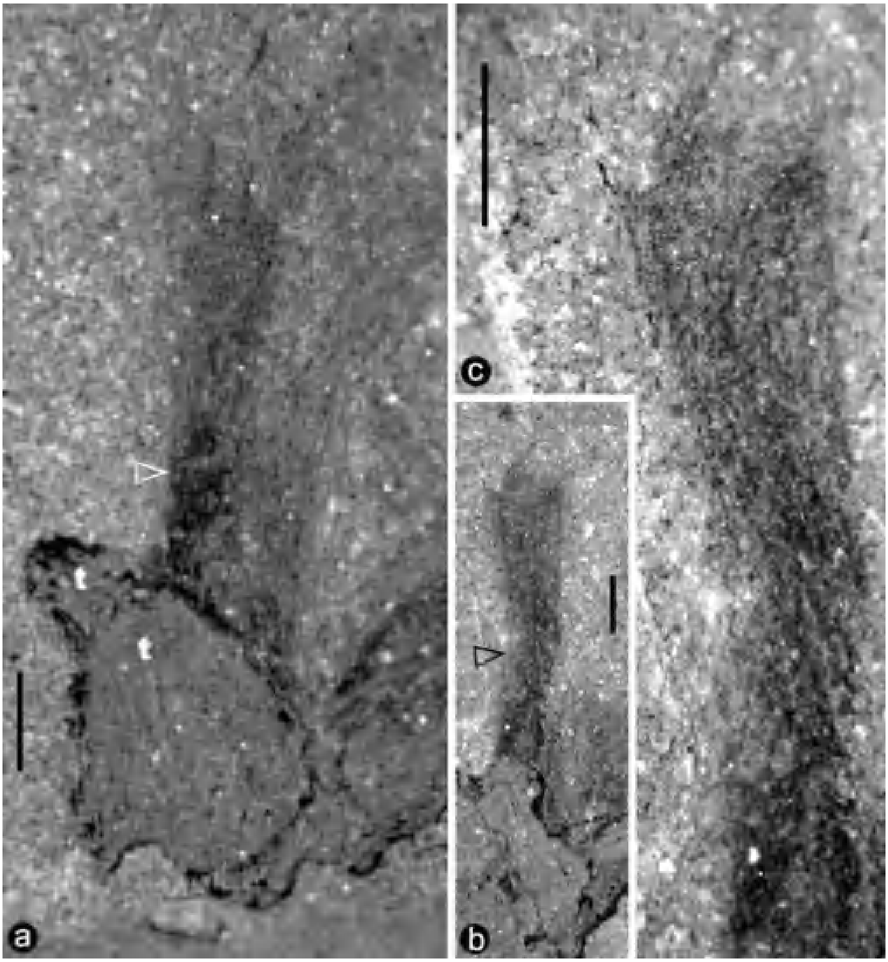

Fig. 6.15 Blooming flowers of S. microstachys and their hairs. BSPG 2009 1 18. (a) The flower marked by black arrow in Fig. 6.10d, with two tepals (t) and apical hair bundles (arrow). Bar = 1 mm. (b) Flower marked by white arrow in Fig. 6.10d, with parallel hairs (arrow). Bar = 1 mm. (c) Detailed view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

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 (Figs. 6.12c, 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) to the apex of the ovary (Fig. 6.13b–d). The septum may be papillate.

Holotype: IBCAS 8604.

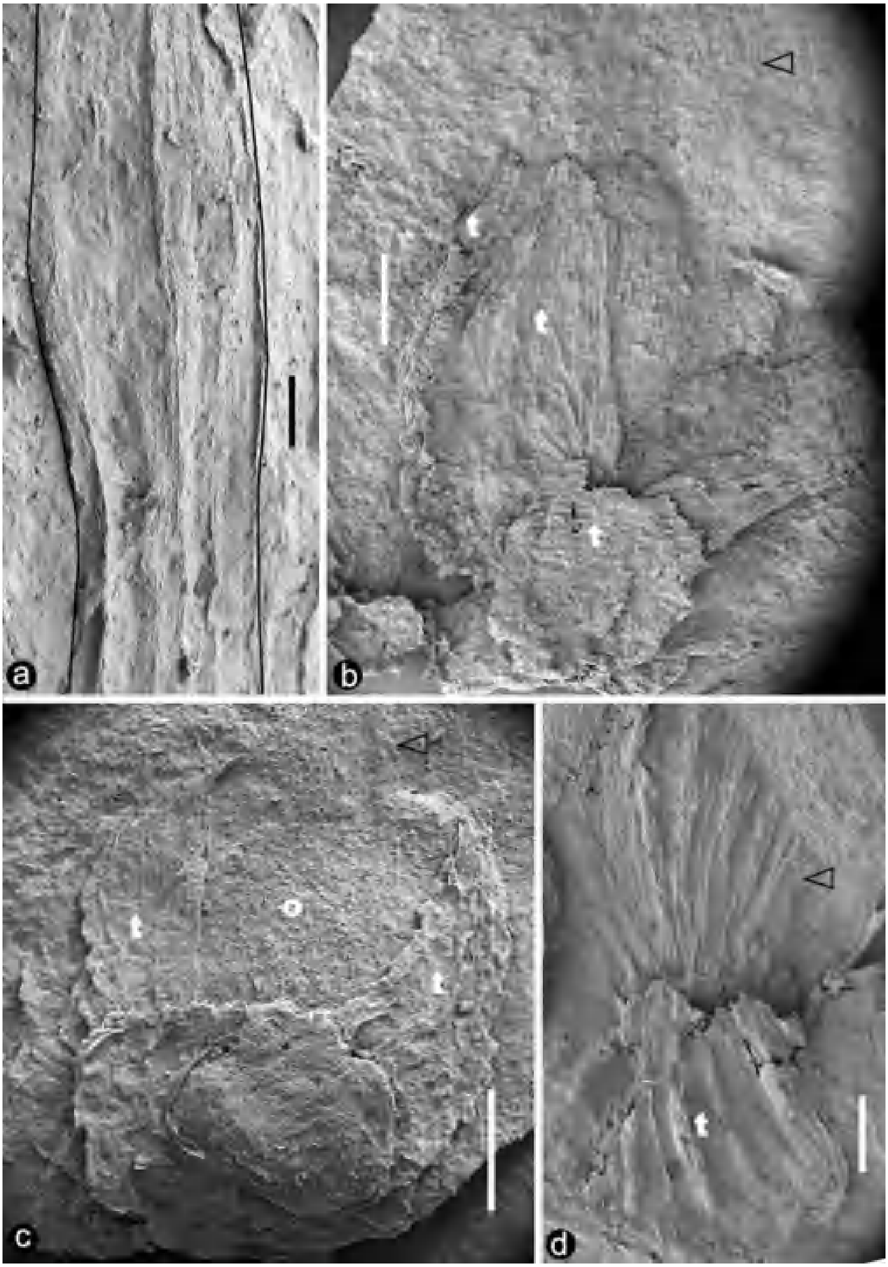

Fig. 6.16 Infructescence axis and tepals in the flowers of S. microstachys. (a) Infructescence axis (outlined by black lines) with longitudinal striations. BSPG 4713. Bar = 0.1 mm. (b) Flower with tepals (t) and parallel hairs (arrow). Note toward to the base there is a tepal (t) of an adjacent flower. 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 Journal of Systematics and Evolution

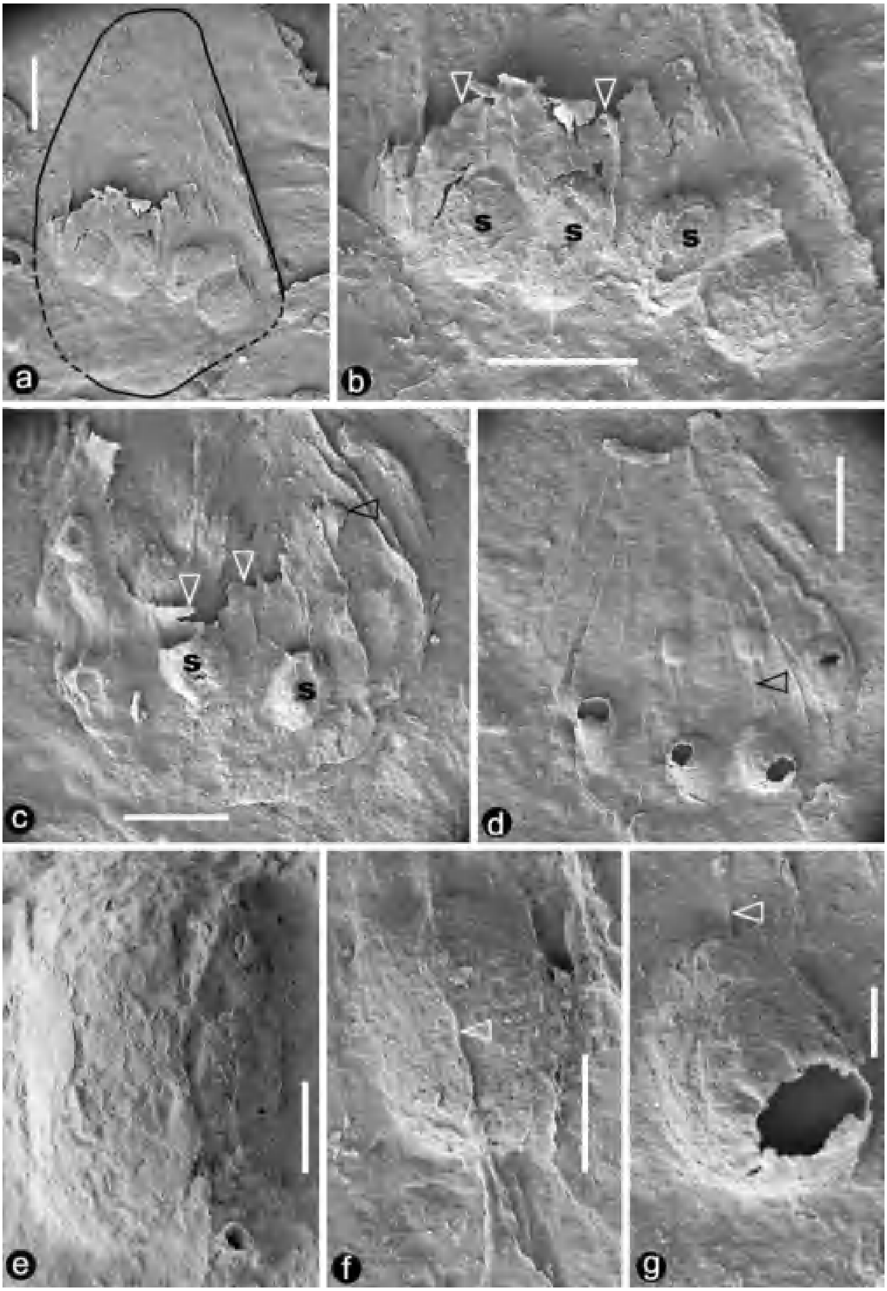

Fig. 6.17 Fruits and in situ seeds of S. microstachys. BSPG 4713. (a) Fruit (outlined by the line) with in situ seeds. Bar = 0.5 mm. (b) Detailed view of the seeds (s) and septum (white arrow) in the fruit shown in a. Note that there still is additional space behind the septum. Bar = 0.5 mm. (c) Another 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 with in situ seeds of variable sizes. Note that there are longitudinal wrinkles (arrow) on the septum. Bar = 0.5 mm. (e) An in situ seed. Note that the seed surface is smooth to the left, but

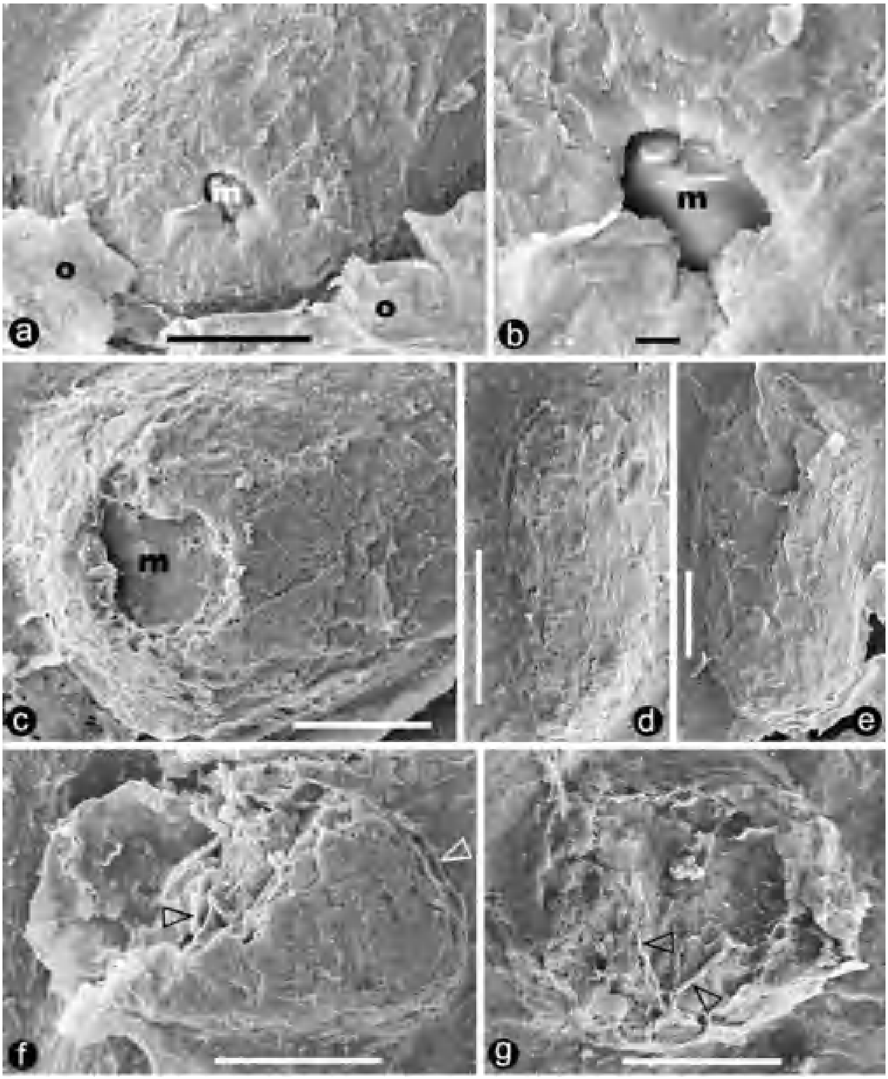

Fig. 6.18 Details of in situ seeds within fruits of S. microstachys. BSPG 4713. (a) Seed with a micropyle (m) within the ovary (O). Bar = 0.1 mm. (b) Detailed view of the micropyle (m) region of the seed in a. Bar = 10 μm. (c) Another seed with a micropyle (m). Bar = 0.1 mm. (d and e) Two elongate-oval shaped in situ seeds. Bar = 0.1 mm. (f) A broken seed with cellular details (arrow). Bar = 0.1 mm. (g) Another broken seed with cellular details (arrow). Bar = 50 μm. Courtesy of Journal of Systematics and Evolution

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Fig. 6.17 (continued) 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 Journal of Systematics and Evolution

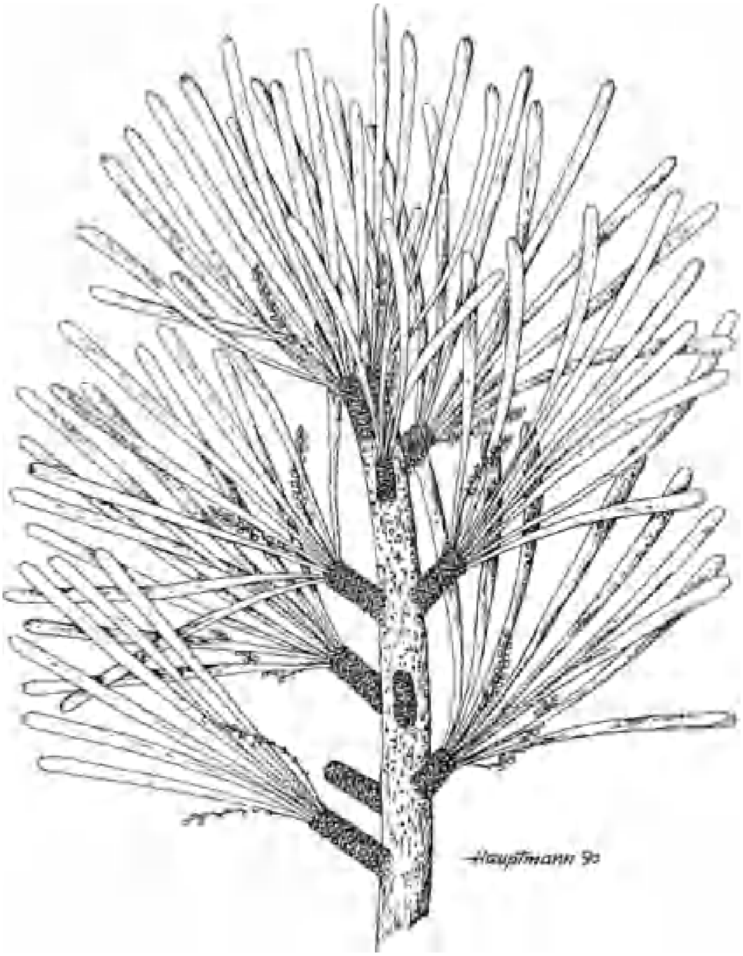

Fig. 6.19 Reconstruction of *S. microstachys*. Note the long shoot, short shoots, and attached leaves and inflorescences (Reproduced from Dr. Schmeißner and Hauptmann 1993; with permission from Dr. Schmeißner and Hauptmann and from Naturwissenschaftliche Gesellschaft Bayreuth)

Holotype locality: Sanjiaochengcun, Jinxi, Liaoning, China.

Stratigraphic horizon: The Jiulongshan Formation (former Haifanggou Formation), the late Middle Jurassic—early Late Jurassic (>162 Ma).

Depository: IBCAS.

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 Germany), and the fact that the number of tepals is hard to ascertain.

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 seed-enclosing fruits of *S. microstachys*, recognized only recently, 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 (Wcislo-Luraniec 1992; Kirchner and Van Konijnenburg-Van Cittert 1994; Wang et al. 2007a, b), 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. 2007a, b; Wang 2009, 2010b).

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 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 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 rigid and regular three-dimensional form (Figs. 6.17e–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. 6.17a–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

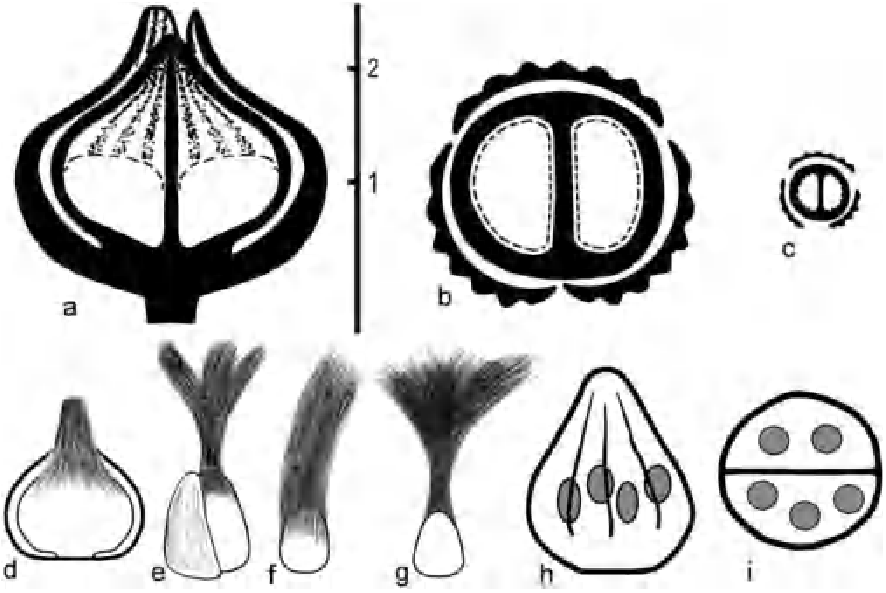

Fig. 6.20 Sketches of the flowers in various stages and perspectives. (a) Longitudinal profile of a flower. Note the tepals surrounding a bilocular ovary, which has a closed apex, is separated by a vertical septum into two locules and contains possible ovules at its base. (b) Cross section of the flower 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 bundles. (f) Flower with a parallel hair bundle. Refer to Fig. 6.14b. (g) Flower with a fanned out hair bundles. 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

6.9a–c). This 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 2010). Wang et al. (2007a) reported a few pollen grains perching on the inner surface of a tepal apex (Fig. 3i–o of Wang et al. 2007a). 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, 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 (Fig. 6.20).

6.1.8 Fruit Dispersal

There is little positive information directly related to the dispersal of Schmeissneria fruits. As implied 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 and thus may be conducive to fruit dispersal by wind.

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 alienated Schmeissneria microstachys from Baiera münsteriana, which was assumed to share the same mother plant with Schmeissneria (Schenk 1890).

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. (2007a) for the first time revealed the internal structure of Schmeissneria′s female flower. Their success can partially be attributed to the fact that the specimens they faced were 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. Recognizing these features took more than ten years. 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 typical angiosperms (Tomlinson and Takaso 2002; Wang et al. 2007a, b, 2015; Wang 2009, 2010b).

In palaeobotany, such a claim by Wang et al. (2007a, b) 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 discussing Schmeissneria after Wang et al. (2007a, b) 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 angiosperms are the only home for it. 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. (2007a, b) is neutrally taken as a plain hypothesis, its validity can easily be tested by further study. If its prediction proves true, then it is valid. Otherwise, it should be discarded. Wang et al. (2007a, b) 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 convincingly 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 on the German specimens, which include many infructescences. According to Wang et al. (2007a, b), 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. At least in term of this point, the hypothesis proposed by Wang et al. (2007a, b) 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 (2010), in which monocolpate pollen grains are the major character used to “confirm” the ginkgoalean affinity of Stachyopitys, a possible male organ of Schmeissneria. However, this conclusion is very shaky because (1) solid evidence of the relationship between Schmeissneria and Stachyopitys is still missing in spite of 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 (Magnoliales and monocots) and Bennettitales [of the latter Van Konijnenburg-Van Cittert was aware clearly as she indicated in her own publication in the preceding year (Zavialova et al. 2009)] is completely ignored and not mentioned at all. Contrary to Van Konijnenburg-Van Cittert′s conclusion, there is evidence showing that Stachyopitys is physically connected with a leaf (Sphenobaiera) (quite different from Glossophyllum? physically connected to Schmeissneria) that is physically connected with a different female organ named Hamshawvia (Anderson and Anderson 2003). Again this fact was known to Van Konijnenburg-Van Cittert who somehow ignored it completely. Such 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 early angiospermous taxa may have been much more diversified and many of them may have gone extinct (Friis et al. 2005) and we have little information of these taxa. Without knowledge of its contemporaneous relatives, extreme caution should be exercised when poorly understood Jurassic angiosperms are compared with extant ones.

6.1.10 Ecology and Environment

There is limited information on the interaction between Schmeissneria and contemporary animals. Van Konijnenburg-Van Cittert and Schmeißner (1999) documented possible 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 preserved in a single specimen (BSPG 4713). There are more than 45 inflorescences on the 32 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 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 theory in Chap. 8 is correct, namely, Cordaitales and others 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, catkin-like reproductive organs, 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 it is conservative enough calling Schmeissneria a Jurassic angiosperm. Although this may appear unexpected to many palaeobotanists, it is in agreement with results from molecular clock studies (Martin et al. 1989a, b; Soltis and Soltis 2004; Bell et al. 2005; Moore et al. 2007;

Prasad et al. 2011) 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. (2007a, b) that Schmeissneria is a Jurassic angiosperm, thus mark a new step in the research concerning the origin and history 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 radiation and diversification of angiosperms in the Early Cretaceous.

6.2 Xingxueanthus

6.2.1 Background

Xingxueanthus is a genus established recently by Xin Wang and Shijun Wang in 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 well-preserved. Its coalified material contrasts well with the light colored sediment matrix and makes its morphology obvious under LM (Figs. 6.21, 6.22, 6.23, 6.24, and 6.27a) and SEM, even without gold coating (Figs. 6.21, 6.22, 6.23, 6.24, 6.25, and 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 proven true. Figure 6.25a, b shows 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

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 Acta Geologica Sinica

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 Acta Geologica Sinica

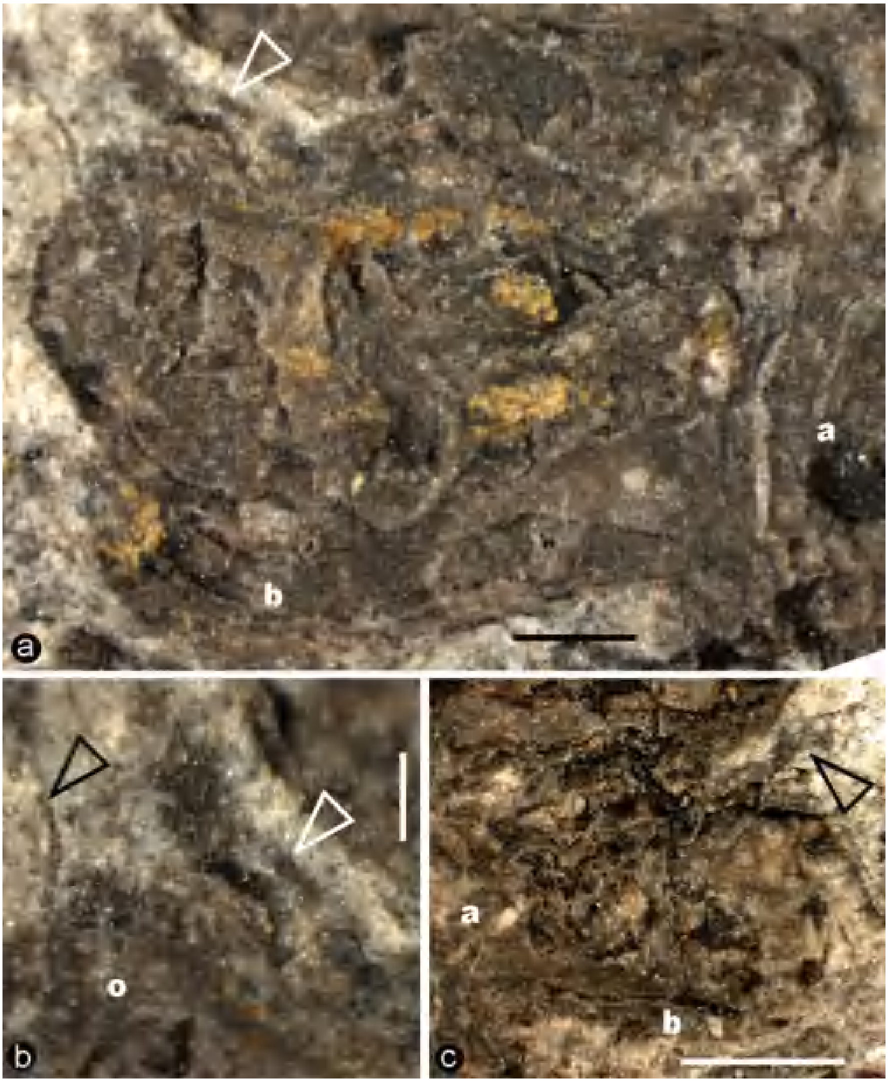

Fig. 6.23 A flower in axil of a bract and its details. (a) Flower 6 in Fig. 6.22. Note the style (arrow) on the top of the ovary, subtending bract (b), and inflorescence axis (a). Bar = 0.2 mm. (b) Detailed view of the style (white arrow) and trichome (black arrow) on the ovary. Note the organic connection 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 Acta Geologica Sinica

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

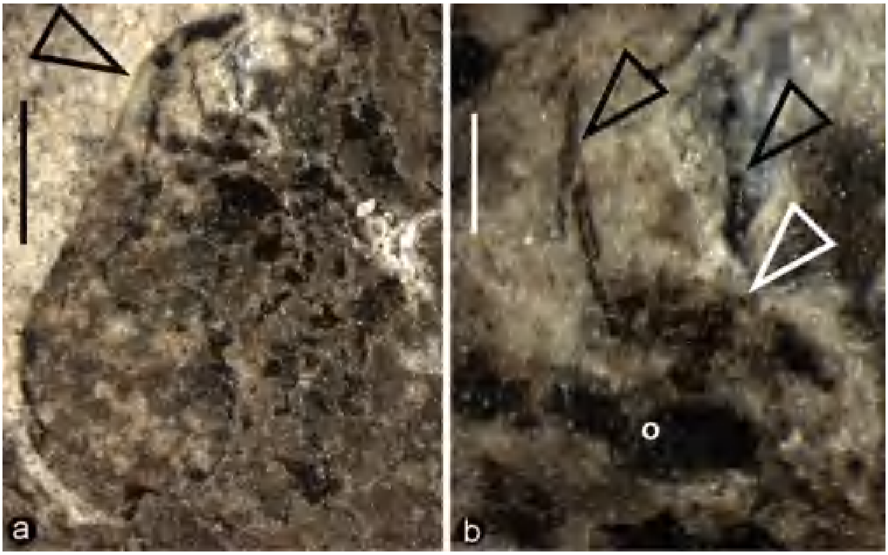

Fig. 6.24 A flower covered by a bract and its details. (a) Flower 5 in Fig. 6.22. Note the bract (arrow) covering the ovary. Bar = 1 mm. (b) Detailed view of the style (white arrow) and trichome (black arrow) on the ovary. Note the organic connection between the ovary (o) and style. Bar = 0.2 mm. Courtesy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

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 conclusion is that it is a female organ of a seed plant.

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 anchoring 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 6.22). The inflorescence includes more than 20 female flowers. The flowers are small in size, only 2–3 mm wide (Figs. 6.23a, c, 6.24a, 6.26a, c, and 6.29a). They are bigger in the proximal and smaller in the distal portion of 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

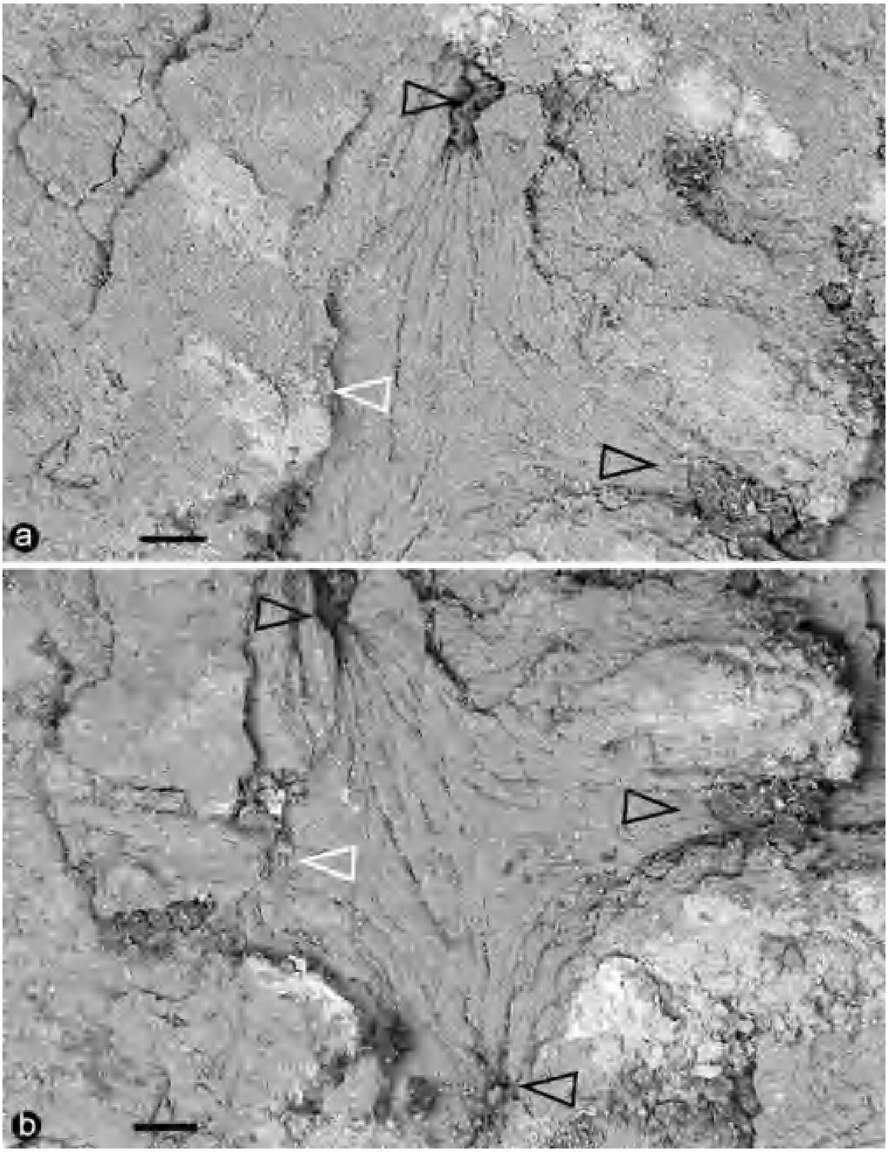

Fig. 6.25 SEM of the placenta in Flower 5 in Fig. 6.22. The funiculi (arrow) with organic relics spirally arranged along the central column. a and b are of almost the same area. One of the funiculi (white arrow) in a is not visible, but is suggested by striations on the central column. This funiculus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

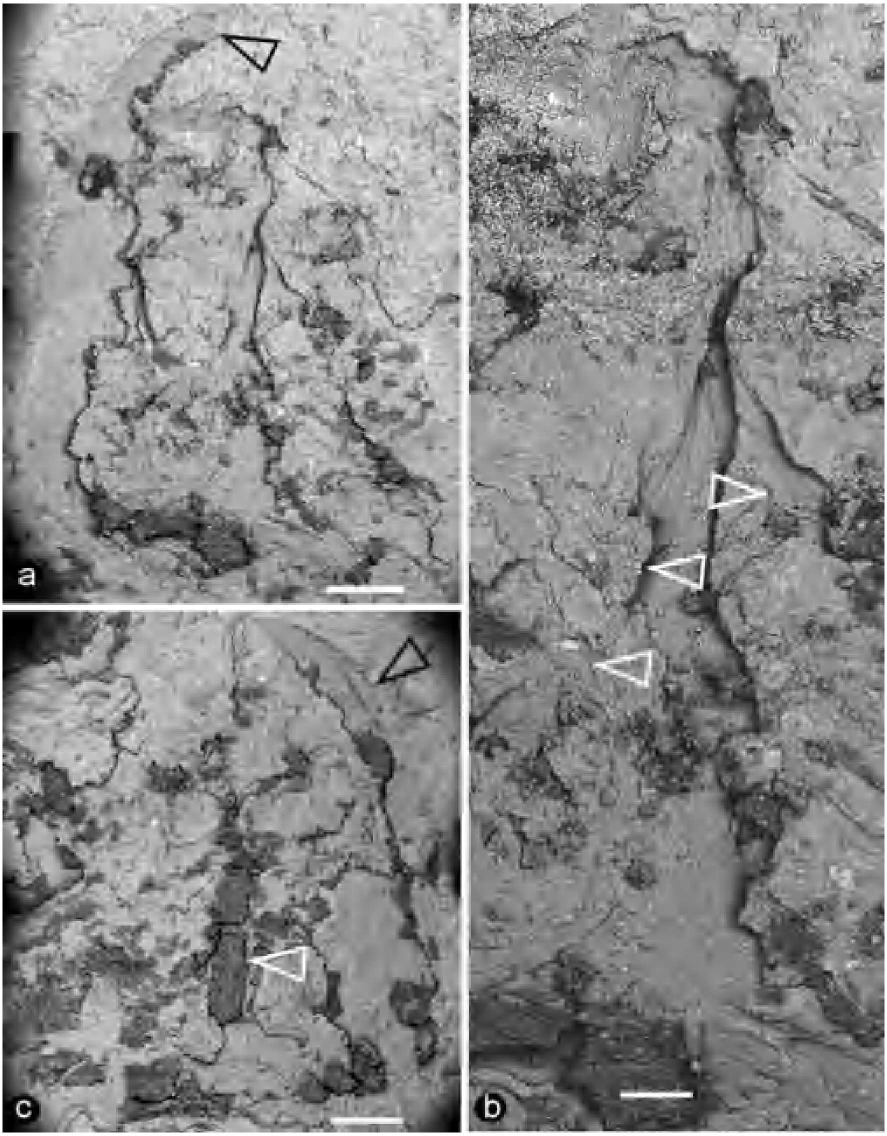

Fig. 6.26 SEM of placenta in flowers. (a) Flower 2 in Fig. 6.21. Note the bract (arrow) covering the ovary and the groove left by the central column that connects the apex and base of the ovary. Bar = 0.5 mm. (b) A detailed view of the placenta of flower in a. Note the funiculi (arrows) attached to the 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 Acta Geologica Sinica

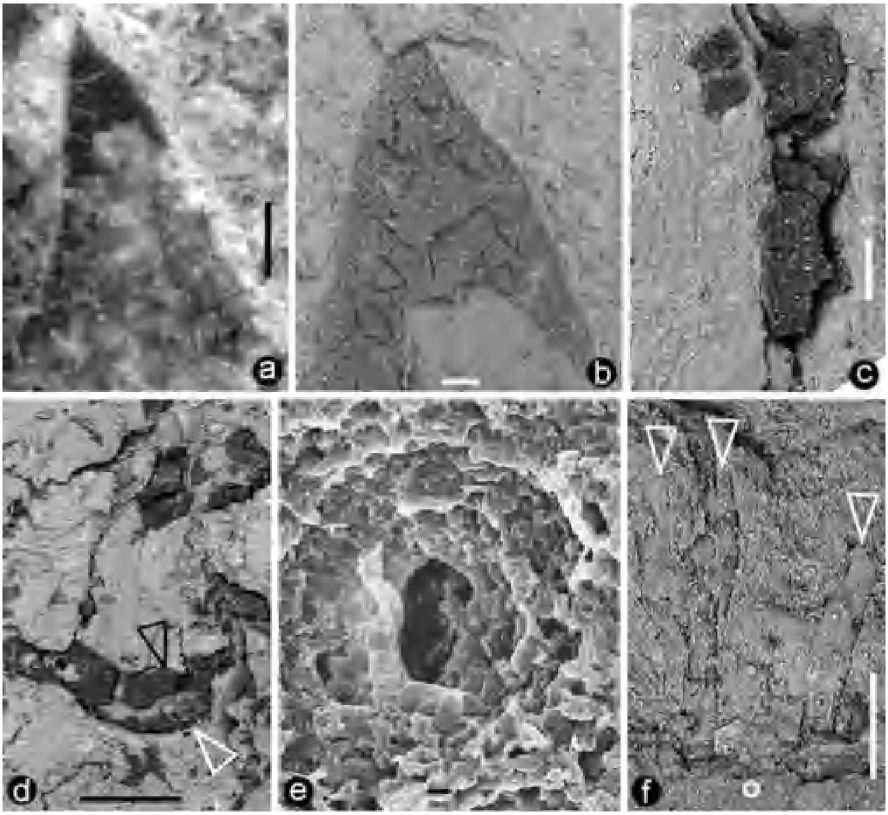

Fig. 6.27 Some details of flowers. (a) One of the bract tips of flower 8 in Fig. 6.22. Note the organic material. Bar = 0.5 mm. (b) Detailed view of the apical portion of the bract in a under SEM. Bar = 0.1 mm. (c) Details of bract near flower 3 in Fig. 6.21. Note the bract of organic material and longitudinal 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 Acta Geologica Sinica

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 distal 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 ovary

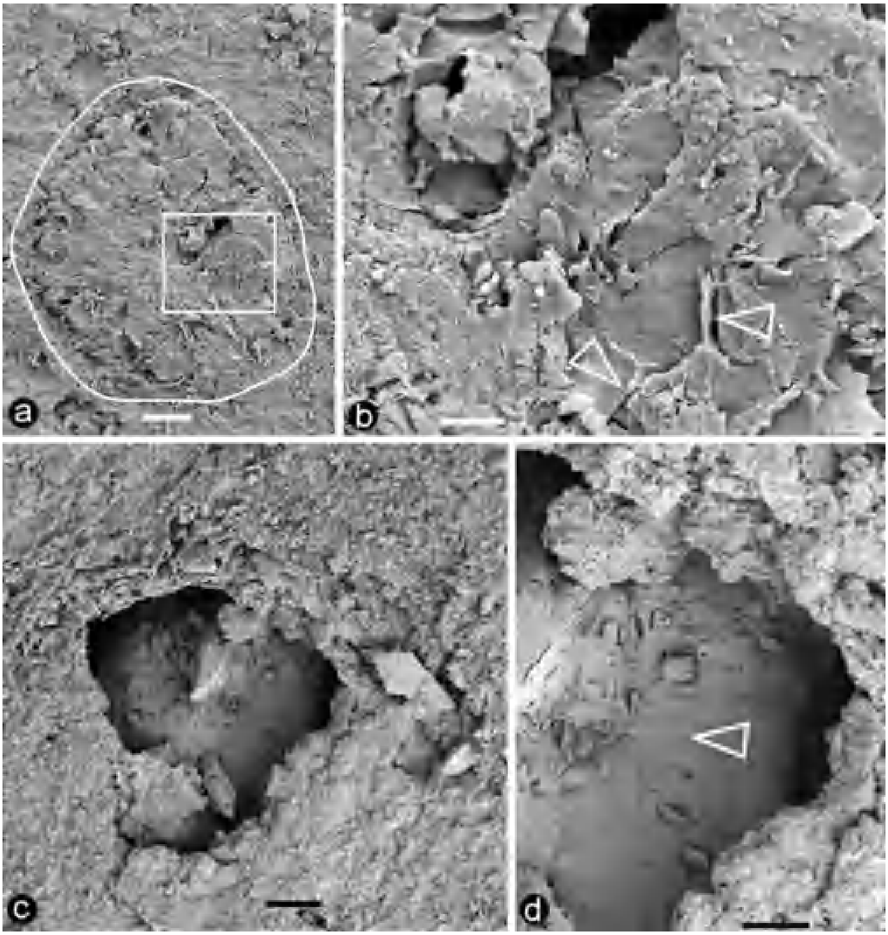

Fig. 6.28 Some details of ovules in flowers from specimen 8703b. (a) Oblique section across an ovule, outlined by the circle. Note the cavity to the middle right of the ovule. Bar = 10 μm. (b) Detailed view of the rectangular region in a. Note the cavity on top, cellular details and cell wall (arrows) 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 Acta Geologica Sinica

(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).

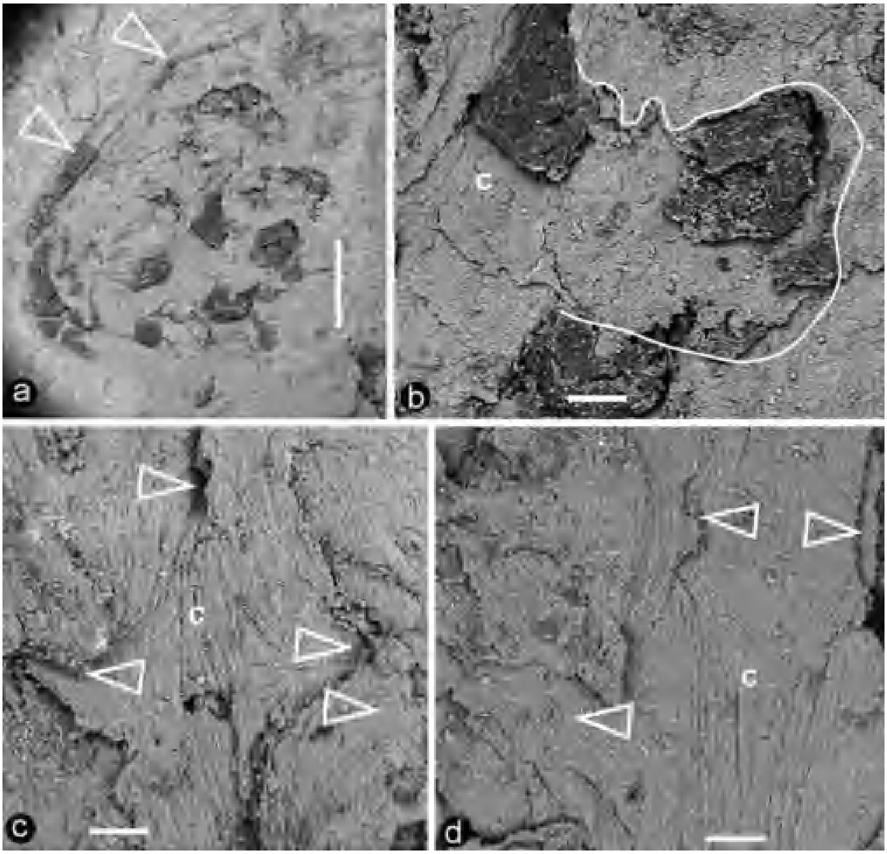

Fig. 6.29 Some details of flower placenta. (a) Flower 1 in Fig. 6.21. Note the bract (arrow) covering the ovary. Bar = 0.5 mm. (b) Detailed view of the ovule in a. Note the ovule (outlined by white line) and its relationship to the central column (c). Bar = 0.1 mm. (c) Placenta of flower 7 in Fig. 6.22. Note the spiral arrangement of funiculi (arrows) 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 Acta Geologica Sinica

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 (Fig. 6.23a, c), and the style is physically connected to the ovary (Figs. 6.23b and 6.24b).

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. 2009a; 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. 2009a) that are distinct from the free central placentation inside the ovary of Xingxueanthus. Bennettitalean seeds also are distinct from Xingxueanthus 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 ovuliferous units and their characteristic decussate arrangement in Gnetales alienate Gnetales from Xingxueanthus (Martens 1971; Biswas and Johri 1997; Wang and Zheng 2010a). After elimination of all these alternatives, the only viable remaining alternative is an angiospermous style.

The presence of such 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 implies 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 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 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). 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 2000; 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 according to the classical theories. 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, this is 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 very derived (Puri 1952). Recently advanced theories based on molecular data and morphological analyses suggest that the most primitive angiosperms had ascidiate carpels with one or two ovules (Endress and Doyle 2009). 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 flawed 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.

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
(Figs. 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, and 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. Multiple 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. 6.21and 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. 6.21and 6.22).

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 distal 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, 6.24a, b, and 6.30a–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

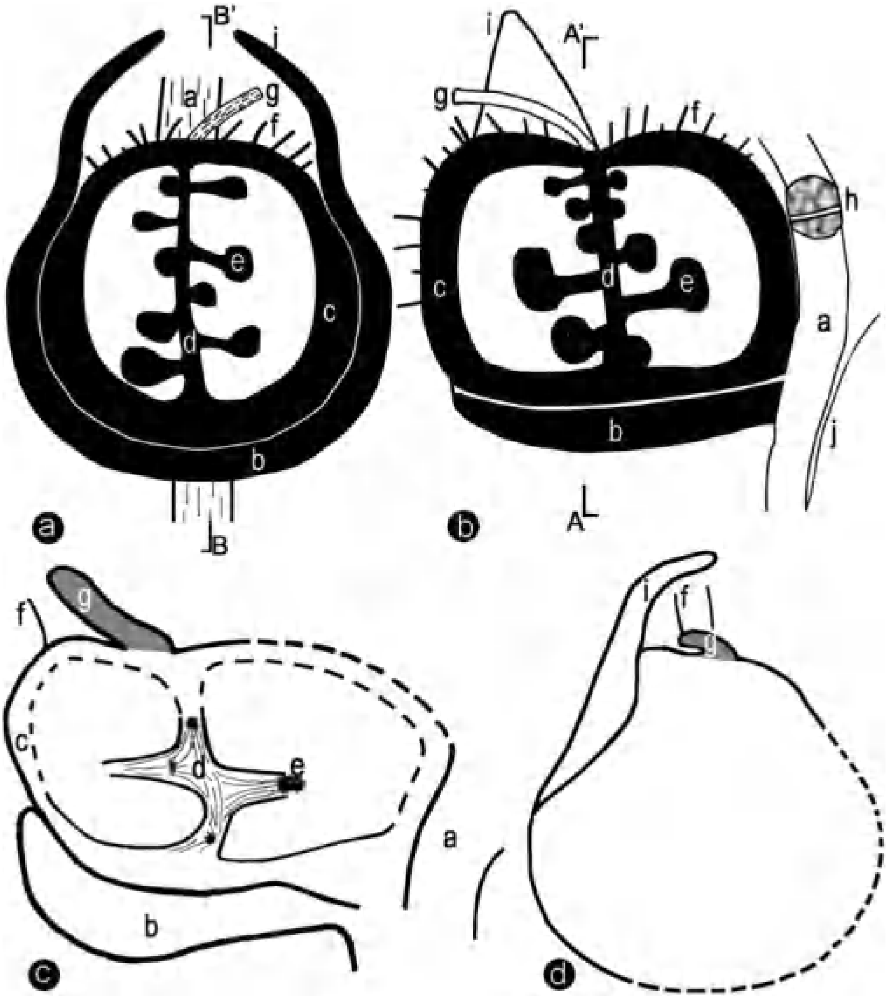

Fig. 6.30 Reconstructions and sketches of the flowers. Labels: inflorescence axis = a, bract = b, ovary wall = c, central column = d, ovule = e, trichomes = f, style = g, scars of the bract and flower = h, bract tip = i, and a portion of another flower = j. (a) Longitudinal section from side to side 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 Acta Geologica Sinica

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). More than three 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 in 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 elongated 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).

Holotype: 8703a.

Paratype: 8703b.

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

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

Stratigraphic horizon: The Jiulongshan Formation (=Haifanggou Formation), late Middle Jurassic to early Late Jurassic (>162 Ma).

Depository: IBCAS.

Remarks: Figure 6.28a–d shows 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 lateral fertile appendages 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 numerous ovules dispersed among interseminal scales spirally arranged on a dome-shaped receptacle

(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 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 1981; 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 living 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 is only found in angiosperms to date. A distal projection at the top of an ovary is a character seen only in angiosperms, Gnetales, Bennettitales, and Erdtmanithecales (Friis et al. 2009a; Rothwell et al. 2009), if the difference between style and micropylar tube is ignored. 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 similar 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. 2007a, b; Wang 2009). It is apparent that the ovule is enclosed in the ovary in Xingxueanthus, satisfying the criterion stipulated for angiosperms in Chap. 3. If accepted as a Jurassic angiosperm, Xingxueanthus, together with Schmeissneria and Euanthus (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. They are joined by Juraherba and Yuhania of similar age (Han et al. 2016; Liu and Wang 2017). This will help to resolve the discrepancy between the molecular clock (Chase 2004; Sanderson et al. 2004; De Bodt et al. 2005; Magallon 2014) and the fossil record (Friis and Crepet 1987; Friis et al. 2005, 2006; 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), Callianthus, Liaoningfructus, Baicarpus and Nothodichocarpum from the Yixian Formation in western Liaoning (Duan 1998; Sun and Dilcher 2002; Sun et al. 1998, 2001, 2002; Leng and Friis 2003, 2006; Dilcher et al. 2007; Wang 2009; Wang and Zheng 2009; Wang and Han 2011; Han et al. 2013, 2017), if the Barremian were 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; Cronquist 1988). The presence of such assumed derived characters in a Jurassic angiosperm casts doubt over the validity of these theories that are mostly based on analyses of molecular and morphological data of living plants. These theories might appear correct in certain contexts but certainly not so if fossil data are taken into consideration. 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 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 will face some challenges in the near future.

Alternatively, if Xingxueanthus were recognized as a new class in seed plants, it would imply that angiospermy/angio-ovuly is not unique to angiosperms 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 these “gymnosperms”. It is conceivable that many proposals will be advanced for such a line. While it is easy to advance a proposal, it is much challenging to reach a new consensus on this a new definition for fossil angiosperms.

6.2.5 Evolutionary Implications

According to the currently dominant evolutionary doctrines, free central placentation is thought derived (Puri 1952; Eames 1961; 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 examine some of the now-unfavored hypotheses or the 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, 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 lost its voice in plant morphology 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 (Rounsley et al. 1995; Roe et al. 1997; 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. The present author does not question their diligence, intelligence, honesty, or reasoning of these botanists. The contradiction may be derived from the simple fact 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 arguments, so only limited trust can be invested in these kinds 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 and other Centrospermales (Joshi 1938), demonstrates exactly what Eames demanded from his opponents, strong evidence 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 origins of the carpel and of angiosperms (see Chap. 8) and its influence may spread to related fields.

6.2.6 Problems Unsolved

Unlike the situation for Schmeissneria, there is limited fossil material of 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 currently a mission impossible. 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: angio-ovuly. Their angio-ovuly 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 ovule protection. Their failure to dominate the vegetation may be due to other factors. The context in which angio-ovuly occurred may be a key factor determining the fate of those 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, the fossil shares arrangement of the whole organ and hexagonal configuration of the “flower”, but details 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. The exact position of the pollen sacs in the fossil was not determined. Currently available information does not allow exclusion or confirmation of the correlation between “synangia” in *Bayeritheca* and ovulate 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). However, they differ in details of 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 an ovulate structure in Solaranthus. The "empty shrivelled sporangia" in Loricanthus (Krassilov and Bugdaeva 1999) and "tepal" in Solaranthus may well be the same thing.

Deng et al. (2014) published a paper on so-called "Aegianthus hailarensis", which might be of Solaranthus in a different developmental stage. The merit of this paper is that they for the first time provide the cuticular information of this genus. Otherwise the treatment in the paper is very dubious. First, due to their limited number of specimen, they over-confidently rejected the existence of tepal-like structure in Solaranthus. Such self-centered academic attitude is detrimental to the accumulation of information about fossil plants. According to their logics, if they had not seen, then there would be no anything. The lack of so-called tepal-like structure is their specimen may well be due to maturity as tepals frequently fall off after anthesis in angiosperms. Second, although they confirmed the existence of monocolpate pollen grains in here-called Solaranthus, they had no idea about where came these pollen grains and the morphology the pollen sacs as the assumed "tepals" are missing in their fossils (Are they studying Solaranthus?). They did not know whether their pollen were in situ, how the pollen sacs were arranged in the organs, there were any trace of female parts in the organ or not. Lack of so much information that had been documented before they did their work makes this paper and its conclusion below the bar in palaeobotany. Therefore the present author would ignore this paper and its conclusion hereafter.

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 except in 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 related information from all these taxa.

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 ovulate structures, filamentous and sessile stamens with in situ pollen grains, young organs, and subtending bracts.

6.3.2.1 Ovulate Structures

Since the male parts, namely stamens, which are self-evident with their in situ pollen grains, have been identified in Solaranthus (see below), ovulate structures in Solaranthus do not have the possibility of being male parts any more. Before going further, it is necessary to eliminate other alternatives and ascertain the identity of ovulate structures first. The ovulate structures in Solaranthus may be alternatively interpreted as fruits, seeds, ovules, or resin bodies. If fruits or seeds, seeds, which would be more likely to fossilize, should have been seen in Solaranthus.

There are no apparent seeds in Solaranthus, but there are subunits that can be interpreted as being ovule-like structures (Fig. 6.41a–d). 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 is not supposed to have internal space, but Fig. 6.41a–d clearly demonstrates the existence of space surrounding a substructure within the ovulate structure. The coherent relationship of this substructure to the ovulate 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-derived structure.

Volcanic ash is ubiquitous in the slab embedding Solaranthus, even inside the tiny cavity under the cuticle (Fig. 6.40g, h). In strong contrast to its apparent ubiquity, the absence of volcanic ash inside the ovulate structure (Fig. 6.40f) becomes especially noteworthy. This situation suggests strongly that the ovulate structure is completely closed in Solaranthus. This feature alone is sufficient to place Solaranthus in angiosperms, considering the presence of ovule-like structure inside. Further examination of ovule-like structures enclosed in ovulate structures (Fig. 6.41a–d) lends more support to the angiospermous affinity of Solaranthus. The ovule-like structures in the ovulate 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 always have surrounding integuments. All these features collectively pin down the angiospermous identity of Solaranthus, according to the definition for fossil angiosperms in Chap. 3.

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 of pollen grains within the fossils. Pollen wall structure and general organization of some fossils are available for comparison now (Kvacek and Pacltov 2001; Deng et al. 2014). 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 vary in morphology. 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 stamens appear virtually identical (Figs. 6.38h and 6.39b, e, h, i).

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 truthful feature of the original pollen grains because a similar pollen wall structure has 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 tie 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 ovulate 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 ovulate 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.

6.3.2.3 Tepals

Deng et al. (2014) cast doubt over the existence of tepals in Solaranthus, based on their observation of lack of tepals in their specimens. To verify their truthfulness, more specimens of Solaranthus were examined, it appears that the tepals are consistently present in many specimens (Fig. 6.44b), in addition to the previous reported specimens (Figs. 6.32a, b, 6.33, 6.34a, b, 6.36b, 6.37b–d, 6.38b, and 6.41a). Therefore the claim by Deng et al. (2014) appears groundless.

6.3.2.4 Bracts

Since the publishing of the first edition of this book, more complete specimens of *Solaranthus* were collected. In several of them, it appears that the whole reproductive organ is subtended by several bracts (Figs. 6.42a, b, 6.43a, and 6.44a), and these bracts may perform the protection function during the early development of the reproductive organs (Fig. 6.43a).

6.3.2.5 Floral Bud

One of the specimens shows the early development of the reproductive organ, in which the bracts are relatively bigger than in others, almost completely covering up the immature organ (Fig. 6.43a, b). Such configuration suggests that during the early development the reproductive is very small and covered up by the bracts. The big size of the reproductive organ is the result of, probably rapid, development of the organ. Similar developmental pattern is frequently seen in angiosperm flowers, in which the flower parts are encapsulated in a small protective calyx and the bloomed flower is much bigger than its flower bud days before.

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, subtended by four or more bracts. Each "flower" including a stalk, a peltate head, ovulate structures, "tepals", and stamens. The peltate head hexagonal or pentagonal in abaxial view. Stamen in fascicles, sessile or filamentous inserted on the periphery 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, inside the cycle of stamens, attached to the adaxial rim of the peltate head. Numerous ovulate 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, and tepal, are put in quotation marks because the stamens, ovulate structures and "tepals" are mispositioned, 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: Young inflorescence is only 14 mm long and 14 mm wide, with several subtending bracts (Figs. 6.42a, b, 6.43a–c, and 6.44a). The bracts are tongue-shaped, with longitudinal ribs (Fig. 6.43a, b). 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, 6.35, 6.42, 6.43, and 6.44) or sparsely spaced (Fig. 6.33) along an axis. The “flower” includes a stalk, a peltate head, stamen, “tepals”, and ovulate structures (Figs. 6.31, 6.32, 6.33, 6.34, and 6.35, 6.36b, 6.41a and 6.44b). The stalk is about 0.5 mm in diameter, connecting the “flowers” to the “inflorescence” axis (Fig. 6.42c). 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, 6.42a, 6.43a, b, and 6.44b). The stamens are grouped in several separate fascicles, distinct, sessile or filamentous, 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 and 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

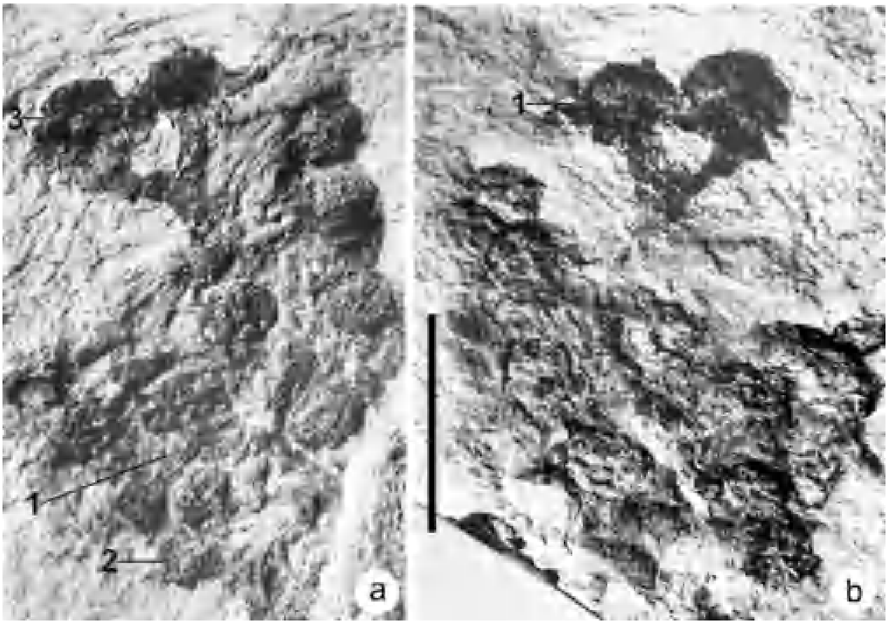

Fig. 6.31 Two facing parts of the same “inflorescence” with more than 13 “flowers”. PB21046a, PB21046b. Bar = 1 cm. Courtesy of Acta Geologica Sinica

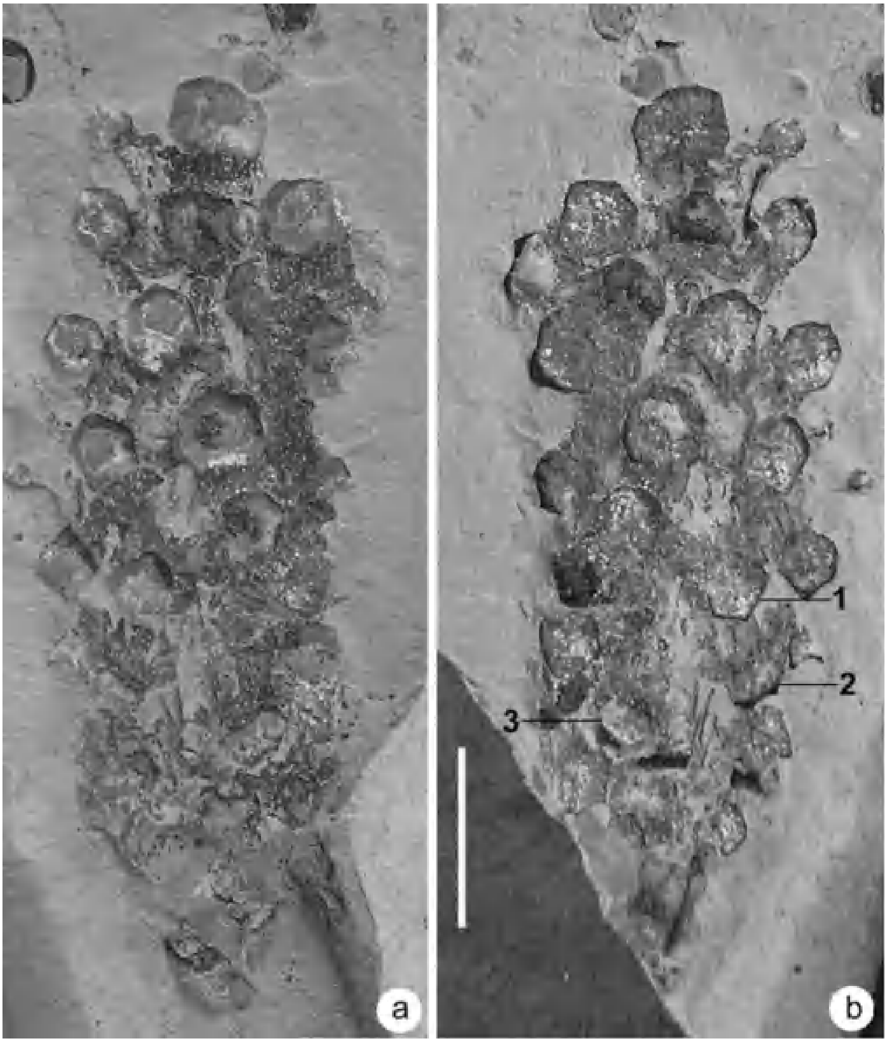

Fig. 6.32 Two facing parts of the same “inflorescence” with up to 27 “flowers”. Note the hexagonal or pentagonal angular profiles of the “flowers”. B0201a, B0201b. Bar = 1 cm. Courtesy of Acta Geologica Sinica

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 rodlets are perpendicular to the foot layer (Fig. 6.39j, k). The “tepals” are inserted on the adaxial rim of the peltate head, one to three per side (Figs. 6.36b, 6.38b, 6.41a, 6.421, and 6.44a, b). 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 cycles

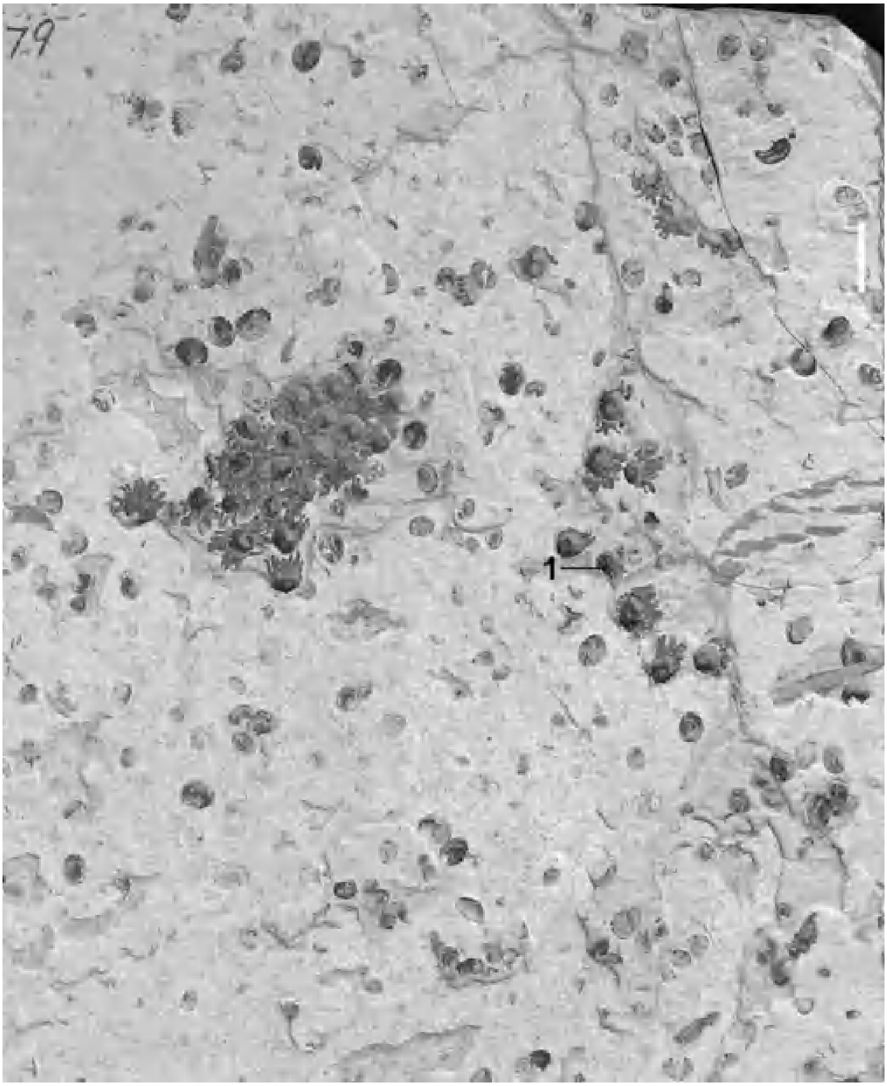

Fig. 6.33 A general view of two to three "inflorescences" on the same slab. Note the varying arrangement of the "flowers", numerous associated conchostracans (Euestheria) and an insect wing (middle right). B0179. Bar = 1 cm. Courtesy of Acta Geologica Sinica

(Figs. 6.36c and 6.37b–d). The gynoecium is up to 3.5 mm in diameter, with numerous ovulate structures inserted on the adaxial surface of peltate head (Fig. 6.40a, d, e). Ovulate 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 ovulate structures (Figs. 6.40b, c, f and 6.41a–d). In a large ovulate structure the ovule-like structure is situated at the "ovary" base, free from the

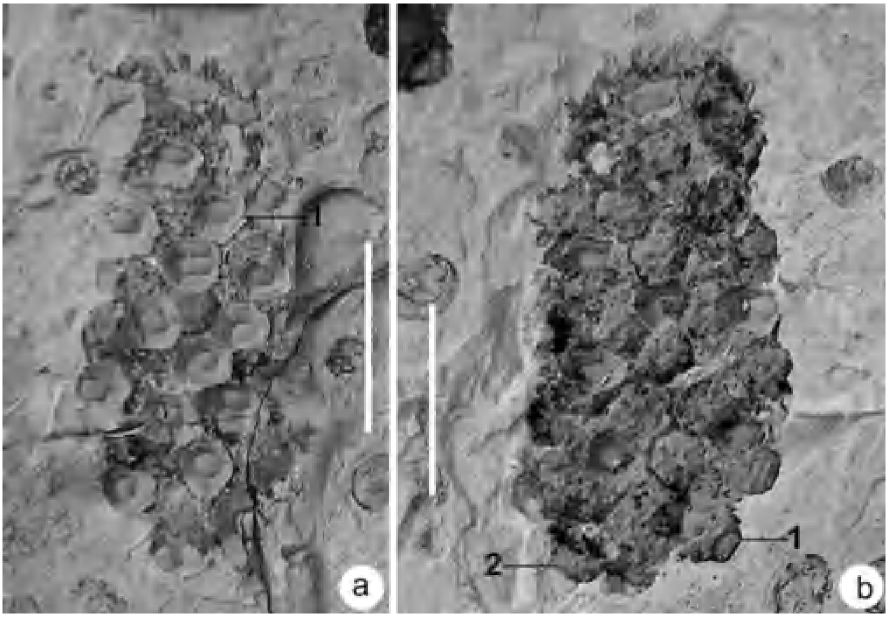

Fig. 6.34 Two facing parts of another “inflorescence”. PB21107b&a. Bar = 1 cm. Courtesy of Acta Geologica Sinica

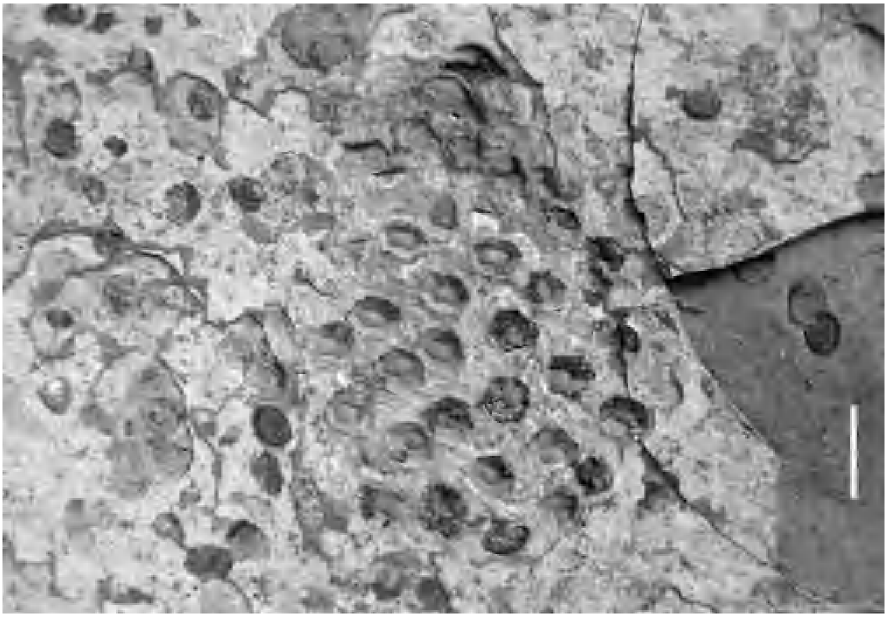

Fig. 6.35 Another “inflorescence” with clustered hexagonal/pentagonal “flowers”. GBM3, SFLBG. Bar = 1 cm

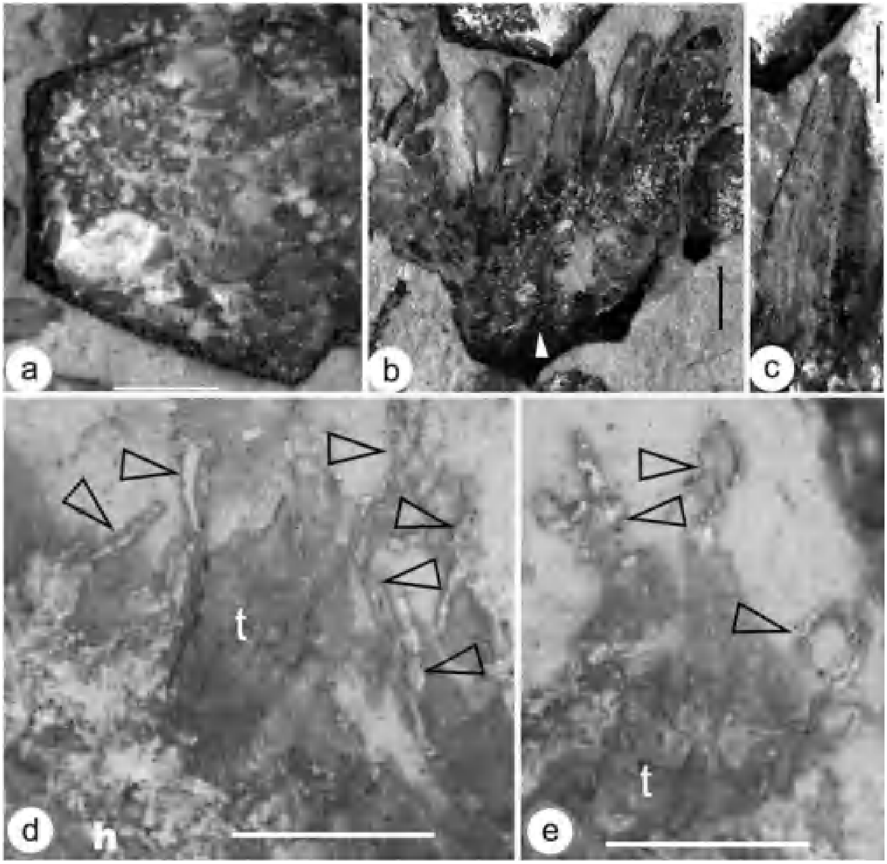

Fig. 6.36 Details of the “flowers”. (a) Transverse view of hexagonal “flower” (No. 1 in Fig. 6.32b). Bar = 1 mm. (b) Longitudinal view of the “flower” (No. 2 in Fig. 6.32b). Note the bottom outline of the “flowers” and attached “tepals”. At least one seed (white triangle) is embedded in the sediment. 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 a “tepal” (t) eclipsing the filaments. Bar = 1 mm. E Stamens (arrows) exserted above the “tepal” (t), from “flower” No. 2 in Fig. 6.31a. Bar = 1 mm. Courtesy of Acta Geologica Sinica

“ovary” wall, 307 μm high and 189 μm wide (Fig. 6.41d). Volcanic ash permeates any non-occluded space (Fig. 6.40f–h) but is absent in the ovulate structure (Fig. 6.40f).

Holotype: PB21046.

Additional specimens: B0179, B0201, PB21107, 47–277, B0007.

Repository: PB21046, PB21107, in NIGPAS; B0179, B0201, in IVPP; 47–277, in STMN; B0007, in LHFM.

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

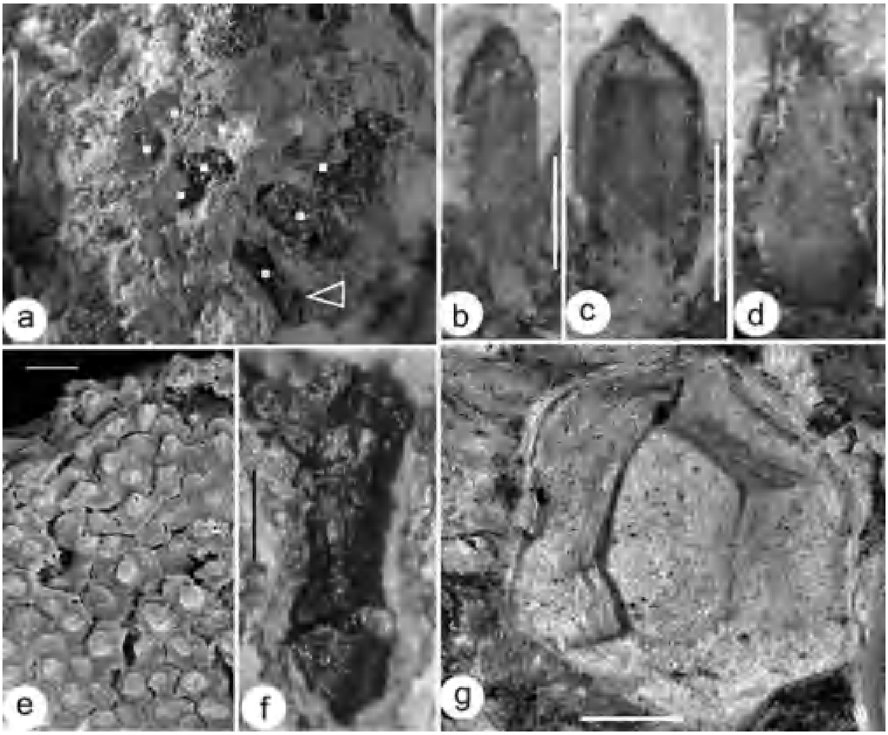

Fig. 6.37 Details of the "flowers". (a) Bottom view of the "flower" No. 2 in Fig. 6.34b, lit from upper left. Ovulate structures left depressions on the sediments and are marked with squares. Bar = 1 mm. (b–d) Three types of "tepals" inserted on the rim of the peltate head. Note their variations in shape, length, and width. Bar = 1 mm. (e) Detailed view of the papillate sculpture on the peltate head surface of "flower" No. 1 in Fig. 6.34b. Note the polygonal outline of the epidermal cells. Bar = 20 μm. (f) Ovulate 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 Acta Geologica Sinica

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 the 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.

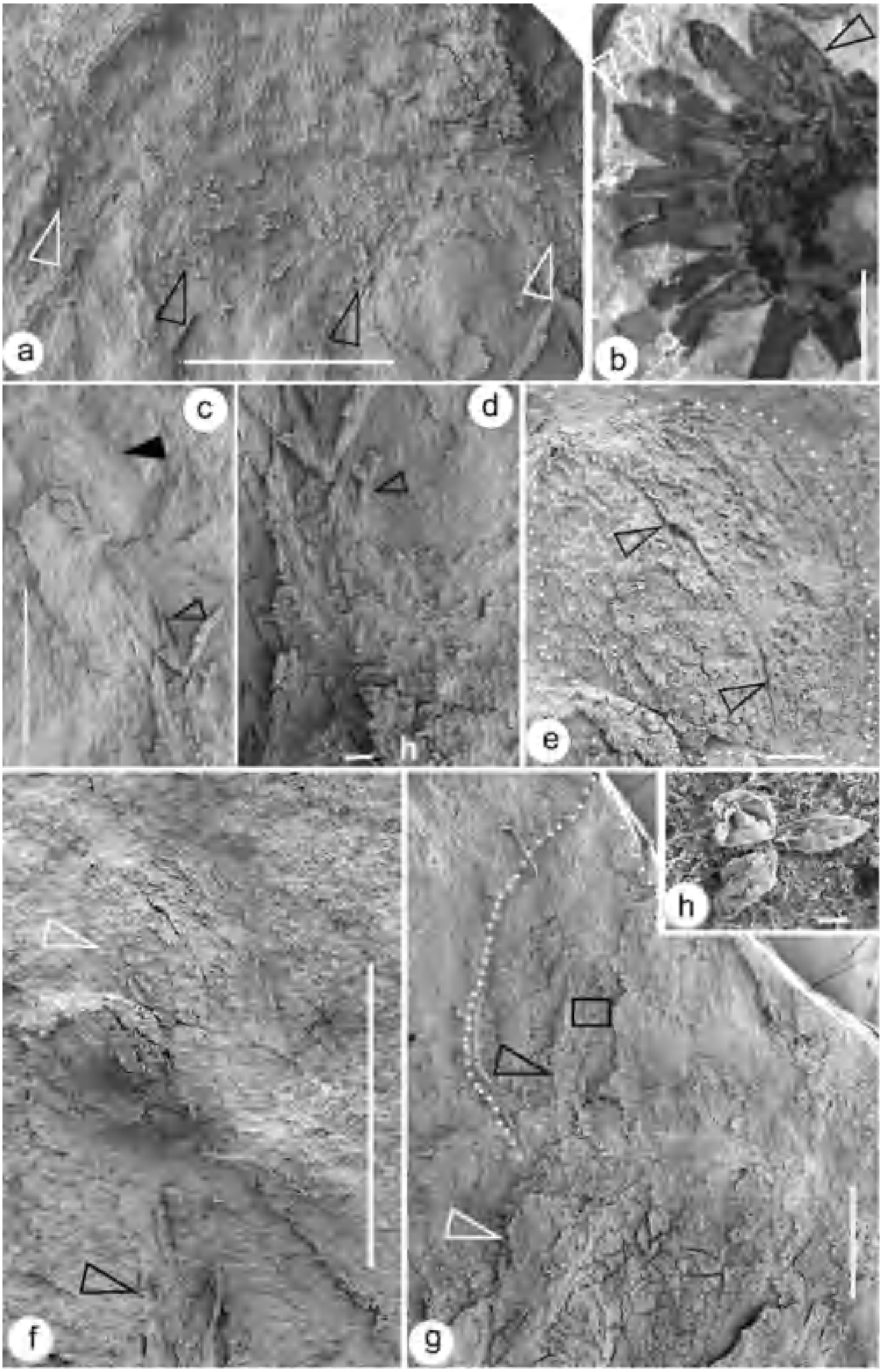

Fig. 6.38 Details of the “tepals” and “stamens”. (a) Four fascicles of filaments (arrows) along the side of the hexagonal peltate head, from “flower” no. 1 in Fig. 6.31b. Bar = 1 mm. (b) “Flower” with more than one cycle of “tepals” of various shapes (arrows) inserted along the adaxial rim of

The general organization of the whole structure and arrangement of peltate heads in Solaranthus are similar to those of equisetalean cones (Oguara 1972; Taylor et al. 2009). 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 permeates any accessible cavity, including the miniscule space under the cuticle layer (Fig. 6.40g, h). They are present in space surrounding the ovulate structures (Fig. 6.40a–c, f), but absent from the ovule-like structure in the ovulate structure (Fig. 6.40f), implying a complete enclosure of the ovule-like structure by the ovulate structure. This inference is in line with the ovule-like structure within the ovulate structure in Fig. 6.41a–d, where the ovule-like structure is coherently attached to the bottom of the ovulate structure. These together prove the existence of an ovule-like structure and its complete enclosure by an ovulate 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 variation 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 extant angiosperms. 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 of a specific group of seed plants (angiosperms).

Fig. 6.38 (continued) the peltate head. Bar = 2 mm. (c) “Stamen” (triangle) and its possible filament at the bottom (arrow), to the right of the “flower” in a, 180° rotated from 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. The region is below that in c. 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 (dotted line) with in situ pollen grains exserted above the “tepal” (white arrow). Note the possible separation (black arrow) 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 rectangle of anther in g. Bar = 10 μm. Courtesy of Acta Geologica Sinica

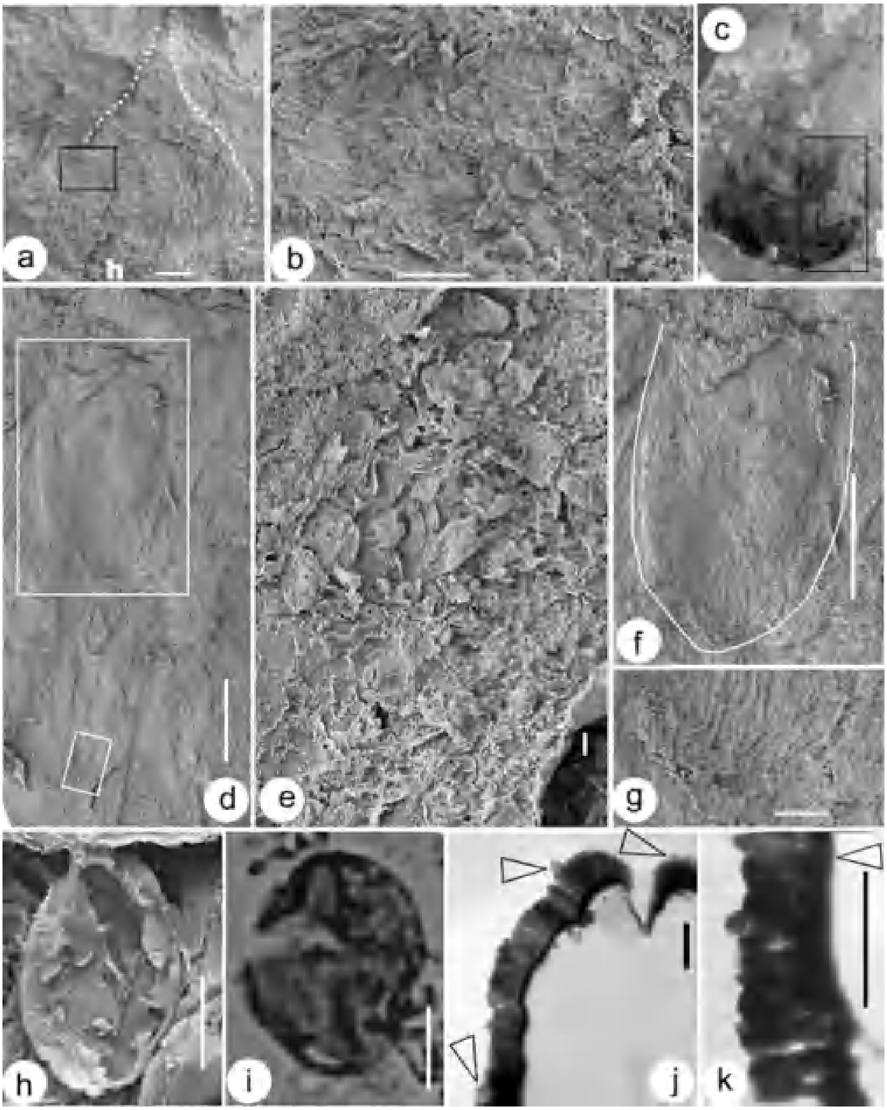

Fig. 6.39 Details of the "tepals" and "stamens". (a) Triangular-shaped sessile "stamen" (dotted line) attached to the adaxial rim of the peltate head (h). Bar = 0.2 mm. (b) Ellipsoid in situ pollen grains, enlarged from the rectangle in a. Bar = 50 μm. (c–g) Physically connected "stamens" and ovulate structures. (c) Replica made from "flower" No. 3 in Fig. 6.31a. Bar = 1 mm. (d) The same "flower" as shown in c, showing "stamen" and ovulate 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) Ovulate structure (white outline) in the "flower", enlarged from the bigger rectangle in d. Bar = 0. 5 mm. (g) Details of the tip of the ovulate structure in f. Note additional material on the ovulate 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 Acta Geologica Sinica

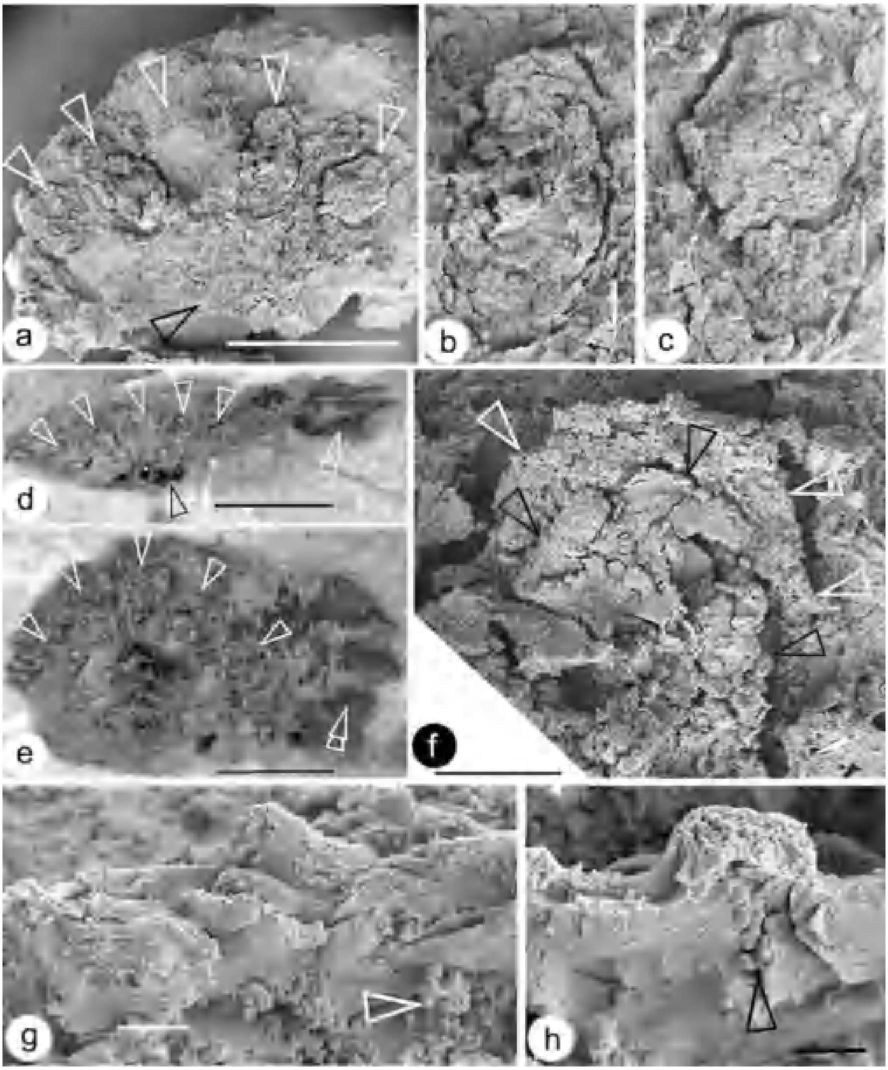

Fig. 6.40 Details of the "gynoecium". (a, d, e) Different views (bottom, side and bottom, respectively) of the same gynoecium of "flower" No. 1 in Fig. 33. Note the center of the gynoecium (black arrow), embedded ovulate structures (white arrows), and impression (central white arrow) left by an ovulate structure, and "tepals" (double white arrows). Bar = 1 mm. (b, c) Details of two ovulate structures shown in a. Bar = 0.1 mm. (f) Detailed view of the ovulate structure in b, not cleaned or processed. Note volcanic ash outside the ovulate structure (white arrows), and their lack on the possible ovule-like structure (black arrows) in the ovulate structure. Bar = 0.1 mm. (g) Epidermis on the top 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 gynoecium in g. Note the tiny granules on its surface and volcanic ash inside (arrow). Bar = 5 μm. Courtesy of Acta Geologica Sinica

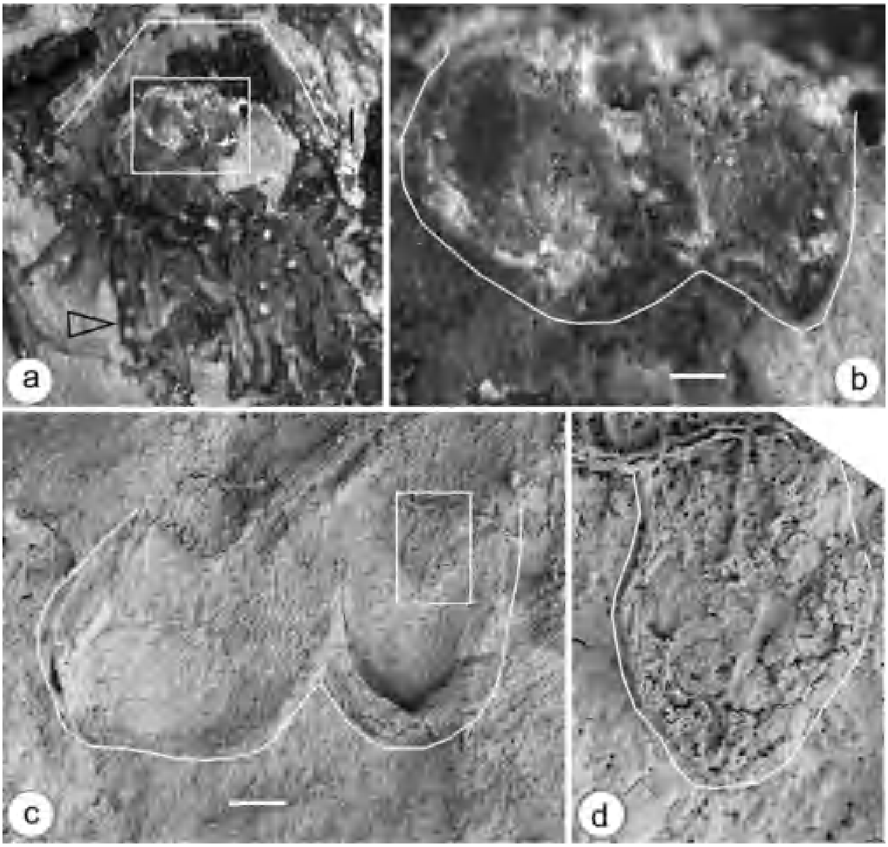

Fig. 6.41 Details of the ovulate structures and an ovule-like structure. (a) Longitudinal view of the "flower" No. 3 in Fig. 6.32b. Note the outline of the peltate head (white line), and "tepals" on the bottom. Bar = 0.5 mm. (b) Detailed view of the rectangle in a. Note the impressions left by two adjacent ovulate structures on the sediment (outlined by the white line). Bar = 0.2 mm. (c) The same two ovulate structures in b. Note the outline (white line) of the ovulate structures. Bar = 0.2 mm. (d) Detailed view of the rectangle in c. Note the smooth outline (white line) of the ovule that is attached to the bottom of the ovulate structure. Bar = 0.1 mm. Courtesy of Acta Geologica Sinica

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 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

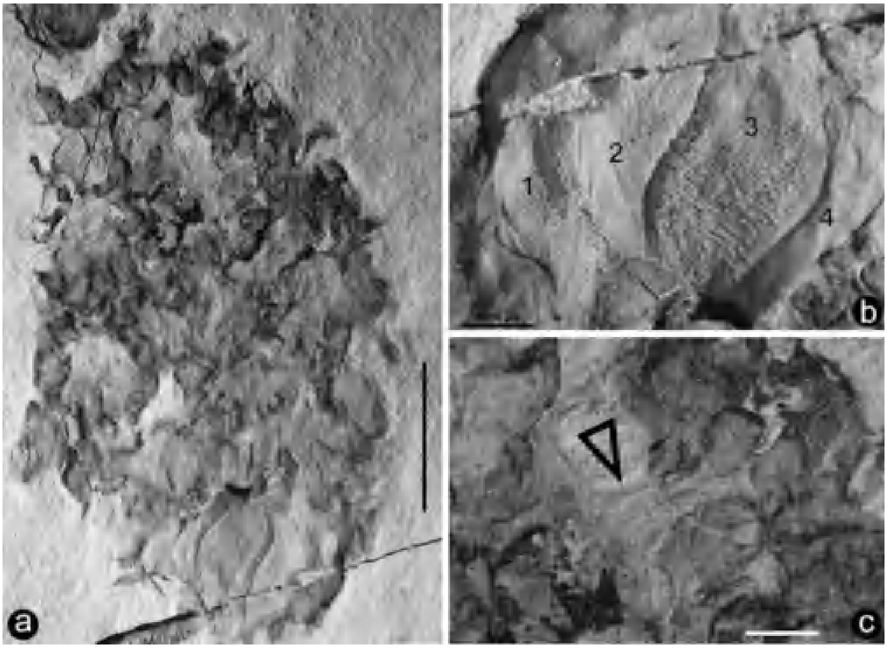

Fig. 6.42 An inflorescence in its early development. (a) several flowers clustered around a central axis. Bar = 2 mm. (b) Bracts (1–4) subtending the inflorescence. Bar = 1 mm. (c) Pedicel (arrow) of a flower attached to the central axis. Bar = 1 mm

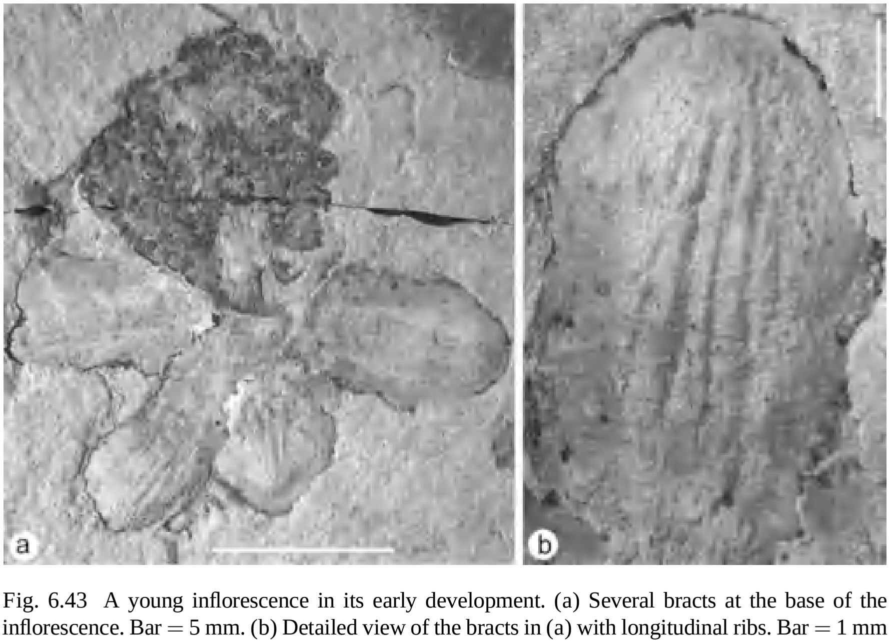

Fig. 6.43 A young inflorescence in its early development. (a) Several bracts at the base of the inflorescence. Bar = 5 mm. (b) Detailed view of the bracts in (a) with longitudinal ribs. Bar = 1 mm

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 ovulate 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 question.

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 we have been braught up, it is in line with the pre-Cretaceous-angiosperm hypotheses based on Jurassic and Early Cretaceous plant reproductive organs (Wang et al. 2007a, b; Wang 2009, 2010b; Wang and Zheng 2009; Wang and Wang 2010; Wang and Han 2011; Han et al. 2013, 2016; Liu and Wang 2016, 2017) and pollen grains (Cornet 1989a; Cornet and Habib 1992; Hochuli and Feist-Burkhardt 2004, 2013). First, these fossils are mutually corroborative. More and more Jurassic angiosperm traces are attracting more and more attention, so ignoring them does not do anything positive 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

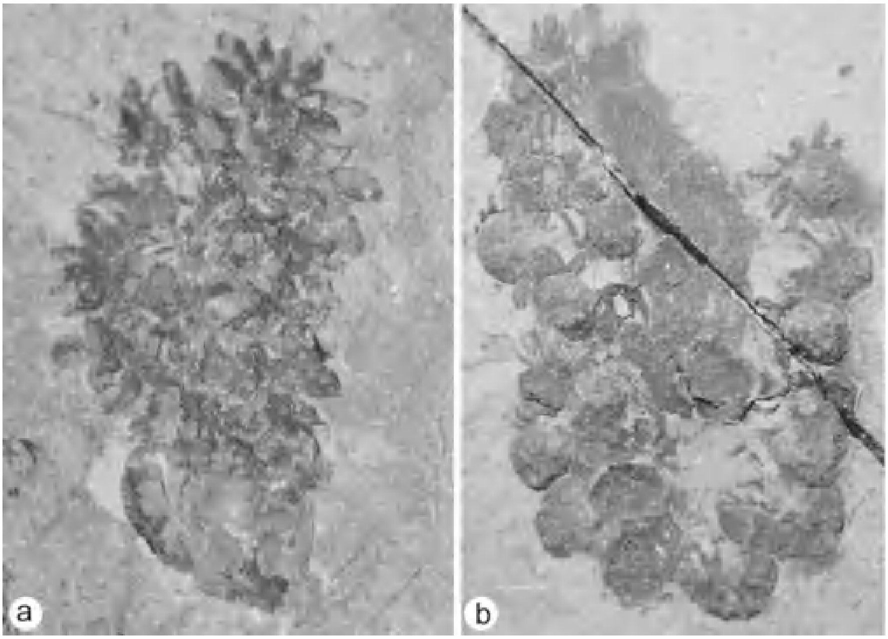

Fig. 6.44 Inflorescences with bracts or tepals. (a) Several bracts at the base of the inflorescence. (b) Several flowers with tepals in a cluster

diversity in the Yixian Formation (Duan 1998; Sun et al. 1998, 2001, 2002; Leng and Friis 2003, 2006; Ji et al. 2004; Wang and Zheng 2009; Wang and Han 2011; Han et al. 2013, 2017), which currently is the oldest strata yielding widely-accepted megafossils of reproductive organs of angiosperms, would be "abominable" and defy an interpretation if there were no pre-Cretaceous angiosperms. It appears most likely that those early angiosperms may have masqueraded in gymnospermous coverage (like Solaranthus) 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 in coniferous cones. Although the gymnospermous appearance and angiospermous identity 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 it. 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 to early angiosperms and their history, and more cryptic "pre-historic" angiosperms will be identified. Third, this non-typical arrangement of floral parts in Solaranthus may well represent the fluidity of organization in early flowers. Similar fluidity has been seen in the gametophyte of the basal angiosperm Amborella (Aulbach-Smith et al. 1984; Friedman and Ryerson 2009) (Fig. 6.45).

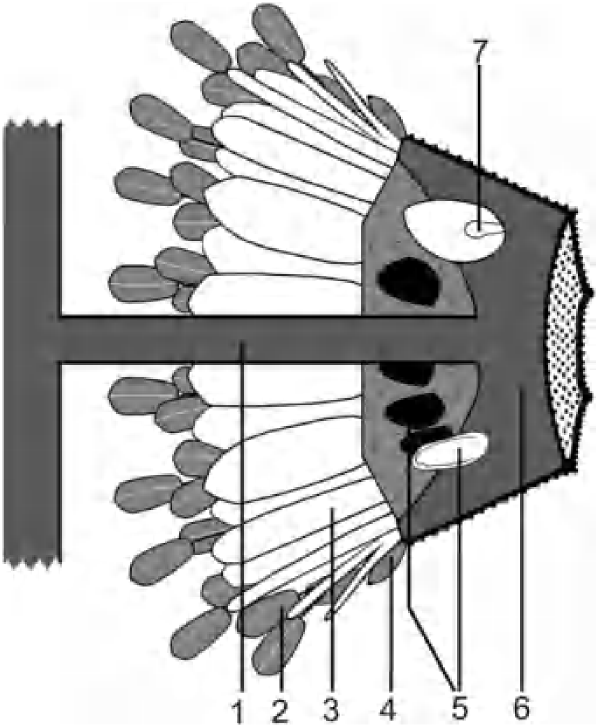

Fig. 6.45 The longitudinal sketch of a "flower". Note the stalk (1) inserted on the inflorescence axis, filamentous stamen (2), "tepals" (3), sessile stamen (4), ovulate structure enclosing ovule-like structure (5), peltate head (6), and an ovule-like structure (7) in a ovulate structure. Courtesy of Acta Geologica Sinica

6.4 Euanthus (Liu and Wang 2016)

The specimen of Euanthus was collected Mr. Kwang Pan (also known as Guang Pan) when he was sent to labor in the countryside in western Liaoning, China during the Cultural Evolution in the 1970s. Mr. Pan had collected large number of fossil plant specimens from the Sanjiaocheng Village area and claimed that there were several angiosperms in his collection (Pan 1983), which, however, was largely either ignored or declined by others (Xu 1987). The Jiulongshan Formation has yielded diversified palaeoflora including Bryophytes, Lycophytes, Ferns, Bennettitales, Cycadales, Ginkgoales, Coniferales, Caytoniales, angiosperms and plants with unknown affinities (Pan 1983; Zhang and Zheng 1987; Kimura et al. 1994; Pan 1997; Wang et al. 1997; Zheng et al. 2003; Wang et al. 2007a, b; Wang and Wang 2010). The fossil plant assemblage suggests a Middle Jurassic age for the Formation which is in agreement with palynological data (Xu et al. 2003), estherian, ostracode, entomofauna, and bivalve assemblage recovered from the Formation (Deng et al. 2003), and further by isotopic datings (Chang et al. 2009, 2014).

6.4.1 Generic Diagnosis

Flower perigynous, with half-inferior ovary, of pentamerous symmetry, with connected calyx, corolla, and gynoecium. Sepals short, stout, with a round distal concave portion and a stout base, attached by its whole base. Petals long, alternate to the sepals, with a round concave limb and a slender claw, and attached by the claw. Androecium with tetrasporangiate dithecate anthers and in situ pollen grains. Gynoecium including a long, slender style covered with hairs and an unilocular ovary enclosing unitegmic ovules inserted on the ovarian wall.

Type species: Euanthus panii (Liu and Wang 2016).
Etymology: Euanthus, for real flower in Latin.
Horizon: The Jiulongshan Formation.
Locality: Sanjiaocheng Village, Huloudao City, Liaoning, China.

6.4.2 Euanthus panii (Liu and Wang 2016)

Specific diagnosis: (In addition to generic diagnosis,) flower about 12 mm long, 12.7 mm wide. Receptacle about 2.3 mm in diameter, pentagonal in cross view. Sepals 3.6–3.85 mm long, 3.6 mm wide, with a round tip and a 1.9 mm-wide base. Petals 5–5.75 mm long, 3.8–4.2 mm wide. Stamen preserved only as anthers. Anther tetrasporangiate, dithecate, about 370 μm wide and 218 μm high, lacking of obvious connective, with in situ pollen grain about 12.6–16.2 μm in diameter. Style 8.5 mm long, 1.4 mm wide, elongate, tapering distally, covered with hairs, of cells with straight walls. Ovary pentermaous, about 2.2 mm in diameter, enclosing unitegmic ovules, with papilae on its inner wall.

Description: Preserved as compression, the specimen has some coalified residue, and it is split as part and counterpart (Fig. 6.46a, c), allowing both the adaxial and abaxial surfaces of the same part to be observed (Fig. 6.46g, h). The flower is about 12 mm long, 12.7 mm wide, including physically connected sepals, petals, possible androecium, and gynoecium (Fig. 6.46a, c). The receptacle is about 2.3 mm in diameter, pentagonal in oblique cross view, with each side about 1.55 mm long, and the angle between adjacent sides is about 110° (Fig. 6.47c, d). Two sepals are visible, 3.6–3.85 mm long, 3.6 mm wide, opposite to a side of the receptacle pentagon and attached with its full base (Fig. 6.46f). A sepal comprises two portions, a 3.6 mm wide, elliptical distal portion and a stout, 1.9 mm-wide, parallel-sided base (Figs. 6.46f and 6.47c). The distal portion is concave when viewed adaxially, with an abaxial keel (Fig. 6.46f). Three petals are visible, alternate with the sepals, 5–5.75 mm long, 3.8–4.2 mm wide, opposite to a corner of the receptacle pentagon (Fig. 6.46a, c, g, h). A petal comprises two portions, a round distal limb and an ob-triangular claw (Fig. 6.46g, h). The limb is 3.2 mm long, 4.2 mm wide, concave when viewed adaxially, with concentric wrinkles at the margin and a round tip, and lacking of an obvious keel (Fig. 6.46g–k). The claw is ob-triangular in shape, narrowing basally, with obvious transverse wrinkles on its distal abaxial (Fig. 6.46g, j). Stamens are inserted between the petals and gynoecium, with only two partially preserved anthers (Fig. 6.49a, d–f). The filament is slender, about 32 wide μm, partially preserved, inferred to be 3.1–3.8 mm long (Fig. 6.49b, c). The anther is tetrasporangiate, dithecate, constricted vertically in the middle, with two adjacent pollen sacs on one side confluent forming an 8-shaped configuration (Fig. 6.49d, h). Pollen sac wall is about 23 μm thick (Fig. 6.49f, h). Possible in situ pollen grains are 12.6–16.2 μm in diameter (Fig. 6.49f, h). The gynoecium is in the center of the flower, including an ovary and a style, with some coalified residue (Fig 6.46a, c). The style is about 10 mm long (Fig. 6.46b, d), visible as two separated segments eclipsed by a sepal in between (Fig. 6.46a, c). The basal segment is physically connected with the ovary, about 1.3 mm wide, elongated, tapering distally, with longitudinal hairs on its surface (Figs. 6.46c, 6.47a, and 6.48f). The distal segment is 5.8 mm long, 0.7 mm wide, tapering distally, with possible secretory structures (Figs. 6.46b, d and 6.48a–d). A hair is about 29 × 33 μm in cross view (Fig. 6.48c, e). The ovary is pentamerous, about 2.3 mm in diameter (Fig. 6.47c, d). Inside the ovary are several protrusions, and at least one of them may be an ovule with a micropyle-like structure (Fig. 6.48g, h). The ovule is 0.2–0.4 mm long, with a pointed micropyle defined by an integument (Fig. 6.48i, j). The integument is 5–8.8 μm thick, covering the

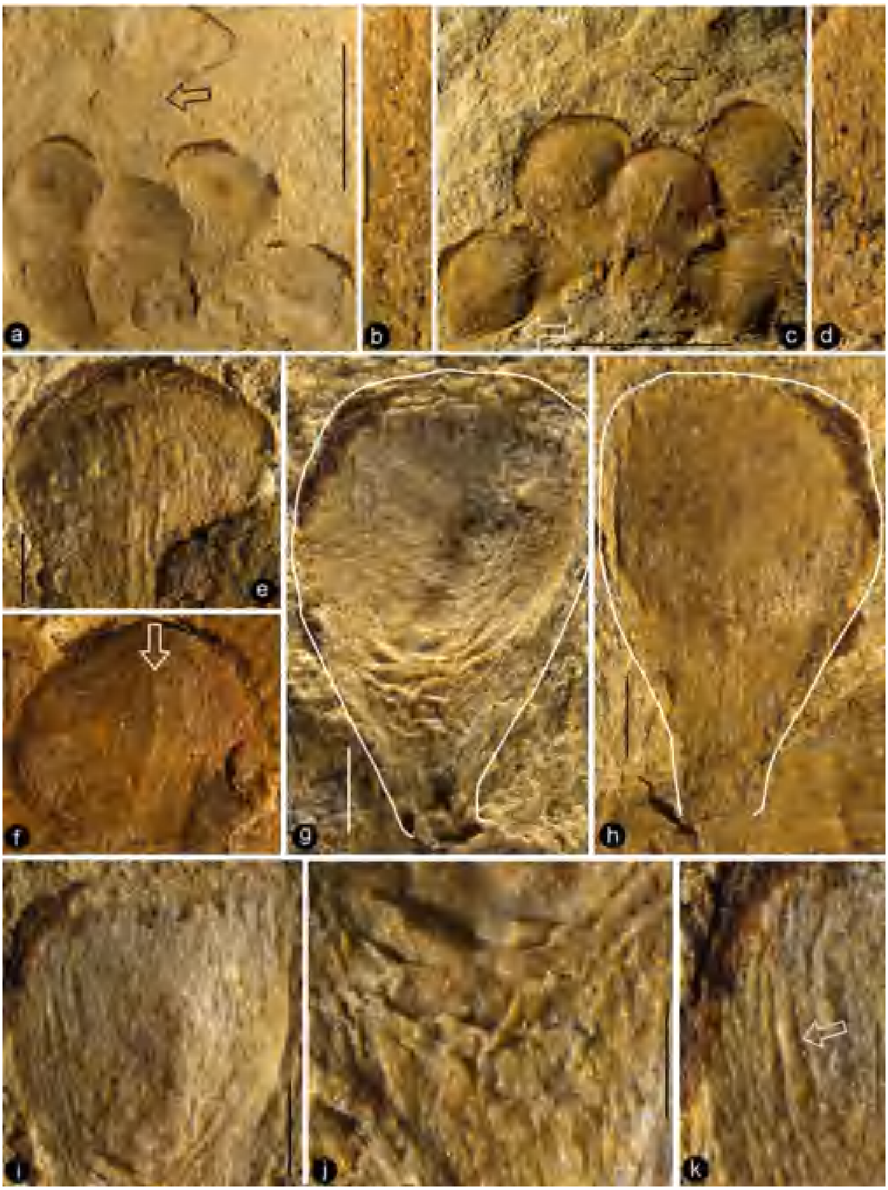

Fig. 6.46 Euanthus panii and its details. Stereomicroscopy. (a, c) The flower in two facing parts. The black arrows mark the style. Holotype. Bar = 5 mm. (b, d) Detailed views of the style in a and c. Bar = 1 mm. (e) Details of a petal pointing to the upper-left in c. Bar = 1 mm. (f) Details of the sepal pointing to the upper-right in c, showing a keel (arrow). Bar = 1 mm. (g) Adaxial view of the petal the right of a, showing a round concave limb and a claw with transverse wrinkles. Bar = 1 mm. (h) Abaxial view of the petal in g, showing the round convex limb and the claw with no wrinkles. Bar = 1 mm. (i) Detailed view of the limb portion of the petal in g. Note the concave smooth central portion and the margin with concentric wrinkles. Bar = 1 mm. (j) Transverse wrinkles on the adaxial surface at the distal portion of the claw in g. Bar = 0.5 mm. (k) Concentric wrinkles on the margin of the limb in i. Bar = 0.5 mm

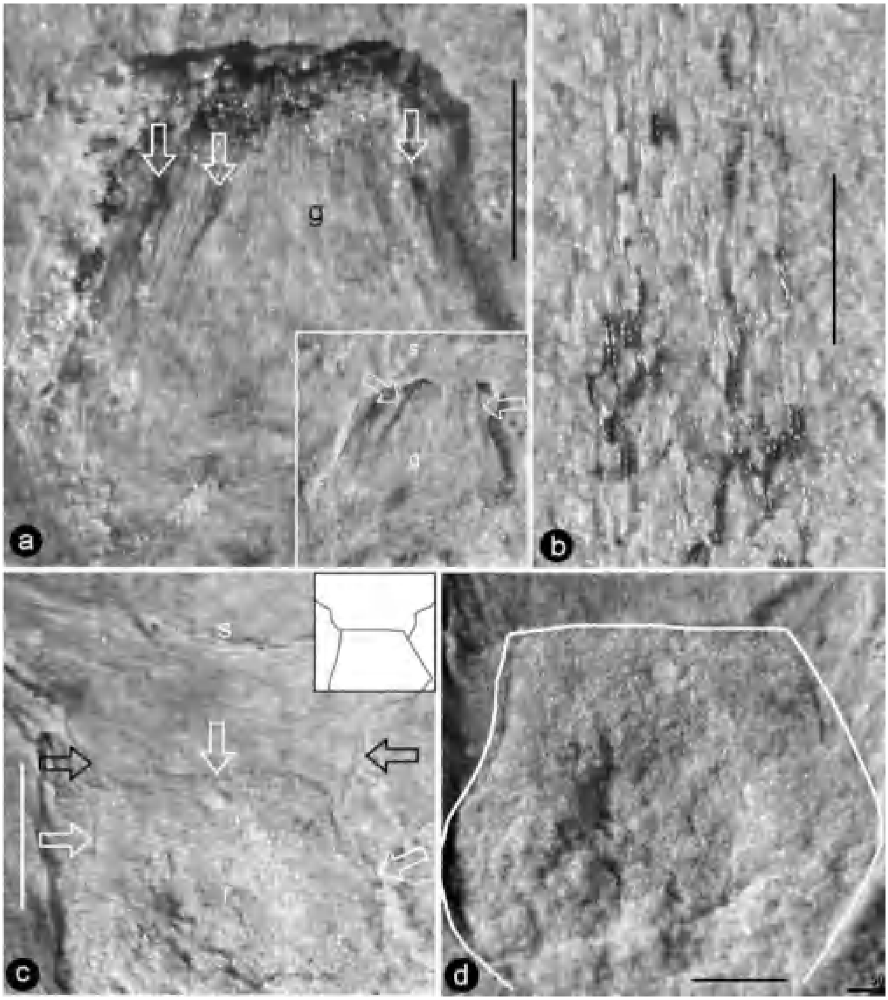

Fig. 6.47 Details of *Euanthus panii*. Stereomicroscopy. (a) Basal segment of the gynoecium (g), with longitudinal hairs (arrows) on its surface. Inset shows the same area before more details are exposed. Bar = 0.5 mm. (b) Detailed view of the style with longitudinal hairs. Bar = 0.5 mm. (c) Detailed view of a sepal (s) with the parallel-sided base (black arrows) joining a side (white arrow) of the receptacle pentagon (r) with its whole base. Outline shown in the upper-right. Bar = 1 mm. (d) Pentagonal receptacle. Bar = 0.5 mm

nucellus (Fig. 6.48i, j). Papillae are seen on the inner wall of the ovary (Fig. 6.48k). Pits are seen on the side wall of a vascular element (Fig. 6.49j, k). The whole flower is sketched in Fig. 6.50a and reconstructed in Fig. 6.50b.

Etymology: *panii* for Mr. Kwang Pan (1920–2014), the collector and donor of the specimen.

Holotype: PB21685 (Fig. 6.46a), PB21684 (Fig. 6.46c).

Depository: the Nanjing Institute of Geology and Palaeontology, Nanjing, China.

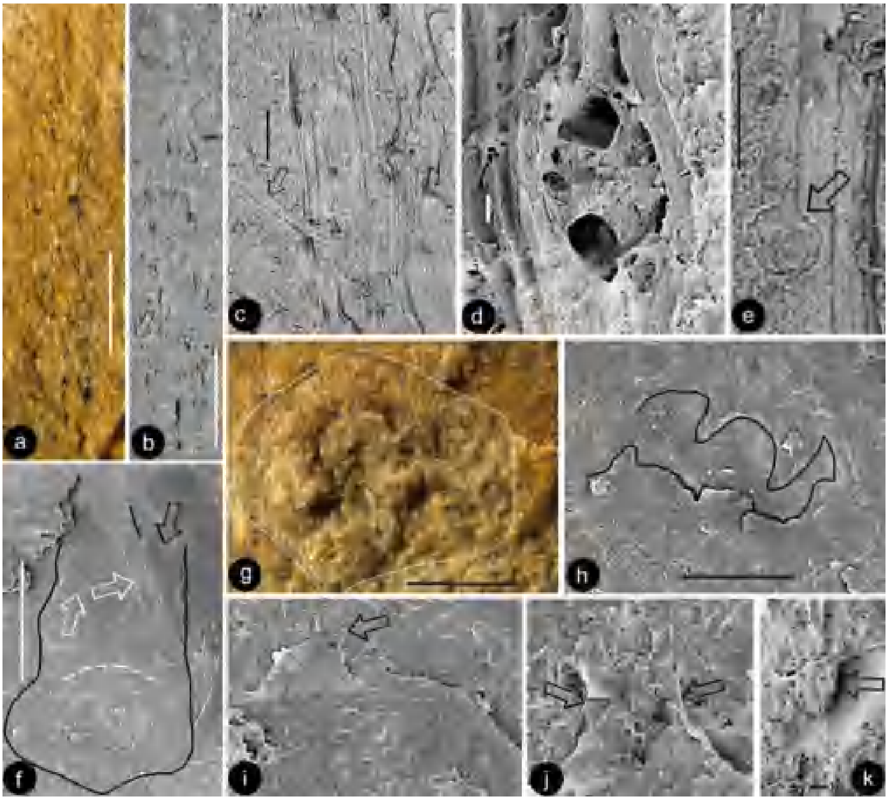

Fig. 6.48 Gynoecium of Euanthus panii. Stereomicroscopy and SEM. (a, b) The distal style with hairs, viewed under SEM (a) and stereomicroscope (b). Bar = 1 mm. (c) A hair (arrow) branching off from the style, enlarged from the arrowed region in B. Bar = 0.1 mm. (d) A possible secretory structure on the style. Bar = 10 μm. (e) Cells in the style with straight cell walls. Note a scar (arrow) left by a fallen-off hair. Bar = 50 μm. (f) The basal portion style and ovary (outlined). Note the branching-off possible filament stub (black arrow) and inner wall (white arrows) of the ovary. Bar = 1 mm. (g, h) Detailed view of the same receptacle and ovary, under stereomicroscope and SEM. Note the pentamerous outline of the receptacle (white line) and protrusions (black lines) on the inner wall of the ovary. Bar = 0.5 mm. (i) The ovule enlarged from h, with a micropyle (arrow). Bar = 50 μm. (j) Details of the micropyle in i. Note that there is only one layer of integument (arrows) covering the nucellus (n). Bar = 20 μm. (k) One of the papillae on the inner ovarian wall. Bar = 10 μm

Remarks: All the parts of Euanthus are physically connected each other, except the male parts the arrangement of which suggests that they are also very likely physically connected although independent of the petals (Figs. 6.46c and 6.49b, c). A possible filament is seen between the gynoecium and petal (Fig. 6.49b, c) and a linear structure (Fig. 6.49a, b) close to the anther (Fig. 6.49a) is very likely a filament.

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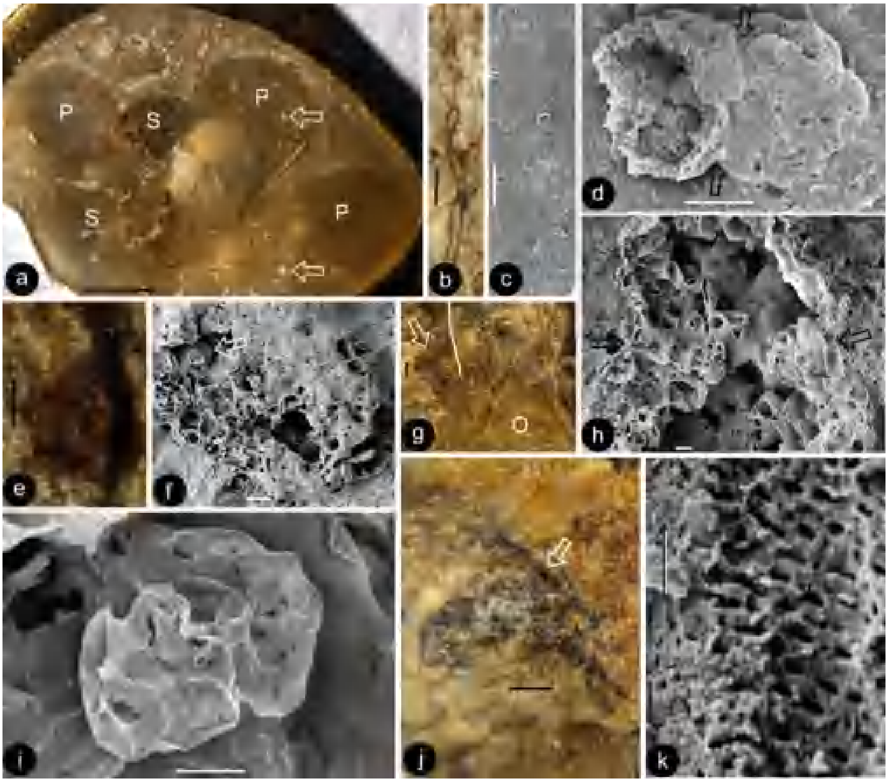

Fig. 6.49 Stamens of Euanthus panii. Stereomicroscopy and SEM. (a) Nitro cellulose replica of the specimen in Fig. 6.46c, showing the positions of two anthers (white arrows) relative to the sepals (S) and petals (P). The white line marks the position of the possible filament shown in b and c. Bar = 2 mm. (b, c) A possible filament on the replica, marked with a white line in a. Stereomicroscopy (b) and SEM (c). Bar = 0.1 mm. (d) The anther marked by a lower arrow in a showing the constriction (arrows) between the left and right halves of the anther. The left half is broken, and its internal details are visible. Bar = 0.1 mm. (e) Dark organic material in the anther marked by the white arrow in Figs. 6.46c and 6.49a. Bar = 0.1 mm. (f) The anther marked by the upper arrow in a, showing a broken anther with possible in situ pollen grains (arrow). Bar = 20 μm. (g) Details of the basal portion of the gynoecium, showing a possible filament stub (arrow) beside the hairy style (to the right of white line) and the ovarian cavity (O). Bar = 0.1 mm. (h) Details of d, showing two confluent pollen sacs in the anther (arrows) and its cellular details. Bar = 10 μm. (i) Detailed view of the possible in situ pollen grains in the anther shown in f. Bar = 5 μm. j Organic material preserved in the flower, arrowed in g. Bar = 0.1 mm. (k) Pitting on a vascular element, enlarged from the arrowed region in (j). Bar = 2 μm

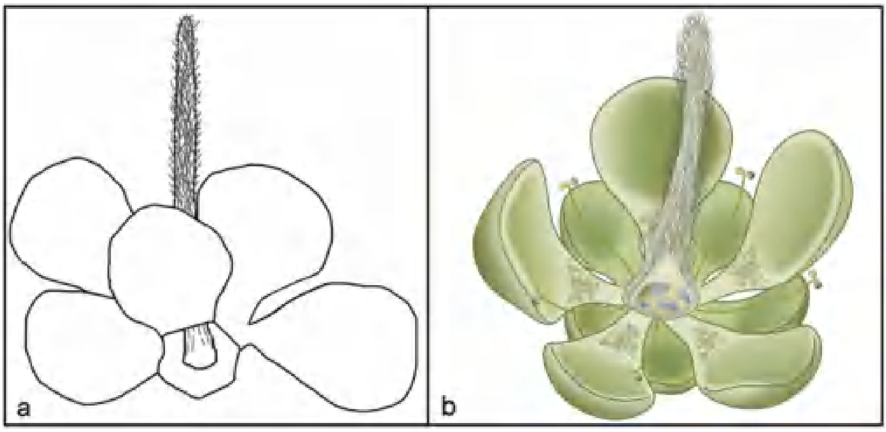

Fig. 6.50 Sketch and reconstruction of Euanthus panii. (a) Sketch of the specimen shown in Fig. 6.46a. (b) Reconstruction of Euanthus panii

6.4.3 Discussions

6.4.3.1 The Age

The Callovian-Oxfordian (Middle-Late Jurassic) age of Euanthus is not claimed by us or any single group alone, but is a consensus reached by various authors working in different fields using different techniques and based on various types of evidence including biostratigraphical as well as isotopic data (Pan 1983, 1997; Zhang and Zheng 1987; Kimura et al. 1994; Wang et al. 1997; Deng et al. 2003; Zheng et al. 2003; Wang et al. 2007a; Chang et al. 2009, 2014; Wang and Wang 2010; Walker et al. 2012). Two isotopic datings have been published to narrow down the scope of the age for the Jiulongshan Formation (Chang et al. 2009, 2014), which has previously yielded several angiosperms including Euanthus, Schmeissneria, and Xingxueanthus. The ^{39}Ar/^{40}Ar datings indicate that these fossil plants are at least 161.8 Ma old (Chang et al. 2009, 2014). Therefore I think that Euanthus is of the Callovian-Oxfordian (Middle-Late Jurassic) in age.

6.4.3.2 The Affinity

People used various characters to define Angiosperms, including vessel elements, reticulate venation, tetrasporangiate anthers, enclosed ovules, and flowers (Wang 2009). Among them, flowers are by far the most reliable and easy-to-accept criterion identifying angiosperms (Thomas 1936), and enclosed ovule before pollination is a defining and sufficient character to pin down angiospermous affinity. Typically, an angiosperm perfect flower includes four whorls of parts, namely, calyx, corolla, androecium, and gynoecium (Judd et al. 1999), with the perianth (foliar parts) arranged around the gynoecium / androecium (Bateman et al. 2006). Euanthus has most, if not all, of the characteristics of typical flowers of angiosperms.

Euanthus can be distinguished from reproductive organs of gymnosperms by various flower features. The perianth of Euanthus is morphologically differentiated into calyx and corolla with different shapes and sizes (Fig. 6.46a, c, e–h), while, in Bennettitales/Gnetales (the only two that are bisexual and frequently related to angiosperms), peripheral foliar parts surrounding female and/or male parts are at most poorly differentiated (Watson and Sincock 1992; Rothwell and Stockey 2002; Stockey and Rothwell 2003; Bateman et al. 2006; Crane and Herendeen 2009). The well-differentiated sepals and petals, transverse wrinkles on the abaxial of its petals, pentagonal receptacle, slender hairy style, and lack of interseminal scales (Fig. 6.46a, c) distinguish Euanthus from the Bennettitales, the reproductive organs of which are round in cross view, with numerous seeds tightly surrounded by interseminal scales on the periphery of the gynoecium (Watson and Sincock 1992; Crane and Herendeen 2009; Friis et al. 2009a; Rothwell et al. 2009). Decussate arrangement of scales/bracts, characteristic of Gnetales, are nothing comparable to the pentagonal configuration of Euanthus (Fig. 6.47c, d). Most importantly, micropylar tube (characteristic of both Bennettitales and Gnetales) is smooth, free of hairs, and not comparable to the style of Euanthus (Fig. 6.46b, d). Finally, ovules with micropyle and integument are enclosed inside the ovary (Fig. 6.48f–j) in Euanthus, sufficient to make a conclusion that Euanthus belongs to angiosperms. Furthermore tetrasporangiate dithecate anther, a feature so far restricted to angiosperms only, reinforces the above conclusion about Euanthus. The pitting pattern seen on the side wall of vascular element in Euanthus (Fig. 6.49j, k) is very similar to the one seen on the intervessel wall of a Miocene angiosperm fossil wood (Ruprechtioxylon multiseptatus, Polygonaceae, Fig. 2h, i of Cevallos-Ferriz et al. 2014).

6.4.3.3 Origin of Angiosperms

Although the widely-accepted record of angiosperms is still restricted to the Early Cretaceous for many. Angiosperms may well have a history extended further beyond the scope of Cretaceous. This is suggested by the unexpectedly high diversity of angiosperms in the Early Cretaceous Yixian Formation (Duan 1998; Sun et al. 1998, 2001, 2002; Leng and Friis 2003, 2006; Ji et al. 2004; Wang and Zheng 2009; Wang and Han 2011; Han et al. 2013, 2017), the existence of angiosperms from the Jurassic (Wang et al. 2007a, b; Wang 2010b; Wang and Wang 2010), pollen grains indistinguishable from angiosperms seen in the Triassic (Hochuli and Feist-Burkhardt 2004, 2013), independent studies (Schweitzer 1977; Cornet 1989a, b, 1993; Chaw et al. 2004; Soltis et al. 2008), recent discoveries of new fossil materials Poales and Solanaceae and related BEAST analyses (Prasad et al. 2011; Wilf et al. 2017). Insects closely related to angiosperms or flowers have been reported from the Middle Jurassic (Wang and Zhang 2011; Hou et al. 2012).

The discovery of Euanthus confirms that flower does exist in the Jurassic. This would help to push the origin of flower back to more ancient times.

The Jurassic age of Euanthus favors an earlier origin of angiosperms suggested by contemporaneous Jurassic angiosperms, including Schmeissneria (Wang et al. 2007a, b; Wang 2010b) and Xingxueanthus (Wang and Wang 2010) recovered from the same locality of the Middle-Late Jurassic. The distinct difference and great diversity in reproductive strategy and morphology demonstrated by these angiosperms suggest that a prior crypt history is necessary to make sense.

Eudicots are characterized by floral pentamerism and tricolpate pollen grains (Doyle 2012). If the pentamerism of Euanthus shared the same origin with eudicots, then either the well-accepted derivedness of eudicots in angiosperms (APG 2009) would face challenges, or the ancestral angiosperm clades must have an unknown history before Euanthus.

6.4.3.4 Evolution of Flowers

The pentagonal configuration of the receptacle in Euanthus (Fig. 6.47c, d) is frequently seen in typical eudicots (Judd et al. 1999). Sepals and petals are of different morphologies and arrangement in Euanthus, a feature relatively derived and not expected for pioneer angiosperms (Doyle and Endress 2000; Doyle 2008; Friis et al. 2010). Their unexpected presence in Jurassic Euanthus constitutes a drastic contrast against the lack of a perianth in Archaefructus and the poorly-differentiated perianth in Callianthus from the Early Cretaceous (Sun et al. 1998; Sun and Dilcher 2002; Ji et al. 2004; Wang and Zheng 2009; Wang and Zheng 2012), creating an anachronism in term of perianth evolution. Maybe these groups are independently evolved and phylogenetically unrelated, or the status seen in those Early Cretaceous angiosperms is secondarily derived, as suggested previously (Friis et al. 2003). Theoretically, undifferentiated perianth must occur before differentiated ones. If so, then the well-differentiated perianth of Jurassic Euanthus implies that there should be a crypt history prior to Euanthus. According to Endress and Doyle (2009), presence of a perianth is a feature for the most recent common ancestor of all angiosperms. If truly phylogenetically related to later angiosperms, Euanthus′ perianth (sepals and petals) seems to favor to Endress and Doyle′s conclusion. However, the situation would be much more complicated if perianth or flowers originated multiple times independently. Answers to these questions lie in future fossil discovery.

The gynoecium with hairy style of Euanthus is located in the center of the flower. The orientations and surface hairs of its both segments of the style are aligned (Figs. 6.46a–d and 6.47a, b), suggesting that both belong to a single style. Similar hairy style has been seen in some angiosperms (especially Poales and Asterales) (Maout 1846; Judd et al. 1999), but almost never seen in any gymnosperms (Maout 1846; Melville 1963; Friis and Pedersen 1996). The function of these hairs may be related to pollen collecting, as in some extant angiosperms

(Maout 1846; Judd et al. 1999). The presence of possible secretory structure in the style (Fig. 6.48d) makes this interpretation more plausible.

6.4.3.5 Summary

Euanthus from the Middle-Late Jurassic is a perfect flower typically restricted to angiosperms. Its occurrence in the Middle-Late Jurassic prompts a re-thinking on the origin and history of flowers and angiosperms. If Euanthus were really related to eudicots, searching for typical eudicot leaves in the Jurassic strata appears promising. The occurrence of a full-fledged flower like Euanthus in the Jurassic undermines the validity of the stereotype “no angiosperms until the Cretaceous”, which is widespread among botanists now. Such a change may trigger a series of far-reaching changes in our perspective on angiosperm evolution, including homology of carpels, possible ancestors, and relationship between angiosperms and gymnosperms.

6.5 Yuhania (Liu and Wang 2016)

Specimen of Yuhania was collected from the Jiulongshan Formation (the Middle Jurassic, >164 Ma) near Daohugou Village of Inner Mongolia, China (119°14′40″E, 41°19′25″N), including various physically connected organs.

6.5.1 Generic Diagnosis

Plant including connected stem, leaves, flowers, aggregate fruits, fruitlets, and seeds in fruitlets. Stem curving, with longitudinal ridges and hairs. Leaves linear, probably spirally arranged, clasping the stem, entire margined, with an acute tip and five to six (rarely seven) parallel veins. Flowers unisexual, female, axillary, including carpels helically arranged along an axis. The carpels rhomboidal-shaped in early stages. Aggregate fruit pedicellate, with helically arranged fruitlets and bracts. Each fruitlet with a cuspidate or rounded tip, enclosing a seed. Seed inserted on the floral axis, on the abaxial of the enclosing foliar part.

Type species: Yuhania daohugouensis (Liu and Wang 2016)
Etymology: Yuhania for Ms. Yuhan Cai, the daughter of Mr. Hongtao Cai who helped collecting the specimen for this study.
Type locality: the Daohugou Village, Ningcheng, Inner Mongolia, China (Fig. 1a, b).
Horizon: The Jiulongshan Formation, Callovian, Middle Jurassic (>164 Ma).

6.5.2 Yuhania daohugouensis (Liu and Wang 2016)

Specific diagnosis: The same as the genus for the time being.

Description: The specimen is preserved as compression and impression, including part and counterpart, with some coalified materials embedded in yellowish tuffaceous siltstone, associated with many conchostracans that are characteristic of some strata of the Jiulongshan Formation near Daohugou Village (Fig. 6.51a). The fossil is 12 cm long, 10 cm wide, including physically connected stem, buds, leaves, flowers, aggregate fruits, fruitlets, and seeds in fruitlets (Fig. 6.51a). The stem is about 2.5 mm in diameter, curving, with leaves probably helically (Fig. 6.51a). The stem bears longitudinal ridges and hairs (Fig. 6.51e, h) or transverse wrinkles (Fig. 6.52f). Lateral bud including helically arranged scales is about 3.3 mm long and 2.3 mm wide at the base, tapering distally (Fig. 6.51f, g). The smallest leaf observed so far is only 0.68 mm long, fringed with dentate protrusions (Fig. 6.52i). The most of leaves are simple, 9–70 mm long, 1.2–4 mm wide, clasping the stem, linear, entire-margined, curving or almost straight (Figs. 6.51a–d and 6.52a–h, j). There are an acute tip, five to six (rarely seven) parallel veins, no midvein in each leaf (Figs. 6.51a–c and 6.52a–f). The veins are 0.1–0.23 mm wide alternating interveins about 0.13–0.34 mm wide, bifurcating only in the basal part of the leaf (Figs. 6.51b, d and 6.52a–e). The veins are obviously parallel in the middle portion of the leaves (Fig. 6.51b, d), but the vein pattern becomes transverse wrinkles in the distal portion of leaves (Fig. 6.52a–c). The regular vein pattern is suddenly lost in the distal of the leaves, probably due to the apical meristematic activity (Fig. 6.52a–c). The adaxial epidermis has longitudinally oriented cells, stomata-free (Fig. 6.52d). The abaxial epidermis has alternating vein and intervein zones (Figs. 6.51d and 6.52e). Stomata are restricted to the abaxial of the leaves, arranged in files between the veins, close to round in shape, about 156–180 μm long and 211–264 μm wide, with pit covered by protrusions or not (Figs. 6.51d and 6.52e, g). The mesophyll includes longitudinally oriented adaxial parenchyma and spongy parenchyma above the abaxial epidermis (Fig. 6.52h). Possible insect damage is seen on some leaves (Fig. 6.52j). At least six aggregate fruits and two flowers are seen physically connected with the fossil (Fig. 6.51a). The pistillate flower are spherical, 1.3–1.46 mm wide and 1.3–1.39 mm long, supported by a stout pedicel, with helically arranged rhomboidal immature carpels (Figs. 6.51g, h and 6.53a–d). The flower pedicel is 0.6–1 mm wide and 0.5–0.7 mm long (Figs. 6.51g and 6.53a). The aggregate fruit pedicel is up to 4.3 mm long and 2.1 mm wide (Fig. 6.51h). A flower is 4–4.5 mm long and 2.6–3.1 mm wide, attached to the stem, with more than 20 fruitlets helically arranged (Fig. 6.53a, d). Each bract has a midrib and a rounded tip, at least 0.9 mm long and 0.9 mm wide (Fig. 6.53h). The bracts and fruitlets point to the proximal of the aggregate fruit (Fig. 6.53d). A young or aborted fruitlet appears triangular in shape, about 0.9 mm long and 0.9 mm wide, widest near the proximal, constricting rapidly to the distal, sometimes broken near the tip

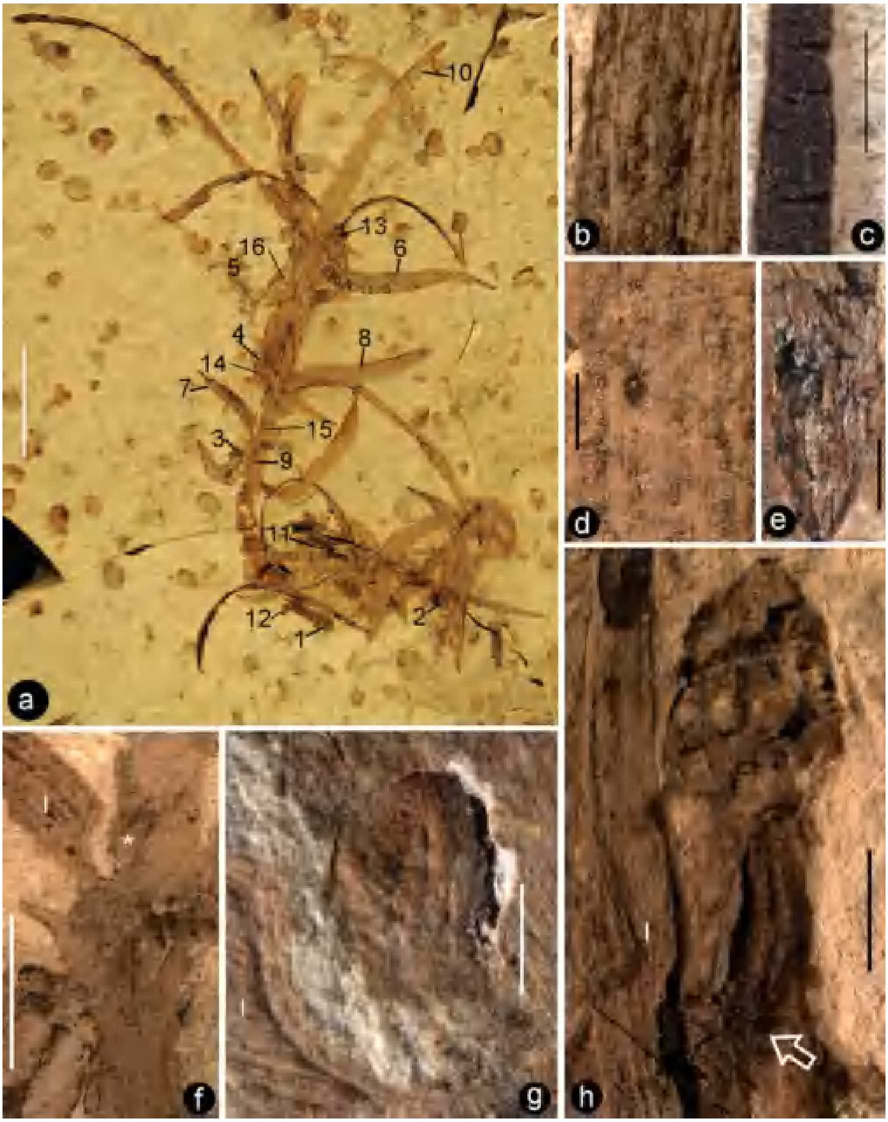

Fig. 6.51 *Yuhania daohugouensis* and its details. Light microscopy. (a) The fossil embedded in yellowish tuffaceous siltstone. Some of the labeled regions are shown in later figures. 1–4 and 12–13 are six aggregate fruits, 14–15 are immature flowers, 5 is an associated lichen [*Daohugouthallus ciliiferus* (Wang et al. 2010)], 6–10 are leaves, and 16 is a lateral bud. Bar = 2 cm. (b) Details of the leaf marked as 7 in a, with parallel veins and entire margin. Bar = 1 mm. (c) A leaf preserved as compression (to the left) and as impression (to the right). Bar = 1 mm. (d) Detailed view of the leaf marked as 8 in a, with entire margin, alternating veins and stomata zones. Bar = 1 mm. (e) Stem with longitudinal ridges, partially embedded in the sediments. Bar = 1 mm. (f) Detailed view of the region as 15 in a, showing an immature flower (asterisk) in leaf (l) axil. Bar = 5 mm. (g) Detailed view of the immature flower in leaf (l) axil in f. Bar = 1 mm. h The aggregate fruit marked as 1 and 12 in a. Note the pedicel connected (arrow) to the stem. Bar = 2 mm

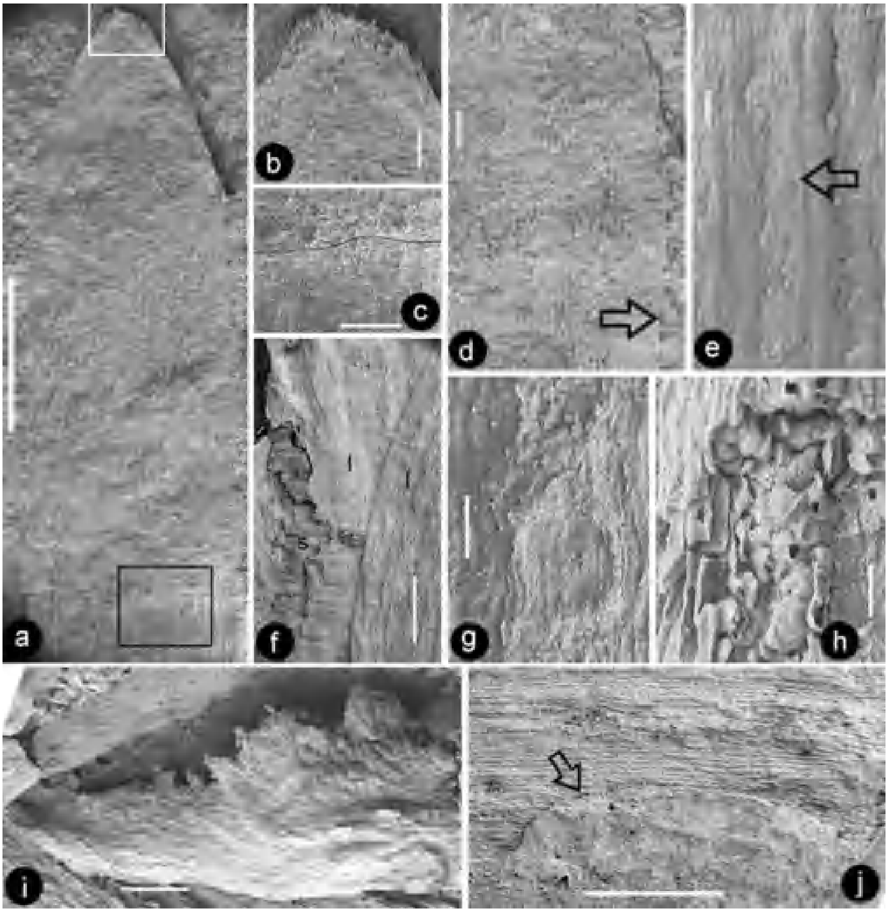

Fig. 6.52 Leaves and their details. SEM. (a) Abaxial view of leaf tip marked as 10 in Fig. 6.51a, showing the entire leaf margin and parallel veins. Bar = 1 mm. (b) Leaf tip with papillae, enlarged from the white rectangle region in a. Bar = 0.1 mm. (c) Leaf texture transitional from regular (below the line) to chaotic (above the line), enlarged from the black rectangle in a. Bar = 0.2 mm. (d) An adaxial view of a leaf, showing longitudinal epidermal cells and entire leaf margin (arrow). Bar = 0.1 mm. (e) An abaxial view of the leaf in Fig. 6.51d, showing well-defined alternating vein and intervein (stomata, arrow) zones. Bar = 0.2 mm. (f) Leaf (l) clasping and diverging from the stem (s) with horizontal wrinkles. Note the leaf texture changes from the horizontal to longitudinal from the bottom up. Bar = 0.2 mm. (g) Detailed view of the stomata arrowed in e. Bar = 0.1 mm. (h) A leaf with elongated epidermal cells (upper-left) and mesophyll aerenchyma. Bar = 50 µm. (i) A leaf in its earliest developmental stage, fringed with dentate protrusions. Bar = 0. 1 mm. (j) Leaf probably damaged by insect (arrow). Bar = 0.5 mm

(Fig. 6.53i). A mature fruitlet is up to 0.9 mm long and 0.7–1.1 mm wide, widest near the distal part, converging rapidly to a cuspidate or rounded tip (Fig. 6.53d–g). A seed with a smooth surface and round shape is inserted on the floral axis, covered by the foliar part bending back down to the proximal, and is visible only when the fruitlet wall is broken (Fig. 6.53e, g).

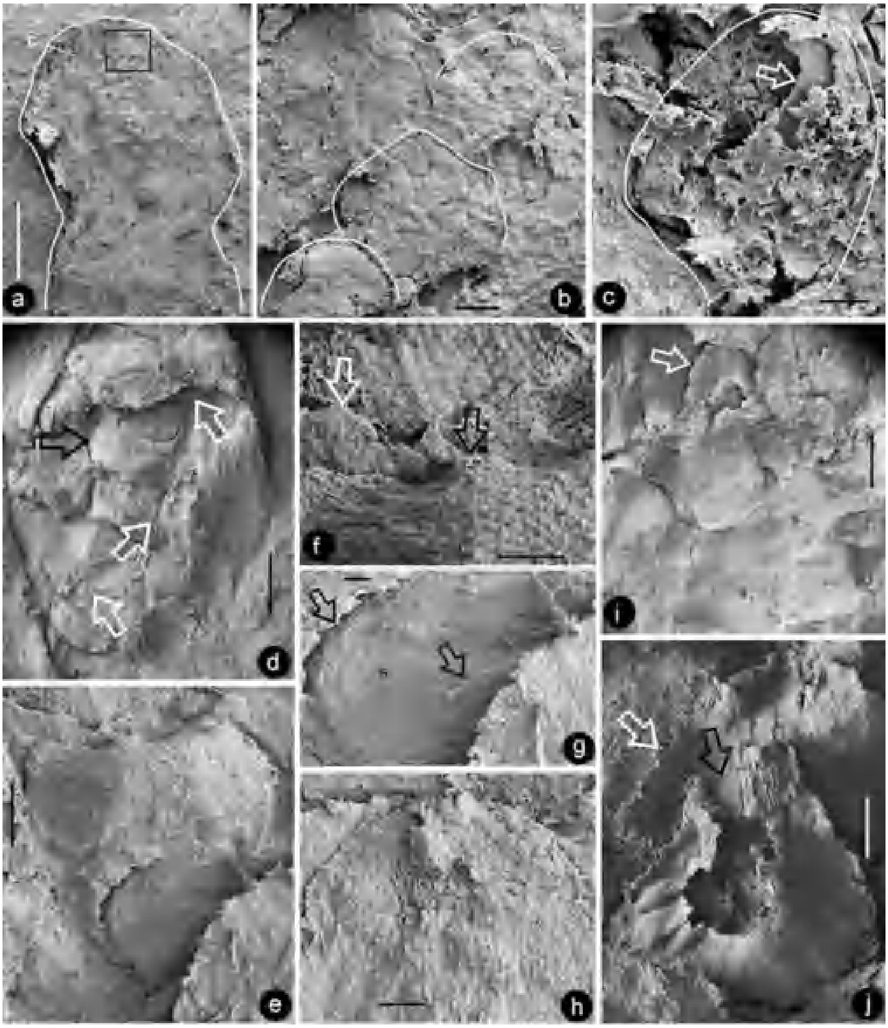

Fig. 6.53 Flower and aggregate fruits of Yuhania. SEM. (a) The immature flower in Fig. 6.51g, with a stout pedicel and spherical receptacle. Bar = 0.5 mm. (b) Detailed view of the rectangle in a, showing outlines of the carpels helically arranged. Bar = 20 μm. (c) The sac-like carpel marked as c in a. Bar = 10 μm. (d) SEM view of the aggregate fruit in Fig. 6.51h, with helically arranged fruitlets. Bar = 0.5 mm. (e) One of the fruitlets from the aggregate fruit in d, with its seed exposed. Bar = 0.2 mm. (f) Detailed view of the distal portion of the fruitlet in e. Note the cuspidate tip (black arrow), the greatest width near the distal of the fruitlet, and a bract (white arrow). Bar = 0.1 mm. (g) Detailed view of the proximal part of the fruitlet in e, showing the broken fruitlet wall (arrows) and exposed seed (s) in the fruitlet. Bar = 50 μm. (h) Rounded tip and longitudinal texture in the middle of a bract. Bar = 0.1 mm. (i) SEM view of the aggregate fruit marked as 2 in Fig. 6.51a. Bar = 0.5 mm. (j) A young “carpel” with a broken tip (black arrow), wide base, and a bract in the background (white arrow). Note the empty space in the “carpel”. Bar = 0.2 mm

Holotype: PB21544, deposited in the Nanjing Institute of Geology and Palaeontology, Nanjing, China.

Isotype: NOCC20130506018, deposited in the Orchid Conservation and Research Center of Shenzhen, Shenzhen, China.

Etymology: daohugouensis for Daohugou Village, Ningcheng, Inner Mongolia, China, where the specimens were collected.

6.5.3 Remarks

Good preservation is the foundation for a robust palaeobotanical interpretation of fossil plants. Normally, fragile parenchyma and young leaves are not preserved in plant fossils. The preservation of mesophyll parenchyma and young leaf in Yuhania (Fig. 6.52h) strongly suggests that preservation of Yuhania implies the faithful preservation of morphology. Furthermore, connection among various parts (including leaves, branches, and fructifications) in a single specimen makes the reconstruction of Yuhania free of imagination and artifacts, and thus more believable.

6.5.4 Consistent Criterion for Angiosperm Recognition

To make claims of early angiosperms more believable, using a consistent criterion that is clearly elaborated is necessary for the sake of communication, examination and testing by the third party. Angio-ovuly before pollination is the criterion used in this book. This is a criterion that has been used for long time in paleobotany. For example, the transferring of former angiosperm Caytonia (Thomas 1925) into gymnosperms is due to the discovery of pollen grains found inside its so-called cupules (Harris 1933, 1940). Another example is Archaefructus, which was recognized as an angiosperm because of enclosed ovules/seeds, as no male part or leaf of Archaefructus was available for Sun et al. in 1998 to identify their fossil.

6.5.5 Female Parts and Implications

An aggregate fruit of Yuhania includes multiple fruitlets (Fig. 6.53d). If these fruitlets are alternatively interpreted as seeds aggregated around an axis, the space inside the assumed seed/ovule is a challenge for this interpretation (Fig. 6.53g, j). The expected seed coat is either broken or lacking in Yuhania (Fig. 6.53e, g). The assumed seed with empty space and internal body can be more rationally interpreted as a fruitlet enclosing a seed in its locule. Therefore I drop this alternative.

The tips of most Yuhania fruitlets are complete and closed, and their seeds are not visible from outside (Fig. 6.53d), suggesting the occurrence of angiospermy in Yuhania. The fruitlet with an exposed seed in Yuhania (Fig. 6.53e, g) does not nullify the angiospermous affinity of Yuhania as seeds of Magnolia are exposed after fruit maturation, only implying that the fruitlet of Yuhania is mature rather than that the ovule is exposed.

A young fruitlets of Yuhania has a breaking tip, probably due to the poorly-developed cuticle as expected for an immature carpel, making the details in a secluded cavity visible. The scar of a possible ovule and adnation of the "carpel" wall to the axis are seen in this "carpel" (Fig. 6.53j). The morphological differences between this young carpel and mature fruitlets (Fig. 6.53e, j) suggests that Yuhania underwent a great developmental change after pollination, which is frequently seen in angiosperms but rarely or never in gymnosperms (Leslie and Boyce 2012). The current available data seem to point to an angiospermous affinity for Yuhania although further evidence and discussion are always welcome to test this hypothesis (Fig. 6.54).

6.5.6 Position of Ovule

Different from all known angiosperms, the abaxial position of ovule relative to its enclosing foliar part in Yuhania is unique or rare in angiosperms or even seed plants. It distinguishes Yuhania from most Coniferales and Cordaitales, in which the ovules are usually borne on secondary axillary shoot in the axil of a bract. In at least most angiosperms, the ovules are adaxial relative to the foliar parts that enclose them. This spatial relationship between ovules and enclosing parts is conceivable and easy to understand considering that, among seed plants, axillary branching is almost ubiquitous. The common spatial relationship between ovules and adjacent foliar parts shared by Yuhania and Corystospermales, on one hand, implies their close phylogenetic relationship, on the other hand, suggests that angio-ovuly and angiospermy may be reached independently by various groups.

6.5.7 Jurassic Monocot?

Parallel venation with files of stomata, longitudinally oriented epidermal cells, alternating leaf zones with and without stomata, linear leaf shape, entire leaf margin, and leaf base clasping stem in Yuhania are frequently seen in monocots (Fahn 1982; Stevens 2008). Despite some of these features are also in some conifers, the morphology of reproductive features of Yuhania makes further considering conifers indecent. Among the above six features, the first four have been considered as basic features or synapomorphies of monocots (Doyle et al. 2008). The presence of fruitlets in Yuhania indicates that the plant was already mature when fossilized. Little or no secondary growth in this mature plant suggests that

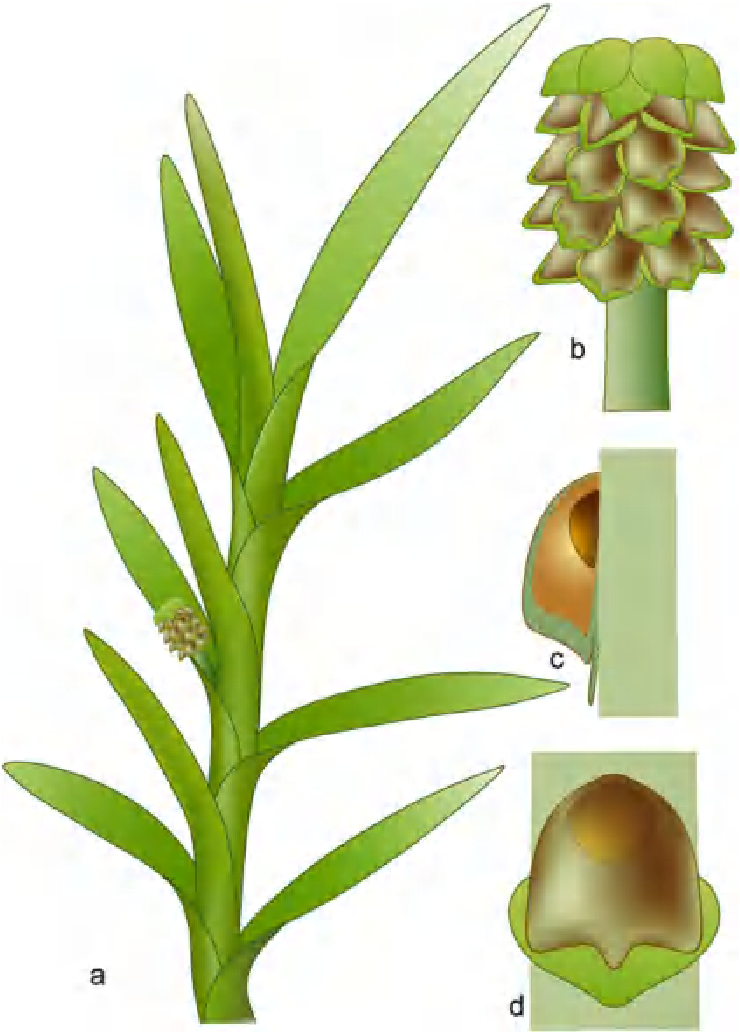

Fig. 6.54 Reconstruction of Yuhania. (a) Shoot with leaves and aggregate fruit. (b) Pedicellate aggregate fruit. (c) Longitudinal section of a carpel/fruitlet, showing an ovule/seed inserted on floral axis and enclosed in ovary. (d) Surface view of a carpel/fruitlet, showing an ovule/seed inserted on floral axis and enclosed in ovary

Yuhania is not woody. This is in line with herbaceous angiosperm Juraherba bodae recovered from the same locality (Han et al. 2016), and early herbaceous angiosperms from the Early Cretaceous (Taylor and Hickey 1990; Sun et al. 1998, 2002; Leng and Friis 2003, 2006).

Monocots are assumed monophyletic derived from the basal clades in angiosperms (APG 2009). If Middle Jurassic Yuhania were related to monocots, then monocots would be more plesiomorphic than previously assumed, or angiosperms would have originated before the Middle Jurassic, or both. However, the unique organization of female parts in Yuhania makes placing it into monocots premature.

6.5.8 Leaf Structure and Habitat

The preservation of delicate aerenchyma in mesophyll of its leaves is a sign suggestive of good preservation for Yuhania. Lack of well-developed palisade in the leaves of Yuhania (Fig. 6.52h) is ecological interest. The presence of lichen, a proxy for humid habitat, in the Daohugou flora (Wang et al. 2010) has suggested that the habitat for the plants is humid and shady. Since well-developed palisade is present under both leaf epidermis in xeromorphic plants (Fahn 1982) and lack of palisade is frequently seen in plants living in wet shady habitat (Feild et al. 2003; Feild and Arens 2007) and many monocots (Fahn 1982; Gu et al. 1993). The organization of mesophyll in Yuhania seems to agree that the habitat of Yuhania is probably humid and shady. Thus the niche of Yuhania is relatively humid and shady, and Yuhania is apparently not the dominating elements exposed to strong sunshine in the ecosystem then.

6.5.9 Origin of Angiosperms

The Jurassic age of Yuhania indicates that angiosperms are true existence in the Jurassic, though more or less surprising to many. Earlier origin time for angiosperms have been repeatedly suggested by various analyses (Wu et al. 2003; Lu and Tang 2005; Soltis et al. 2008; Hilu 2010; Prasad et al. 2011). The recently discovered angiosperm-like pollen in the Triassic (Hochuli and Feist-Burkhardt 2004, 2013), Schmeissneria microstachys from the Early Jurassic (Wang 2010b), Euanthus panii from the Middle Jurassic (Liu and Wang 2016), rice tribe (Changii indicum) in the Late Cretaceous (Prasad et al. 2011), and herbaceous angiosperm (Juraherba bodae) from the Middle Jurassic, seem to agree with Yuhania and all these push the origin of angiosperms to an earlier time. The BEAST analysis (Prasad et al. 2011) suggests that monocots can be traced back to the Middle Jurassic (145–161 Ma). The 164+ Ma age of Yuhania seems to agree with this analysis, making the former conception “No Angiosperms Until the Cretaceous” vulnerable to further doubt.

Despite long existence, angiosperms seem to not gain ecological importance until much later in the Early Cretaceous. The unique Bau-plan of the reproductive organs of Yuhania seems to suggest that it has little phylogenetic relationship with other known angiosperms. If angiosperms were monophyletic, then the divergence of these groups must have occurred much long before. However, if angiosperms were polyphyletic, then the origin time may not need to be too early and angio-ovuly could be taken as a result of convergence of parallel-developed lineages. The silent evolution of angiosperms before the Cretaceous makes the evolution of angiosperms more mysterious. Whether Yuhania left any offspring angiosperms or it simply represented a dead-end in plant evolution is a question awaiting answers.

6.5.10 Conclusion

With various parts physically connected, well-preserved Yuhania sheds unique light on the early angiosperms. Although remote from any known angiosperms, Yuhania, and together with other pioneer angiosperms, suggests that angio-ovuly appears to be an evolutionary grade for plants, which may have been reached by the Cretaceous independently in various groups at different times. The formerly assumed one-episode radiation of angiosperms in the Early Cretaceous appears to be an over-simplified story of angiosperms, which awaits further deepened careful investigation on early angiosperm fossils to reveal.

6.6 Juraherba Han and Wang

By outgroup comparison with woody gymnosperms, it is inferred that woody plants were ancestral among angiosperms in the previous evolutionary theories (Cronquist 1988; APG 2009; Chamberlain 1957; Bierhorst 1971; Biswas and Johri 1997; Taylor et al. 2009). Herbaceous plants as important elements in the current ecosystem that are necessary for the human beings and global ecosystem have left few fossils even in the Cretaceous. Although truthful herbaceous habit is restricted to angiosperms among seed plants and ecophysiological analyses of extant and fossil plants suggest that pioneer angiosperms may well be herbaceous (Stebbins 1981; Taylor and Hickey 1990, 1992, 1996; Carlquist 1996; Royer et al. 2010), and Archaefructus from the Early Cretaceous (Sun et al. 1998, 2001, 2002; Ji et al. 2004; Wang and Zheng 2012) is also herbaceous, all these evidence does not alter the woody image of ancestral angiosperms, which is deeply rooted in the mind of botanists previously. Herbaceous angiosperms were not known in the Jurassic until Juraherba was recovered from the Middle Jurassic of Inner Mongolia, China (Han et al. 2016). The fewness of herbaceous angiosperms can be partially attributed to their lower fossilizing potential (Jacobs et al. 1999). Fossil plants with various parts connected are among the most sought palaeobotanical materials due to its error-proofing in reconstruction. The small size of herbs, although a disadvantage otherwise, is conducive to whole plant preservation and reliable reconstruction.

The specimen of Juraherba is preserved as a compression with some coalified residues embedded in tuffaceous siltstone. Replicas of nitro cellulose (Zhu 1983) made on the specimen enables detailed observation using a Leo 1530 VP SEM. Dissecting one of the fructifications reveals the internal details (including seed) otherwise invisible to observers.

6.6.1 Description

Juraherba Han and Wang

Generic diagnosis: Herbaceous plant, small, including physically connected roots, stem, leaves, and fructifications. Root minute, borne on the bottom of the plant. Stem straight, bearing helically arranged leaves. Leaves linear, entire margined, with a midvein and an acute tip. Fructification on a long scape. Fruits enclosing ovules/seeds, surrounded by foliar parts, with longitudinal ridges and wrinkled surface. Fructification scape with scaly leaves and longitudinal ridges.

Type species: **Juraherba bodae** Han et Wang

Etymology: **Jura**-, for the Jurassic, the age of the fossil; -**herba**, for the herbaceous habit of the plant.

Type locality: the Daohugou Village, Ningcheng, Inner Mongolia, China.

Horizon: The Jiulongshan Formation, Middle Jurassic (>164 Ma).

Juraherba bodae Han and Wang

Specific diagnosis: as of the genus.

Description: Preserved as an impression/compression, the specimen is embedded in grey tuffaceous siltstone, with some coalified residue preserved in the lower portion and fructifications (Fig. 6.55a). The fossil comprises physically connected roots, a stem, leaves, fructifications, and it is associated with an insect (Fig. 6.55a). The specimen is 38 mm long and 12 mm wide, including at least twelve leaves and four fructifications physically connected with a root at the bottom (Fig. 6.55a). There is a constriction between the root (lower portion) and the shoot (Fig. 6.55a, f). The root is oval-shaped, 0.79 mm high and 1.16 mm wide, with scales and hairy roots (Figs. 6.55f and 6.56a). The scales have integral surfaces and bear vertically oriented hairy roots up to 121 μm long and 33 μm wide at the bottom (Figs. 6.55f and 6.56a, j, k). The leaves are helically arranged on the stem with irregularly wrinkled surface, simple, linear, up to 40 mm long and only 1.3 mm wide, entire-margined, with a midvein and an acuminate tip, usually eclipsing the stem, and older leaves tend to abscise at the bases (Figs. 6.55a and 6.56a–e, g). In the middle portion of the leaves, the midvein is 0.3 mm wide and the lateral zone is 0.42 mm wide, both tapering distally (Fig. 6.56b, e). Stomata are arranged along both sides of the midvein and restricted to the abaxial surface of leaves (Figs. 6.56d, e and 6.58a, c). The adaxial leaf epidermial cells have rectangular outlines (Fig. 6.56d) while the abaxial ones bear longitudinal striations, both surfaces are relatively smooth compared to the wrinkled surface of stem and fructifications (Fig. 6.56b–e, g and 6.58g). Frequently insect damages [DT138, according to Labandeira et al. (2007)] occur on the leaves (Fig. 6.58d). Four fructifications are present in the plant and inserted basally, arranged nearly at the same horizontal level (Fig. 6.55a). The fructifications are fusiform, 2.2–4.1 mm long and 1.4–2.2 mm wide, on long scapes, and surrounded by foliar parts (Figs. 6.55a, c, d and 6.57a, d, g). Different foliar parts can be discerned by their surface texture (Fig. 6.57g). The scapes may be up to 14–15.5 mm long, longitudinally

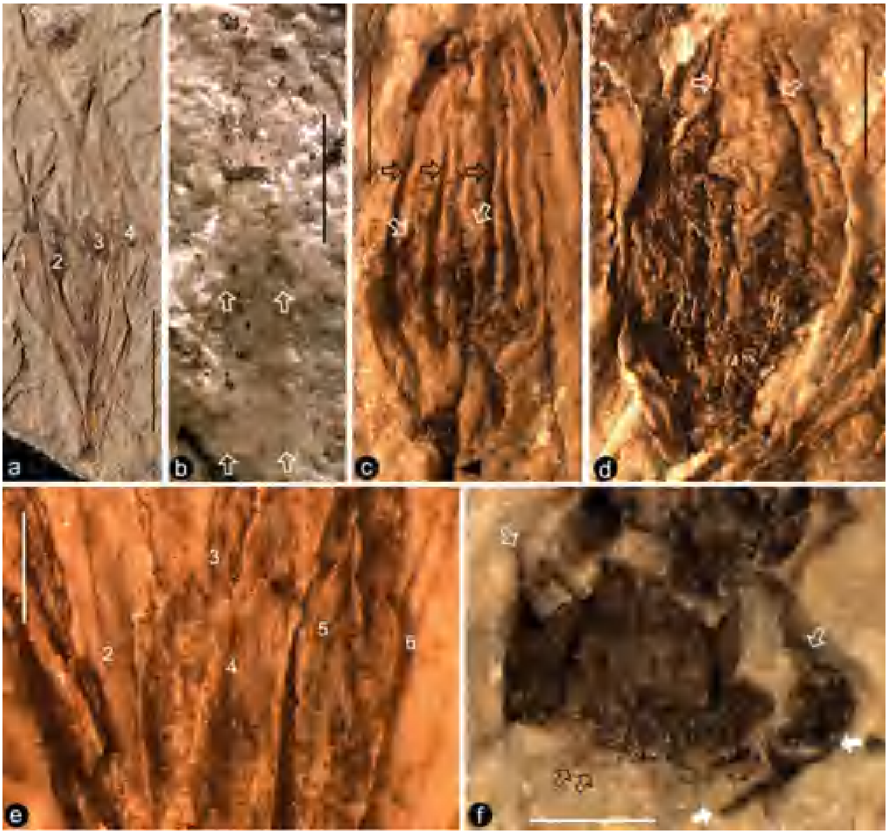

Fig. 6.55 General morphology and details of Juraherba. All stereomicroscopy. (a) Whole plant with physically connected parts including root, stem, leaves, and fructifications (1–4). Note an associated fossil insect (arrow) at the top. Bar = 10 mm. (b) Acuminate leaf tip (black arrow) and entire margins (white arrows). Bar = 1 mm. (c) Fructification 1 in a, on its scape (triangle). Note the longitudinal ridges (black arrows) and upper margins of the perianth (white arrows). Bar = 1 mm. (d) Fructification 3 in a, with longitudinal ridges (arrows) and coalified material at the lower-left. Bar = 1 mm. (e) Spiral arrangement of leaves (1–6). Bar = 0.5 mm. (f) Coalified root with attached scales (white arrows), and root hairs (black arrows). Bar = 0.5 mm

ridged, with sparsely helically arranged scaly leaves (Fig. 6.57c, d). The fructification terminus has an irregular margin, probably due to abscission of the distal part (Fig. 6.57b). Each fructification has several longitudinal ridges and irregular wrinkles on its surface (Fig. 6.57a, d, g). An ovule/seed 339 μm long is seen anchored to an internal structure and embedded in the fructification tissue (Fig. 6.57h). Another ovule appears in the same fructification (Fig. 6.57f, i). An oval body (possible seed) is seen in another fructification after removing the covering tissue (Fig. 6.58e, f).

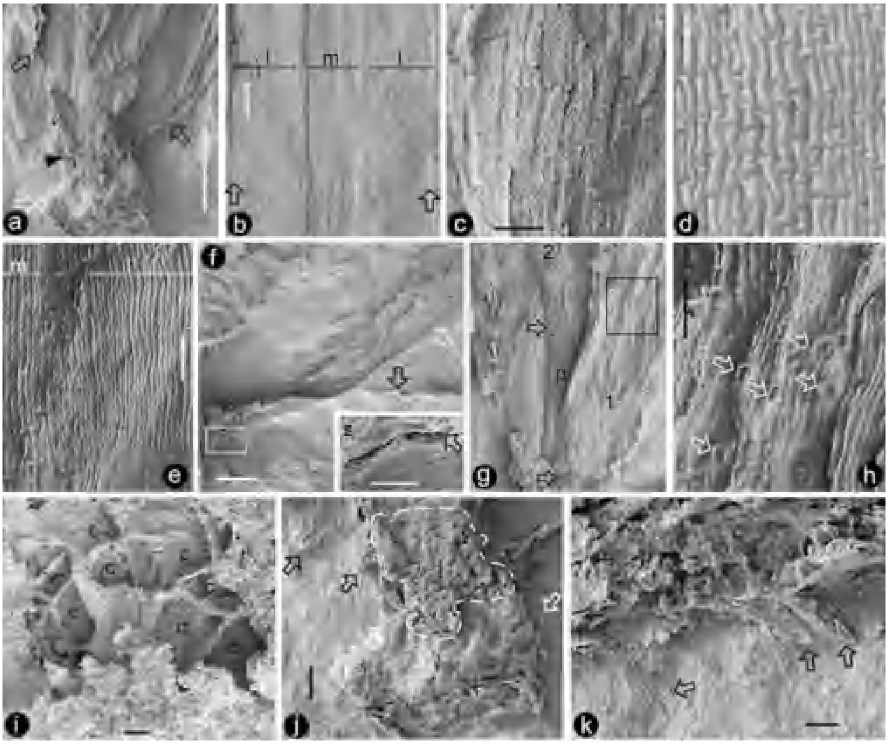

Fig. 6.56 Details of Juraherba's leaves and root. SEM. (a) Basal portion of the plant, with root (white arrow), connected scapes (black arrows), scape scar (black triangle), stem, and leaves. Bar = 1 mm. (b) Abaxial view of the middle portion of a leaf, with parallel entire margins (arrows), longitudinal striations on midvein (m) and lateral zones (l). Bar = 0.2 mm. (c) Texture on the adaxial leaf epidermis near the bottom. Bar = 50 μm. (d) The adaxial leaf epidermis near the tip. Bar = 50 μm. (e) Abaxial leaf epidermis in the middle, showing midvein (m), lateral zone (l), and stomatal zone in between. Bar = 0.1 mm. (f) Details of the right scape in a, showing scape (white arrow) and a subtending leaf (black arrow). Bar = 0.2 mm. The inset enlarged from the rectangle, with a 50 μm bar, shows the separation (arrow) between the scape (s) and subtending leaf. (g) Leaf arrangement near the base of the plant. Note broken surface (arrows) between the leaves (1–2) and stem (p). Bar = 0.2 mm. (h) Rectangular region in g, showing scattered stomata (arrows) on the leaf. Bar = 0.1 mm. (i) Cells (c) in a leaf. Bar = 10 μm. (j) The root and associated organs. Note the disarticulated leaf (black arrows), outline of a scape scar (white broken line), and scales (white arrows). Bar = 0.2 mm. (k) Root hairs (arrows) attached to the integral surface of the root, enlarged from bottom of (j). Bar = 50 μm

Etymology: bodae, dedicated to Boda (the Chinese abbreviation of Bohai University), the affiliation of Dr. Gang Han.

Holotype: PB21415, deposited in the Nanjing Institute of Geology and Palaeontology, CAS, Nanjing, China.

Remarks: The irregularly wrinkled surfaces of the stem and fructifications form strong contrast against the relatively smooth leaf surface, implying the volume of these parts has been reduced during the fossilization and these parts used to be more or less fleshy in live form.

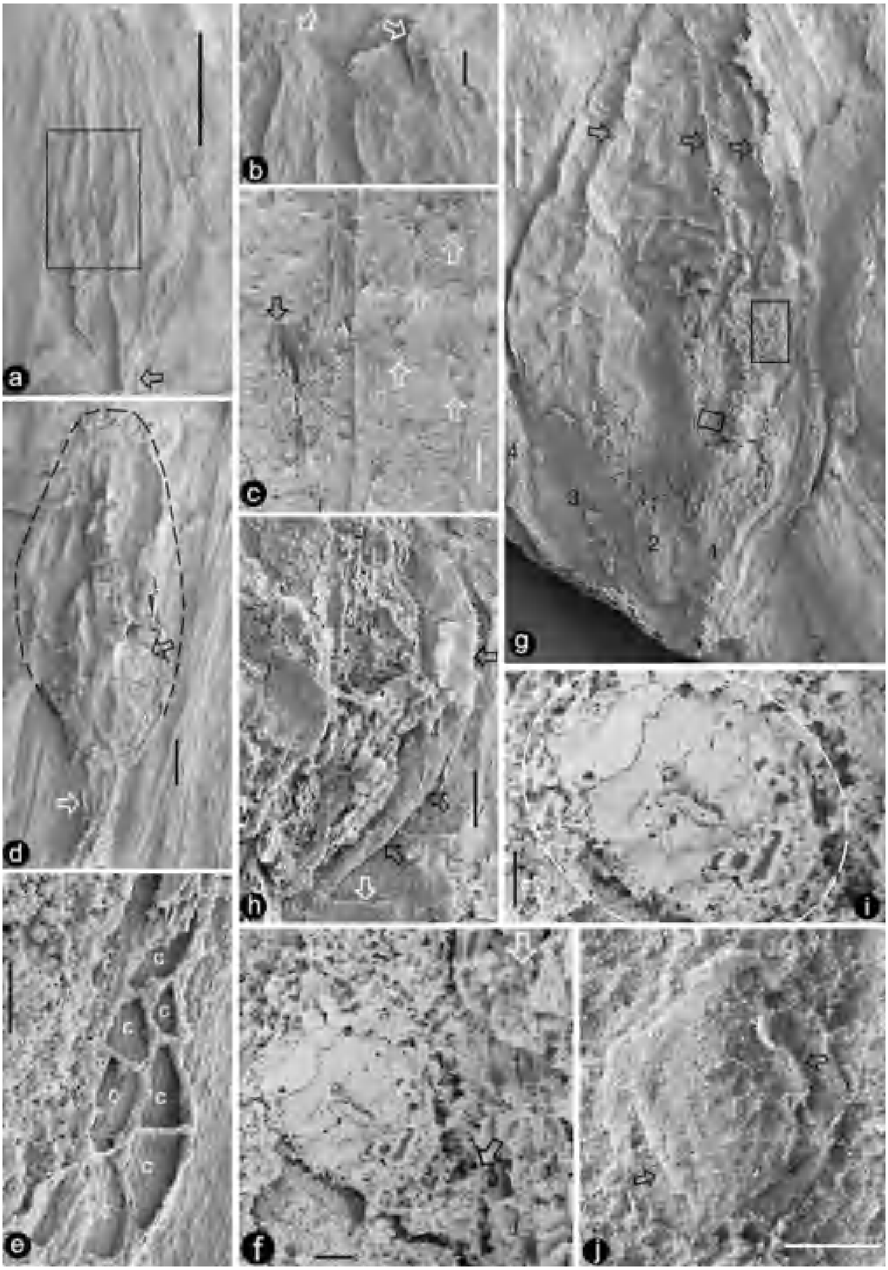

Fig. 6.57 Details of Juraherba's fructifications. SEM. (a) Fructification 1 in Fig. 6.55a. Note its fusiform shape, longitudinal ridges, and scape (arrow). Bar = 1 mm. (b) Tip of the fructification in a, with a terminal scar (arrows). Bar = 0.1 mm. (c) Scape of the fructification in a, with scaly leaf (black arrow) and stomata (white arrows). Bar = 50 µm. (d) Fructification 2 with a scape (arrow) in Fig. 6.55a. Bar = 0.5 mm. (e) Two layers of cells (c) of the perianth member in d. Bar = 0.1 mm.

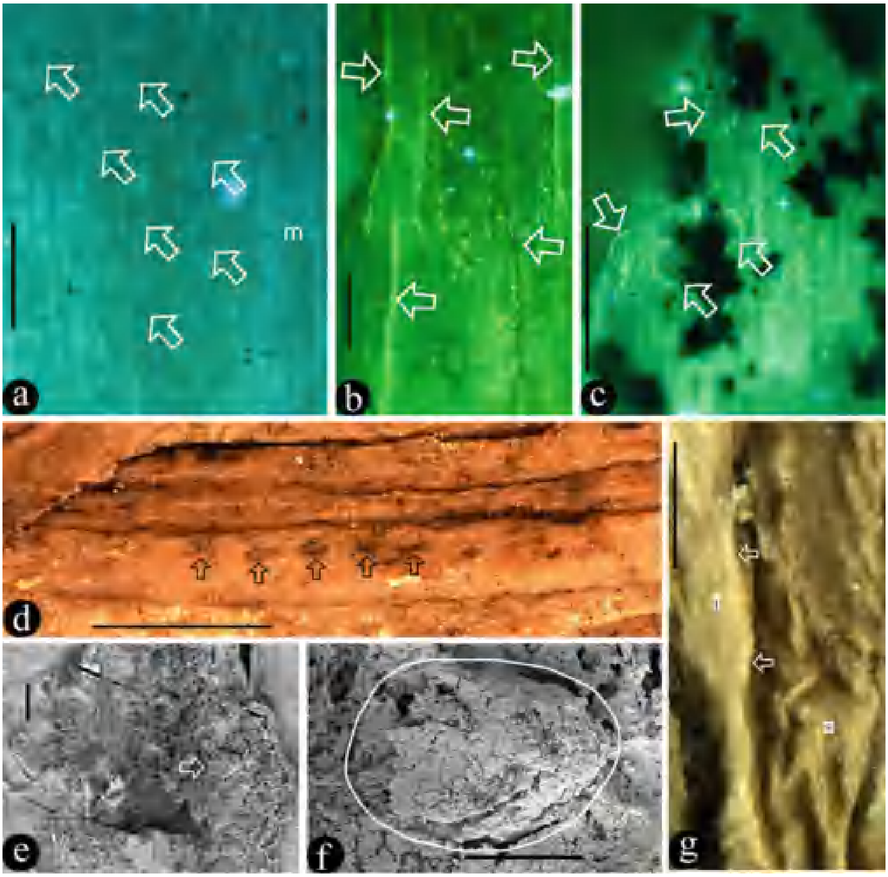

Fig. 6.58 Fluorescent micrographs of leaf, pedicel, and surrounding foliar parts on the fructification. (a) Possible stomata (arrows) near the midvein (m) on the abaxial leaf surface. Bar = 0.1 mm. (b) Longitudinal ridges (arrows) on a fructification pedicel. Bar = 0.1 mm. (c) Epidermal cells and possible stomata (arrows) on a foliar part surrounding the fructification. Bar = 0.1 mm. (d) One of the leaves with an array of insect damages (arrows). Bar = 1 mm. (e) Internal details of the portion of fructification shown in Fig. 6.57d, after removing the covering tissue. Bar = 0.2 mm. (f) A possible seed (oval body outlined) inside the fructification, enlarged from the arrowed region in e. Bar = 0.1 mm. (g) Margin (arrows) of a leaf (l) with smooth surface, and the stem (s) with rough surface. Bar = 0.5 mm

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Fig. 6.57 (continued) (f) An oval body (ovule/seed) exposed from region marked by lower rectangle in g, after removing the covering tissues. Bar = 0.1 mm. (g) Fructification 3 in Fig. 6.55a. Note the wrinkles and three longitudinal ridges (arrows), and distinct perianth members (1–4). Bar = 0.5 mm. (h) Details in the upper rectangle in g. Note the smooth outline of an ovule/seed (black arrows) embedded in tissues, and its attachment (white arrow). Bar = 50 μm. (i) Details in the ovule/seed in f. Bar = 20 μm. (j) An associated disulcate pollen grain. Bar = 10 μm

6.6.2 Discussions

6.6.2.1 Eliminating Alternatives

The fructifications surrounded by foliar parts (Fig. 6.57g) without any trace of spores in Juraherba are clearly different from sori or sporangia of ferns, in which sori and sporangia are usually closely related to pinnae (Haupt 1953; Smith et al. 2006a, b). Fructification scapes with scaly leaves (Fig. 6.57c) are distinct from smooth setae or pseudopodia of bryophytes (Gradstein et al. 2001), eliminating the relationship between Juraherba and bryophytes. In short, these differences distinguish Juraherba from bryophytes and most ferns (Fig. 6.59).

It is necessary to distinguish Juraherba from contemporaneous frequently seen fossil taxa. Some short shoot of Czekanowskiales (including Phoenicopsis, Czekanowskia, and Tianshia) in the Mesozoic (Zhou and Zhang 1998; Sun et al. 2009) might be taken as herbaceous, if found isolated. However, the single vein and acute leaf tip of Juraherba are distinct from the multiple veins and rounded leaf tips of Phoenicopsis and Tianshia (Zhou and Zhang 1998). The linear, non-branching leaf shape of Juraherba is distinct from the filiform, branched leaf of Czekanowskia (Sun et al. 2009). Furthermore the distinction between the terminal fusiform fructifications surrounded by foliar parts in Juraherba and lateral naked bivalvate units in Leptostrobus (Czekanowskiales) eliminates any relationship between these two. If really belonged to Czekanowskiales, then the base of Juraherba should be truncated and broken with rough surface and no hairs. However, observation on Juraherba indicates that the base of Juraherba is integral and bearing hairy roots (Fig. 6.56a, j, k). Therefore, Juraherba is a whole plant rather than a short shoot of any plants.

6.6.2.2 Herbaceous Habit

An herbaceous habit is suggested from Juraherba by its small size of whole plant as Juraherba is only 38 mm tall. This conclusion is favored by comparison with other examples of big herbaceous and small woody plants. On one hand, primary growth may produce organs bigger than that of Juraherba. The early land plant Rhynia may produce an axis up to 3 mm in diameter (Edwards 2003), in contrast to only 1.16 mm wide lower portion of Juraherba, suggesting that the size of Juraherba is within the scope of primary growth. On the other hand, plants with little secondary growth may produce axes much thicker than that of Juraherba. The lower portion of Juraherba is much smaller than that of the so-called “herbaceous” conifer (Aethophyllum stipulare, Plate I, Fig. 3, Rothwell et al. 2000), the fertile one of the latter is more than 30 cm tall, suggesting that smaller Juraherba has no secondary growth. In the meantime, shrubby Ephedra (Gnetales) is much bigger than Juraherba and does have an active cambium (Martens 1971). These comparisons indicate that mature Juraherba (as implied by its fructifications) is truthfully herbaceous. Thus this herbaceous habit alone can distinguish Juraherba from all known gymnosperms (Bierhorst 1971; Biswas and Johri 1997).

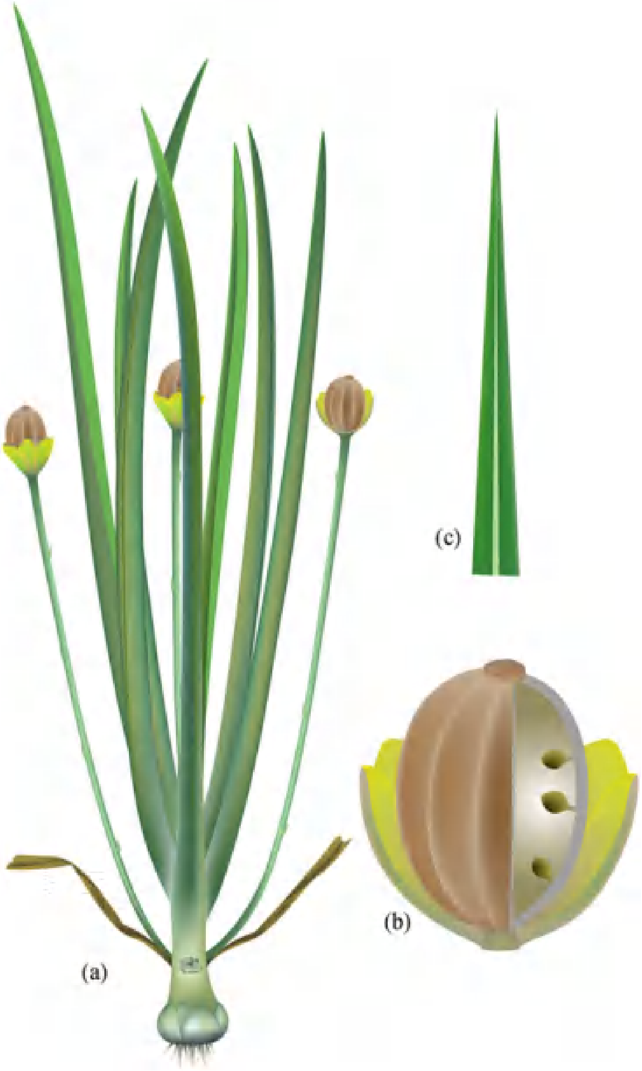

Fig. 6.59 Reconstruction of whole plant, fructification, and leaf of Juraherba. Not to scale. (a) Reconstruction of Juraherba including roots, stem, leaves, and fructifications. (b) Fructification showing surrounding foliar parts, fruit with longitudinal ridges, and ovules/seeds inside the fruit. (c) Leaf with a midvein and lateral zones, tapering distally

6.6.2.3 Ecological Implication

The tiny size and herbaceous habit suggests that Juraherba may have a short life cycle, an ecological strategy that contributes to the radiation and success of angiosperms (Stebbins 1981). Some strategy is obviously adopted by some basal angiosperms such as the Hydatellaceae (Gandolfo et al. 1998; Saarela et al. 2007).

Ecophysiological analyses of extant and fossil plants conclude that herbaceous habit may well have been adopted by early angiosperms (Stebbins 1981; Taylor and Hickey 1990, 1992, 1996; Carlquist 1996; Royer et al. 2010). Juraherba not only confirms the conclusion of the above analyses and but also indicates that this strategy has been adopted at least back to the Middle Jurassic (Fig. 6.55a), although the ecological success of angiosperms did not come until much later. Juraherba marks the earliest record of herbaceous angiosperms, adding first-hand material for studying the origin and evolution of herbs and calling for serious attention to the Paleoherb Theory that was advanced decades ago.

6.6.2.4 Affinity

Identifying the oval bodies inside the fructification is of crucial importance for determining the affinity of Juraherba. The oval bodies in the fructification seen in Fig. 6.57f, h, i cannot be interpreted as either microspores or pollen grains because of their large size (over 300 μm long, far beyond the scope of microspores), therefore they have to be interpreted as either seeds, ovules, or megasporangia rather than microspores/pollen grains. Besides seed plants, megaspores are seen in Lycophyta, Sphenophyta, and Salviniales (Scott 1962; Smith et al. 2006a, b; Taylor et al. 2009). The reproductive organs of Lycophyta and Sphenophyta are usually organized in cone-like structures (Scott 1962; Taylor et al. 2009), and completely different from those of Juraherba. Salviniales can be easily distinguished from Juraherba by their leaf morphology (Smith et al. 2006a, b). Although it may be interpreted as an insect egg laid inside the fructification, the shape of the oval body in Juraherba (Fig. 6.57h) is not as symmetrical as an insect egg. Instead the oval body is anchored and embedded in the fructification tissue in Fig. 6.57h. This interpretation is further strengthened by another similar structure embedded in the same fructification (Fig. 6.57f, i), which is a mass of dense organic material anchored by a pedicel. The lack of obvious testa in both cases implies that it is either an ovule or a seed in its very early development. Finally, one more oval body that was formerly covered inside the fructification became exposed after the covering tissue was removed (Fig. 6.58e, f). The spatial positions of these oval bodies within the fructification (angiospermy) is rather significant because it is where an ovule is expected in angiosperms.

The irregular scar at the fructification tip (Fig. 6.57b) suggests that there used to be a distal part (probably style) that has fallen off in Juraherba. Abscised styles are frequently seen in angiosperms after pollination but never in gymosperms (Goldschmidt and Leshem 1971; Simons 1973; Keighery 2004), thus this features favors a placing of Juraherba in angiosperms. Among angiosperms, Juraherba resembles Hydatellaceae (one of the basal-most angiosperms) in general morphology and habit (Rudall et al. 2007; Sokoloff et al. 2013), although the differences between them are also obvious. Lack of both herbaceous habit and angio-ovuly in gymnosperms helps to reinforce the angiospermous affinity for Juraherba. Apparently, Juraherba is a Jurassic herbaceous angiosperm deserving further investigation.

6.6.2.5 Aquatic Habitat

The hairs on the roots of **Juraherba** are very tiny in size, simple in organization, only about one-cell wide (Fig. 6.56k). Such poorly developed roots imply that **Juraherba** probably lives in an environment with little water stress where requirement for strong anchorage and mechanical support are unnecessary. All four fructifications arranged nearly at the same horizontal level in **Juraherba** implies that these reproductive organs might be close to the water surface when pollinated. All these features converge to that **Juraherba** is most likely aquatic.

6.6.2.6 Interaction with Animals

The wrinkled fructification surface of **Juraherba** (Fig. 6.57g), in contrast to the smooth leaf surface (Fig. 6.56c, d) in the same fossil, suggests that **Juraherba**′s fructifications may be fleshy and dispersed by some animals. Study of early angiosperms (Eriksson et al. 2000) indicates that some animals may well have involved in the dispersal of fleshy diaspores of angiosperms as early as in the Early Cretaceous. Thus the occurrence of fleshy fructifications in the Jurassic is not too surprising. The Middle Jurassic age of **Juraherba** suggests that the co-evolution between fleshy fructifications of angiosperms and animals can be dated at least back to the Middle Jurassic. Previously, Na et al. (2014) reported the first ovipositional scars on **Sphenobaiera** from the same locality, Daohugou Village. Oviposition scars in rows were found on leaves of **Schmeissneria** (Van Konijnenburg-Van Cittert and Schmeiβner 1999). The traces of insect damages on the leaves of **Juraherba** (Fig. 6.58d) as well as **Schmeissneria** (Van Konijnenburg-Van Cittert and Schmeiβner 1999) imply that the interaction between angiosperms and insects may be much longer than previously assumed.

6.6.2.7 Summary

Juraherba bodae from the Middle Jurassic of Inner Mongolia, China is preserved as a whole plant, including root, stem, leaves, and fructifications. The small size of **Juraherba** with fructifications enclosing ovules/seeds and lacking secondary growth indicates that **Juraherba** is a truthful herbaceous angiosperm. Its Middle Jurassic age makes **Juraherba** the earliest herbaceous seed plant and angiosperm. Analyses indicate that **Juraherba** lived in an aquatic habitat. The unexpected morphology of **Juraherba** undermines the mainstream thinking about angiosperm evolution. Fleshy fructifications and insect damage seen in **Juraherba** suggest that animal-angiosperm interaction history may be much longer than previously assumed.

6.7 General Summary

The plant fossils documented in Chaps. 5 and 6 represent a subset of many angiosperms from the Jurassic and Early Cretaceous. These plants are placed in angiosperms because they have demonstrated the existence of angio-ovuly. Angio-ovuly currently is a feature restricted to angiosperms. Angiosperms have occurred in the Jurassic, much earlier than the widely-accepted age for angiosperms. These fossil plants and the conclusion here 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, which were unknown previously. The age and morphology of these early angiosperms will influence the rivaling balance among existing evolutionary theories and hypotheses.

Although the interpretations in this book may be subject to debate and discussion, the fossils are not. They are not ignorable, and ignoring these fossils can be taken as a criterion differentiating a real botanist and a botanist who takes botany as a religion rather a science (Fig. 6.60).

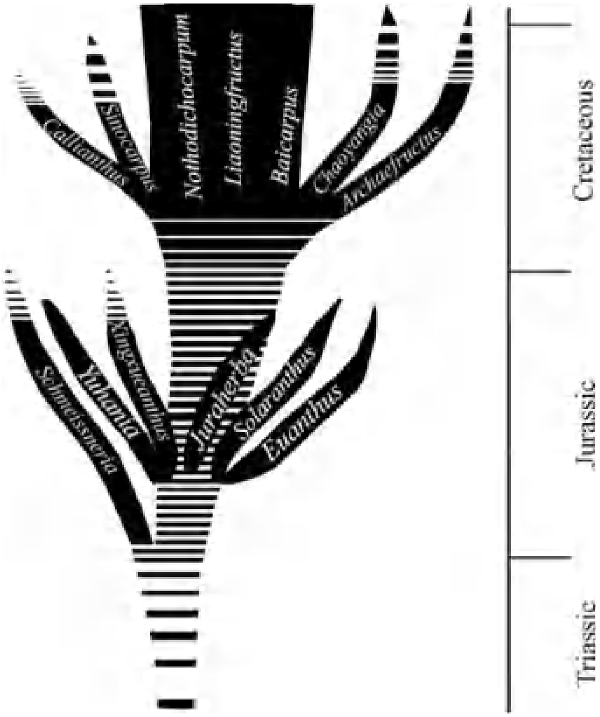

Fig. 6.60 A scenario of diversification of angiosperms in the Mesozoic

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Chapter 7
Fossil Plants Possibly Related to Angiosperms

In addition to those fossil plants that can be put in angiosperms with confidence, there are more fossil plants that are more or less related to angiosperms, but the current knowledge on them does not allow the author to put them in angiosperms according to the criterion presented in Chap. 3. In this chapter, four of these plants are briefly documented. These fossils show combinations of characters that are never seen in typical gymnosperms but are frequently seen in angiosperms. Their trans-angiosperm-gymnosperm traits prompt the author to share their information with the readers. It is hoped that future study will elucidate on their position in the evolutionary map of angiosperms and seed plants.

7.1 Taxon A

Specimens of Taxon A include two facing parts of the same fruit-like organ (Fig. 7.1a, b), distinct from any other fossil or living plants known in the Daohugou 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.

7.1.1 Diagnosis

Taxon A
(Figs. 7.1, 7.2, and 7.3)

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

X. Wang, The Dawn Angiosperms, Springer Geology,
DOI 10.1007/978-3-319-58325-9_7

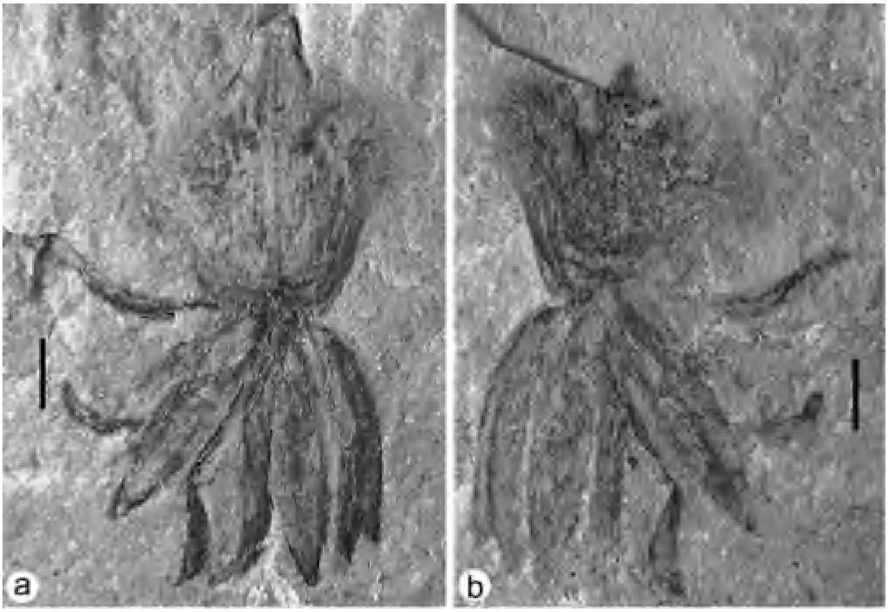

Fig. 7.1 Two facing parts of Taxon A. Stereomicroscopy. Note the apical fruit and drooping tepals in the base. All bar = 1 mm

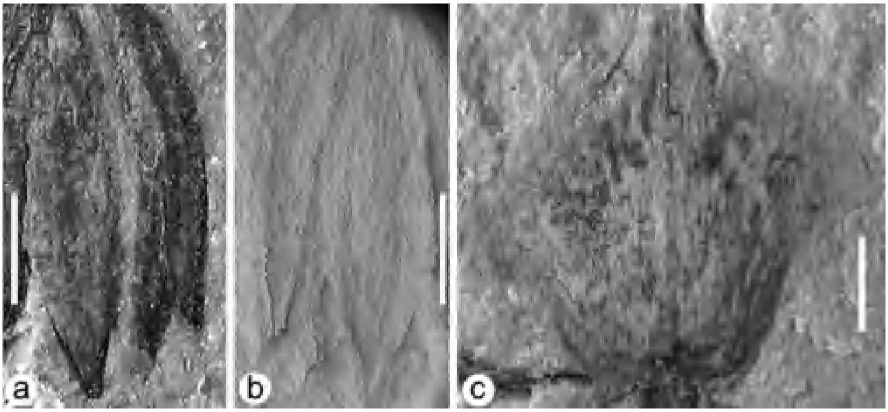

Fig. 7.2 Details of Taxon A. (a) Detailed view of the lanceolate tepals. LM. (b) Mirror image of the same region as in a. Note the tepal margins and rugose surface. SEM. (c) Detailed view of the apical fruit. Note the shape and cellular details on the surface. LM. All bars = 1 mm

Description: The whole organ is about 8.1 mm long and 5.8 mm wide (Fig. 7.1a, b). The organ consists of two parts, an apical fruit and cycles of tepals at the base (Figs. 7.1a, b and 7.2a–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/

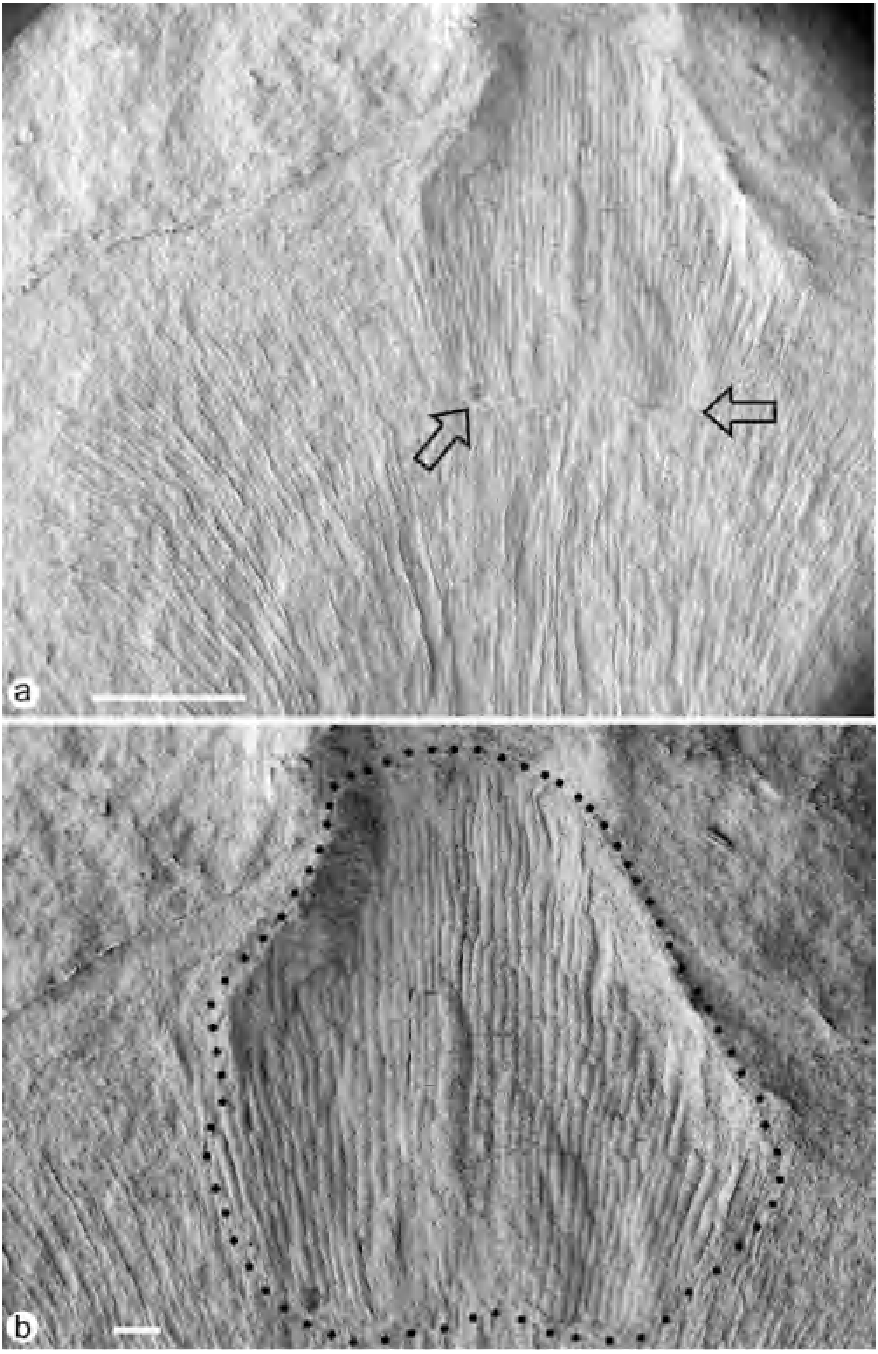

Fig. 7.3 Details of Taxon A. SEM. (a) Further detailed view of the fruit. Note the radial arrangement of cells. Bar = 0.5 mm. (b) Close-up of the apical region of the fruit. Note the cells within the dotted line are different and separate from other cells. Bar = 0.1 mm

broken tip and a base about 2 mm wide (Figs. 7.1a, b and 7.2a–c). There are well defined cellular details on the surface of the fruit (Figs. 7.2c and 7.3a, b). The cells in the apical region are delimited from other regions by evident changes in cell arrangement (Fig. 7.3a, b). The cells in this region are about 70~162 μm long and 14~38 μm wide, much wider than cells in other regions. Tepals are about 3.7 mm long and 0.85 mm wide, lanceolate, probably in more than one cycle (Figs. 7.1a, b and 7.2a, 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 projection on the top of the fruit. Considering style-like projections are only seen in angiosperms, Gnetales, Erdtmanithecales, and Bennettitales (the three of latters are apparently out of the question here) and the cellular details at the fruit apex do not show anything similar to the micropylar tubes in BEG clade (Friis et al. 2009), which usually is bracketed by an outer envelope (a separate layer), Taxon A appears very likely to be an angiosperm.

The tepals appear to drop and overlap each other (Fig. 7.2a, b), suggesting that there are more than one cycles of such 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 angiosperm leaves or scales. Similar arrangement of the tepals is never seen in gymnosperms. All these strongly suggest that Taxon A is very likely an angiosperm fruit.

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

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

7.2 *Pseudoephedra* (Liu and Wang 2016)

Pseudoephedra paradoxa was recovered from the outcrop of the Yixian Formation near Dawangzhangzi, Lingyuan, Liaoning, China. Its affinity is mysterious as the fossil demonstrates a chimeric character combination spanning Ephedraceae (gymnosperms) and angiosperms. If placed it in gymnosperms (Ephedraceae), it would make BEG group lacking of a synapomorphoy. If placed in angiosperms, it would make some angiosperms hard to distinguish from Ephedraceae. Apparently, this combination of characters of *Pseudoephedra* challenges the classical thinking about relationship between Angiosperms and Ephedraceae.

Archaefructus (Sun et al. 2002; Ji et al. 2004) and Sinocarpus (Leng and Friis 2003, 2006) have been found from the same locality. The age of 122–125 Ma (the Barremian or Aptian, Early Cretaceous) is an age that is widely accepted for the Yixian Formation (Swisher et al. 1998; Leng and Friis 2003; Dilcher et al. 2007).

7.2.1 Pseudoephedra (Liu and Wang 2016)

Generic diagnosis: Bracts oppositely arranged along the main axis with obvious joints and internodes. Female parts axillary, more or less pedicellate, surrounded by narrow elongated scales, including a central unit and two surrounding envelopes. Central unit including a proximal oval body and an apical projection. Oval body locular, surrounded by a thin wall. An apical projection solid, long, exserted, with a truncated tip.

Type species: Pseudoephedra paradoxa Liu and Wang.

Etymology: Pseudo- for fake in Latin; -ephedra for the genus Ephedra in Gnetales.

Horizon: The Yixian Formation, Barremian–Aptian, Lower Cretaceous (122–125 Ma).

Locality: Dawangzhangzi Village, Lingyuan City, Liaoning Province, China.

Remarks: Chengia and Siphonospermum are two fossil genera related to Gnetales from the Lower Cretaceous Yixian Formation of Liaoning, China (Rydin and Friis 2010; Yang and Wang 2013). Both resemble Pseudoephedra in term of axillary female parts subtended by oppositely arranged bracts, apical projection, obvious joints and internodes (Rydin and Friis 2010; Yang and Wang 2013). Furthermore Siphonospermum shares with Pseudoephedra two envelopes surrounding the apical projection, elongated pedicel of female part, and elongated apical projection (Rydin and Friis 2010). But Siphonospermum is compared to Gnetum-Welwitschia clade (Rydin and Friis 2010) whereas Pseudoephedra here demonstrates more resemblance to Ephedra. Both publications of Chengia and Siphonospermum suffer from lack of detailed information about their apical projections, being tubular or solid, making further comparison with Pseudoephedra impossible.

7.2.2 Pseudoephedra paradoxa (Liu and Wang 2016)

Specific diagnosis: (In addition to that of the genus) Plant part 51 mm long, 17 mm wide. Main axis about 1.5 mm wide. Internode up to 19 mm long, shortening distally. The proximal oval body 1–1.8 mm in diameter. Apical projection 1.6–2.6 mm long, 48–120 μm wide.

Description: Specimen of Pseudoephedra is preserved as part and counterpart, red in color, preserved as compression, embedded in slightly yellowish siltstone (Fig. 7.4a, b). All appendages are physically connected to a common axis

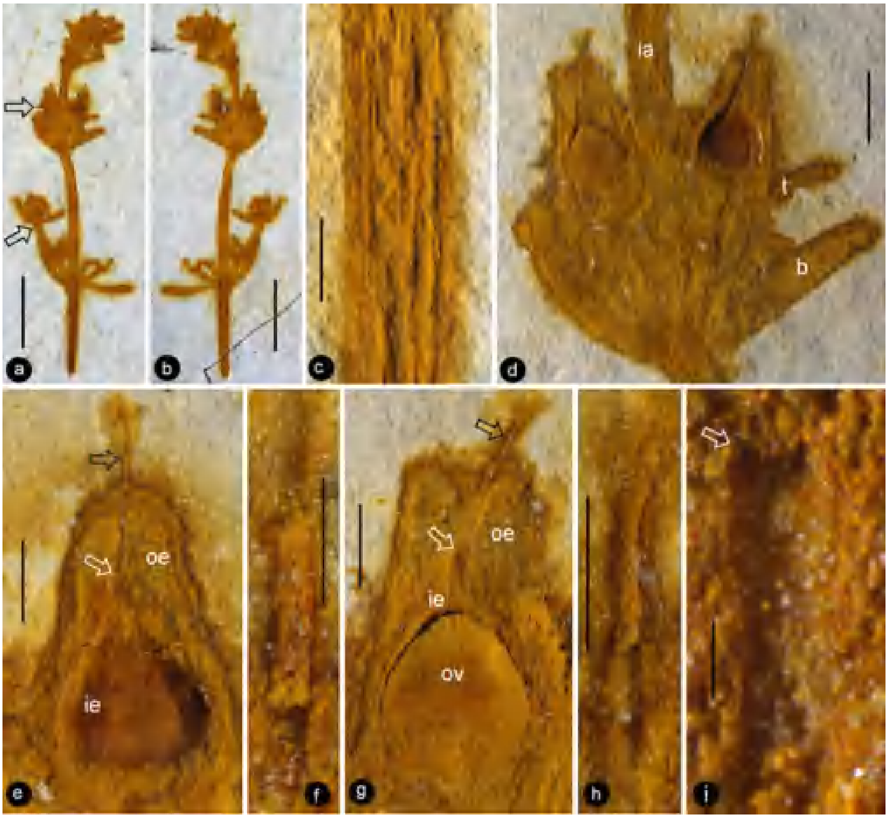

Fig. 7.4 Pseudoephedra paradoxa and its details. Stereomicroscopy. (a) An inflorescence. Note the straight inflorescence axis, decussate arrangement of "flowers", which become smaller and less mature to the distal. Bar = 1 cm. (b) The counterpart of the one shown in a. Bar = 1 cm. (c) Longitudinal ridges along the inflorescence axis. Bar = 1 mm. (d) Two "flowers" in axils of bracts (b) oppositely arranged along the inflorescence axis (ia), enlarged from a. Note the tepals (t) subtending the envelopes. Bar = 2 mm. (e) A "flower" broken along its longitudinal axis, showing the inner envelope (ie) and outer envelope (oe) surrounding the style (black arrow). Note the terminal of the inner envelope (white arrow). Bar = 1 mm. (f) Detailed view of the style in e. Note part of the cylindrical style either leaves a groove in the sediments (to the top and bottom) or rises above the sediment surface (the middle). Bar = 0.25 mm. (g) A "flower" broken along its longitudinal axis, showing the inner envelope (ie) and outer envelope (oe) surrounding the ovary (ov) and style (black arrow). Note the bulging ovary inside the inner envelope and the terminal of the inner envelope (white arrow). Bar = 1 mm. (h) Detailed view of the style in g. Note the cylindrical style either leaves a groove in the sediments (to the bottom) or rises above the sediment surface (to the top). Bar = 0.25 mm. (i) A depression on the sediment left by a style. Note stigma (arrow) at a style terminal and the dark shadow implying the groove left by the style. Light from left. Bar = 0.1 mm. Courtesy of Palaeoworld

(Fig. 7.4a, b). The axis is slender and straight, about 50 mm long and 1.5 mm wide, with longitudinal ridges (Fig. 7.4a, b). Distinct joints and internodes are seen (Fig. 7.4a, b). An internode is up to 19 mm long, becoming shorter distally (Fig. 7.4a, b). Bracts are strap-like, about 8 mm long and 1.1 mm wide, oppositely arranged along the axis (Fig. 7.4a, b). A female part is up to 8 mm long and 5 mm wide, in the axil of the subtending bract, either sessile (Fig. 7.4a, d) or on a pedicel up to 13 mm long (lower arrow in Fig. 7.4a, b), becoming smaller distally (Fig. 7.4a, b). Female parts have lanceolate scales surrounding their central units (Fig. 7.4a, b). The scales are about 4 mm long and 0.7 mm wide (Figs. 7.4d and 7.6a–e). The central units are surrounded by two envelopes (Figs. 7.4d, e, g, 7.5a, e, and 7.6a–d). The outer envelope is up to 3.5–4 mm long, 0.75 mm thick at the distal, with ground tissue of isodiametric cells about 20 μm in diameter (Figs. 7.4e, g and 7.5a, e). The inner envelope surrounds the central unit, crateriform, 0.76 mm above the oval body, and buttresses only the proximal portion of the apical projection (Figs. 7.5a, e and 7.6a–d). The oval body is 1–1.8 mm in diameter, solid, surrounded by a wall about 117 μm thick, separated from the inner envelope (Fig. 7.4e, g). The apical projection protrudes through both envelopes, and is cylindrical, solid, straight or slightly curved, up to 2 mm long and 83 μm in diameter (Fig. 7.4d–i). The projection includes epidermis and ground tissue inside, either preserved as a solid cylinder raised above the sediment matrix or leaving a groove on the sediment when missing (Figs. 7.4f, h, i and 7.5a–c, f–g). The ground tissue in the apical projection is of isodiametric cells 18–19 μm in diameter (Figs. 7.5a, b, f, g). The terminus of the apical projection appears truncated (Figs. 7.4f, h and 7.5f, h).

Etymology: Paradoxa for the mysterious affinity of the fossil.

Holotype: NOCC201204261301 (Fig. 7.4a, b).

Paratype: NOCC201204261302.

Depository: The National Orchid Conservation Center of China, Shenzhen, China (NOCC).

Remarks: Both the distal (apical projection) and proximal (oval body) parts of the central unit are bulging above the sediment surface when preserved or leaving depressions on the sediment when missing. Their three dimensional configurations constitute a strong contrast against the axis, which demonstrates a less bulging form. This contrast implies that the apical projection is truly solid and more robust than the axis in Pseudoephedra.

The general configuration of the female parts varies from the bottom to the top of the fossil. For example, the pedicel is obvious in the basalmost pairs of female parts but almost non-existing in the topmost pair (Fig. 7.4a, b). This difference can be attributed to the maturity and development of the organs.

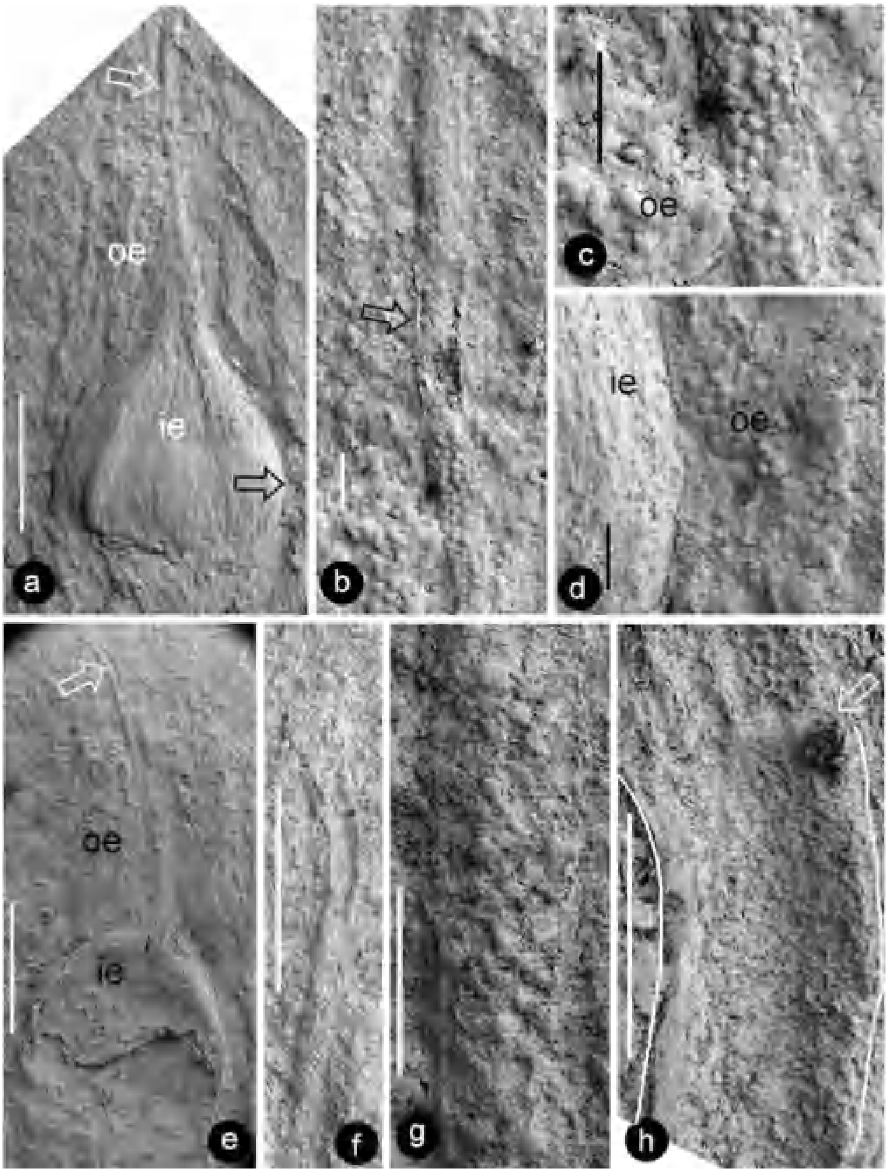

Fig. 7.5 Details of P. paradoxa. SEM. (a) The flower shown in Fig. 7.4e, showing the inner envelope (ie) and outer envelope (oe) surrounding the style. Bar = 1 mm. (b) Detailed view of the style shown in a. Note the epidermis and ground tissue of the style. Bar = 0.1 mm. (c) Detailed view of the ground tissue of isodiametric cells in the style, enlarged from the lower part of b. Bar = 0.1 mm. (d) Detailed view of the ground tissue of isodiamteric cells in the outer envelope (oe) marked by black arrow in a. Bar = 0.1 mm. (e) A flower with empty ovary surrounded by inner envelope (ie) and distal style (arrow) bracketed by the outer envelope (oe). Bar = 1 mm. f Detailed view of the style shown in e. Bar = 0.5 mm. (g) Detailed view of the style shown in (f), showing the isodiametric cells in ground tissue of the style. Bar = 0.1 mm. (h) Detailed view of a style with slightly expanded tip (arrow). Bar = 0.1 mm. Courtesy of Palaeoworld

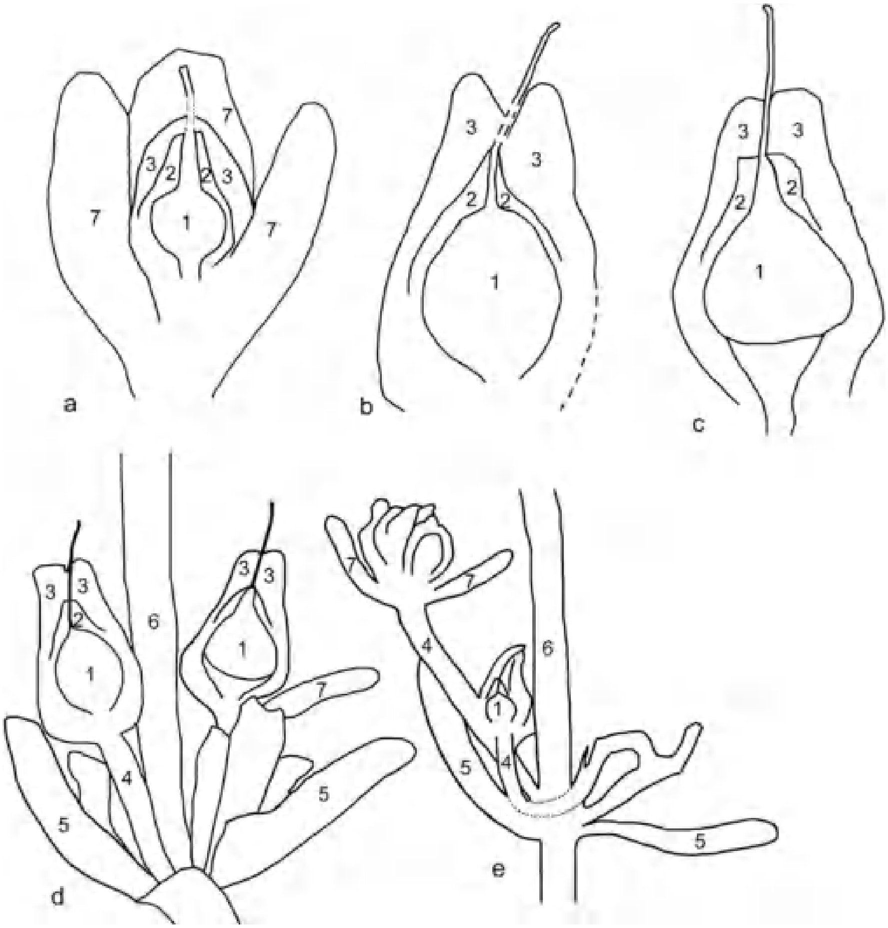

Fig. 7.6 Sketches of P. paradoxa, showing details of female parts. Labels for all: 1 oval body, 2 inner envelope, 3 outer envelope, 4 pedicel, 5 bract, 6 axis, 7 scale. (a) The immature female part with the central unit surrounded by two envelopes. (b) and (c) Female parts with its central unit surrounded by two envelopes. (d) The pair of female parts oppositely arranged in axils of subtending bracts. (e) A female parts oppositely arranged in axils of subtending bracts, note the elongated pedicels and one of them bending to the opposite side. Courtesy of Palaeoworld

7.2.3 Discussions

The oval body of the central unit is situated in the center of the female part in Pseudoephedra. The homology of this oval body is hinged with the affinity of Pseudoephedra, for which the vegetative features are helpless in this special case. Given its huge size, position, and morphology, male part is apparently out of the question, and the oval body in Pseudoephedra could only be plausibly interpreted either as (1) a nucellus with a beak, (2) an ovule with a micropylar tube, or (3) an ovary with a style. We will discuss each alternative, its implications and credibility below.

7.2.3.1 First Alternative

A nucellus with an apical beak has been seen in certain gymnosperm taxa. The Devonian proto-ovule Runcaria has a distal projection similar to that of Pseudoephedra (Gerrienne and Meyer-Berthaud 2007). Since how Runcaria is related to later evolved seeds is still unknown, its Devonian age and unknown vegetative parts prevent further comparison with Cretaceous Pseudoephedra. In Cycas and Zamia, the nucellus has its beak exserted above the integument and is exposed to the exterior (Zhang 2013). If such cycad nucellar beak became more elongated, it might give rise to the solid apical projection of Pseudoephedra. Two envelopes surrounding the apical projection, decussate branching pattern, and general morphology are sufficient to distinguish Pseudoephedra from any cycads. In addition, various nucellar beaks are frequently seen in gymnosperms (e.g., Stephanospermum, Feruglioclådus, Otovicia) (Archangelsky and Cuneo 1987; Drinnan et al. 1990; Kerp et al. 1990; Spencer et al. 2013). But these nucellar beaks are very short and always hidden in the micropyles rather than exserted as in Pseudoephedra. A typical nucellus does not have a separable wall around, conflicting with the presence of a thin wall around the oval body in Pseudoephedra [Fig. 2k of Liu and Wang (2016)], therefore nucellar beak is not an ideal candidate for the distal projection in Pseudoephedra. Therefore the distal projection of Pseudoephedra has little to do with the nucellar beaks seen in some gymnosperms.

7.2.3.2 Second Alternative

If the oval body with distal projection in Pseudoephedra were compared to an ovule with micropylar tube, then the female part of Pseudoephedra would be very similar to that of Ephedra, namely, an ovule surrounded by envelopes. This comparison appears favorable if the general morphology of Pseudoephedra is taken into consideration. The characters shared between Pseudoephedra and Ephedra (Ephedraceae) include dioecy, growth habit, opposite branching pattern, obvious joints and internodes, envelopes free from the nucellus except at the base, obvious apical projection (Chamberlain 1957; Bierhorst 1971; Martens 1971; Rydin and Friis 2010; Rothwell and Stockey 2013), suggesting that Pseudoephedra appears to fall well into the scope of the Ephedraceae. This rational-appearing placement remains plausible until detailed information of the apical projection is taken into consideration. The apical projection in Pseudoephedra is solid as other alternatives can be eliminated easily. (1) The apical projection is a micropylar tube filled up with pollen grains or sugar/starch. This interpretation sounds plausible considering the size of the granules in the apical projection (about 20 μm in diameter, Fig. 7.5c, g) matches well with that of pollen grains. However, this alternative becomes absurd when similar granules are also seen in the outer envelope of Pseudoephedra, where pollen grains are not expected (Fig. 7.5d). Furthermore micropylar tubes

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have never been reported completely filled up with pollen grains yet. Sugar or starch is present in pollination drop of Gnetales, but such sugar/starch, if preserved, should not be granular and micropylar-tube-full-filling, and they should not be seen in the tissue of outer envelope, either. Therefore this alternative is dropped. (2) Micropylar tube in Pseudoephedra is blocked after pollination, as in Gnetales and Erdtmanithecales (Friis et al. 2007; Rothwell and Stockey 2013). However, the blocking of micropylar tube in Gnetales and Erdtmanithecales is restricted to the segment of micropylar tube bracketed by the outer envelope and the distal portion of micropylar tube remains open (Friis et al. 2007, 2011). The “blocking” in Pseudoephedra is seen in the whole length of the apical projection (Fig. 7.5b, c, f, g), thus distinct from the cases in Gnetales and Erdtmanithecales. Three dimensionally preserved apical projection of Pseudoephedra shows no trace of tubular structure, as it shows little deformation in spite of the vertical pressure from the overlying strata. The apical projection of Pseudoephedra, when missing, leaves a groove on the sediment (Fig. 7.5f, h); it may be preserved as a cylinder bulging above the sediment, when preserved (Fig. 7.4f, h), implying that the apical projection of Pseudoephedra is a solid rather than tubular structure. This character alone prevents placing Pseudoephedra in Ephedraceae.

Apparently, forcing Pseudoephedra into the Ephedraceae (Gnetales) is not an acceptable treatment. Solid apical projection implies angio-ovuly in Pseudoephedra. If it were forced into Ephedraceae, it would mean that the ovules have no chance to be exposed at pollination in Ephedraceae and the pollination has to be fulfilled in a mode typical of angiosperms. This treatment would bridge angiosperms and Gnetales, in which Gnetum is similar to eudicots in almost all aspects. On the other hand, the BEG group (Bennettitales, Erdtmanithecales, and Gnetales) has only one synapomorphy, micropylar tube (Friis et al. 2007; Friis et al. 2009). Lumping Pseudoephedra without micropylar tube into Ephedraceae (Gnetales, BEG clade) would destroy the only synapomorphy of whole BEG clade. This undermines the validity of BEG clade, as pointed previously (Rothwell et al. 2009; Tekleva and Krassilov 2009). Considering all, Pseudoephedra is hard to place in Gnetales.

7.2.3.3 Third Alternative

If the oval body with distal projection in Pseudoephedra is taken as an ovary with a style, then the female part of Pseudoephedra is comparable to a female flower of angiosperm. The scales surrounding the female part may be interpreted as perianth elements, the apical projection the style, and the whole fossil an inflorescence. This interpretation is favored by the solid nature of the apical projection and thin wall around the oval body of Pseudoephedra [Fig. 2k of Liu and Wang (2016)]. The solid nature of the apical projection makes gymnospermous pollination impossible. Different pollination modes have been used to distinguish angiosperms and gymnosperms for more than a century (Arber and Parkin 1907; Martens 1971; Cronquist 1988; Biswas and Johri 1997; Tomlinson and Takaso 2002): the ovules in angiosperms are typically pollinated by sperms transported through pollen tubes that penetrate style tissues. The famous Mesozoic plant Caytonia had once been put in angiosperms due to its enclosed seeds (Thomas 1925) but later transferred into gymnosperms due to the presence of pollen grains in the cupules (Harris 1933, 1940). Similarly, despite its eudicot-like morphology, Gnetum is rationally placed in gymnosperms because of its pollination mode. These examples demonstrate clearly that only complete enclosure of ovules before pollination ensures an angiosperm affinity for a plant, and other characters are only of limited value in determining angiospermous affinity. The solid nature of the apical projection in Pseudoephedra makes pollen grains impossible to enter the oval body. The thin wall around the oval body [Fig. 2k of Liu and Wang (2016)] strengthens that the oval body actually may be an ovary, and the thin wall may be the ovarian wall completely secluding the interior space, suggestive of angio-ovuly. Thus placing Pseudoephedra in angiosperms appears rational. The challenges for this interpretation include Ephedra-like morphology and two surrounding envelopes of Pseudoephedra. Ephedra-like angiosperms have been seen among extant angiosperms, for example, Anabasis (Amaranthaceae) is a eudicot that is hardly distinguishable from Ephedra. Early Cretaceous Chaoyangia was also frequently placed in Gnetales due to its Ephedra-like decussate branching pattern although Chaoyangia is proven a monoecious angiosperm (Duan 1998). Two envelopes surrounding an ovary is rare but not unseen in angiosperms, for example, the ovary with distal style in Fagaceae and Juglandaceae (Bhattacharyya and Johri 1998) is surrounded by additional layers. Thus it seems decent placing Pseudoephedra in angiosperms, although this treatment may blur the boundary between angiosperms and gymnosperms, a situation expected by Darwinism.

Treated as incertae sedis by Liu and Wang (2016), Pseudoephedra awaits new light on its affinity from future research.

7.2.4 Conclusions

Pseudoephedra is an enigmatic Early Cretaceous plant demonstrating a great resemblance to Ephedraceae. Instead of micropylar tube, the occurrence of solid apical projection in Pseudoephedra makes it more comparable to angiosperms. Placing Pseudoephedra in any known group of seed plants is currently premature.

7.3 Problematospermum

Problematospermum is an enigmatic seed originally described from the Karatau of Kazakhstan (Turutanova-Ketova 1930). Currently known records of Problematospermum range from the Middle Jurassic to Early Cretaceous (Turutanova-Ketova 1930; Krassilov 1973a, b, 1982; Liu 1988; Wu 1999; Sun et al. 2001). The long pre-Cretaceous history makes *Problematospermum* interesting because of it was interpreted as an angiosperm by Krassilov (Krassilov 1973a, b). The material reported here are of *Problematospermum ovale* from two localities in the Middle Jurassic of China. *Problematospermum* has a tuft of filamentous appendages attached to its base and a stout projection with a central canal at its apex. *Problematospermum* demonstrates a chimeric combination of features scattered in Gnetales, Bennettitales, and Erdtmanithecales.

Total 71 individual seeds of *Problematospermum* were recovered from the Jiulongshan Formation near Sanjiaocheng Village in western Liaoning, and Daohugou Village in eastern Inner Mongolia, China.

7.3.1 Problematospermum

Generic Diagnosis: Seed composed of a short stalk, and a seed body with a long apical projection and basal filamentous appendages. Seed body round to elliptic, with short blunt processes in rows and files. Projection straight, with a central canal. Filamentous appendages attached to the base of seed body, diverging upward, becoming detached when the seed is mature. Seed coat composed of three layers.

Type species: *Problematospermum ovale*.

Locality: Gansu, Liaoning, Inner Mongolia, China; Karatau, Kazakhstan; Mongolia.

Age: the Middle Jurassic to Early Cretaceous.

7.3.2 Problematospermum ovale

Synonyms:

Problematospermum ovale Turutanova-Ketova (1930, p. 160, Plate 4, Fig. 30, 30a).

Problematospermum elongatum Turutanova-Ketova (1930, p. 161, Plate 4, Fig. 29, 29a).

Problematospermum ovale Turutanova-Ketova, Krassilov (1973b, p. 1, Plate 1, Figs. 1–12; Plate 2, Figs. 13–22).

Problematospermum ovale Turutanova-Ketova, Krassilov (1973a, p. 170, Fig. 4a–d).

Typhaera fusiformis Krassilov (1982, p. 35, Plate 19, Figs. 247–248, 250–251).

Problematospermum sp. Krassilov (1982, p. 36, Plate 19, Fig. 252).

Carpolithus longiciliosus Liu (1988, p. 97, Plate 1, Fig. 22).

Typhaera fusiformis Krassilov, Wu (1999, p. 22, Plate XVI, Fig. 3, 3a; Plate XVIII, Figs. 3,3a, 6, 6a).

Problematospermum ovale Turutanova-Ketova, Sun et al. (2001, p. 110, Plate 25, Figs. 3–4; Plate 66, Figs. 3–11).

Problematospermum ovale (Turutanova-Ketova), Wang et al. (2010, p. 448, Figs. 1–3).

Holotype: *Problematospermum ovale* Turutanova-Ketova (1930, p. 160, Plate 4, Fig. 30, 30a).

Type locality: Karatau, Kazakhstan (Turutanova-Ketova 1930; Krassilov 1973a, b).

Other localities: Gurvan-Eren Mountain, Mongolia (Krassilov 1982); Niuposigou, Shenyu and Wangjiagou, Wubu Village, both in Huating County, Gansu, China (Liu 1988); Huangbanjigou, Beipiao, Liaoning, China (Wu 1999; Sun et al. 2001); Daohugou Village, Ningcheng, Inner Mongolia, China (Wang et al. 2010); Sanjiaocheng Village, Jinxi, Liaoning, China (Wang et al. 2010).

Age: The Middle Jurassic to Early Cretaceous.

Stratigraphic horizon: Karatau Shales (Upper Jurassic) in Kazakhstan; Gurvan-Eren Formation (Lower Cretaceous) in Gurvan-Eren Mountain, Mongolia; Huanhe-Huachi Formation (Lower Cretaceous) in Huating County, Gansu, China; Yixian Formation (Lower Cretaceous) at Huangbanjigou, Liaoning, China; Jiulongshan Formation (Middle Jurassic) at Daohugou Village, Inner Mongolia and Sanjiaocheng Village, Liaoning, China.

Specimen number: PB20716, PB21108-PB21114, PB21117, PB21121-PB21128, PB21130, PB21132-PB21136, PB21139-PB21140, PB21145, PB21148-PB21167, PB21176, from Daohugou Village; PB21115-PB21116, PB21118-PB21120, PB21129, PB21131, PB21137-PB21138, PB21141-PB21144, PB21146-PB21147, PB21168-PB21175, from Sanjiaocheng Village.

Specific Diagnosis: In addition to the generic diagnosis, the size of the seeds from all localities ranges from 3.5 to 21.3 mm long; the elongated seed body is 1.6–8.4 mm long and 0.48–2.4 mm wide; the apical projection is 0.6–14.5 mm long and 0.14–0.7 mm wide.

Description: The seed consists of four parts, namely, basal stalk, seed body, apical projection, and basal filamentous appendages (Fig. 7.7a–d). In many specimens some of the projections and filamentous appendages may be detached or missing, naked seed bodies without filamentous appendages or apical projections are frequent among the newly recovered specimens (Fig. 7.7e–h). The maturity of the seeds is suggested by their size and attachment of filamentous appendages. Larger specimens without filamentous appendages are considered more mature than smaller specimens with filamentous appendages still attached.

The stalk is about 0.5–0.9 mm long, 0.2 mm wide (Fig. 7.7a–h). The seed body is long-elliptical, ranging from 1.6 to 8.4 mm (average 5.485 mm, 54 measurements) in length, and from 0.48 to 2.4 mm (average 1.23 mm, 59 measurements) in width (Fig. 7.7a–c, e–i). The apical projection ranges from 0.6 to 14.5 mm

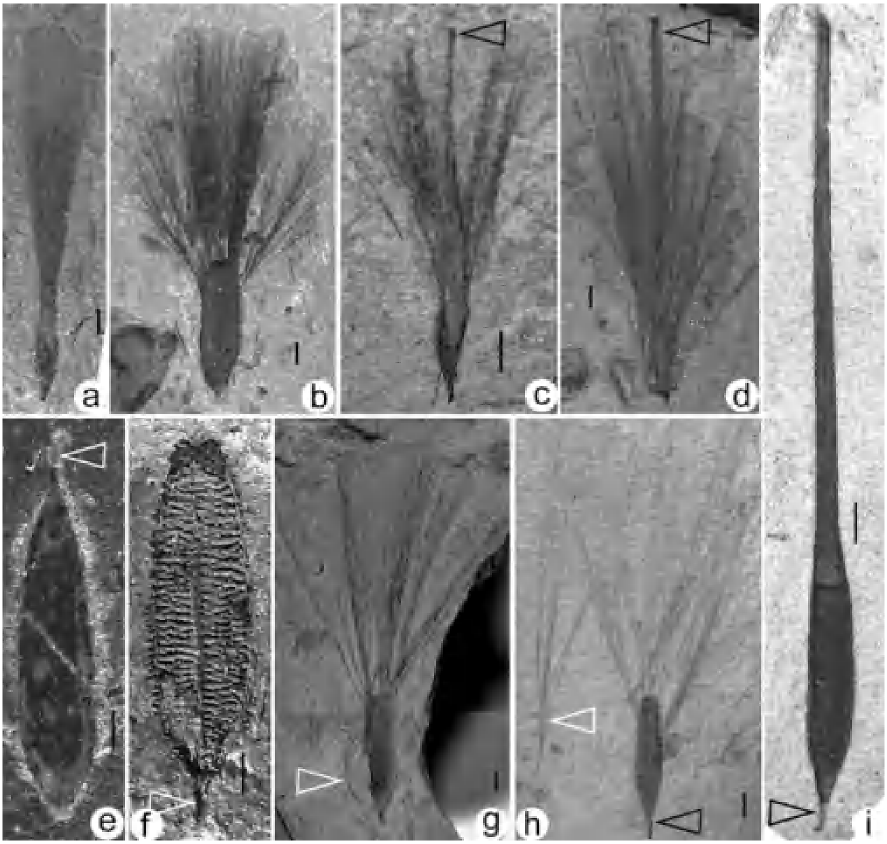

Fig. 7.7 *Problematospermum ovale*. Nine seeds preserved in various stages. All from Daohugou Village, Inner Mongolia except Fig. 7.7e from Sanjiaocheng Village, Liaoning. All stereomicrographs. All bar = 1 mm. (a) Seed probably in early stage, note filamentous appendages not widely spread above seed body. PB21112. (b) Seed including seed body and filamentous appendages. Projection not visible. PB21110. (c) Seed with under-developed seed body, filamentous appendages, and a central rigid straight projection (arrow). PB21132. (d) A seed with basally attached filamentous appendages, and a central rigid straight projection (arrow) with a truncated tip. PB21109. (e) A seed including seed body and remnant of projection (arrow). Note dark material of seed content. PB21116. (f) A seed including seed body and remnant of stalk (arrow). PB21176. (g) Seed with truncated apex, stalk, basally-fixed filamentous appendages (arrow), and lack of projection. PB21113. (h) A seed and detached filamentous appendages (white arrow). Note the truncated apex and stalk (black arrow), basally-fixed filamentous appendages, and lack of projection. PB21114. (i) A seed without filamentous appendages. Note stalk (arrow), seed body, and rigid straight projection with truncated tip. PB20716. Courtesy of International Journal of Plant Sciences

(average 4.675 mm, 24 measurements) in length, and from 0.14 to 0.7 mm (average 0.332 mm, 27 measurements) in width (Fig. 7.7c–e, i). Filamentous appendages range from 6.8 to 20.5 mm (average 12.99 mm, 34 measurements) in length (Fig. 7.7a–d, g, h).

Fifty-nine seeds have been observed and measured. The largest specimens (presumably mature seed body) is elliptic but slightly wide in the lower middle (Fig. 7.7a–c, e–i). The apex is notched or truncated when the apical projection has fallen off (Fig. 7.7b, f–h). The seed body is longitudinally ridged, with short blunt processes arranged in rows and files on the surface (Figs. 7.7f, i, 7.8k, and 7.9b). Frequently short blunt processes are arranged in rows and merge horizontally with each other (Figs. 7.7f, i, 7.8k, and 7.9b). Seed coat includes Layer I with short hairs, Layer II, and Layer III (Fig. 7.9b,

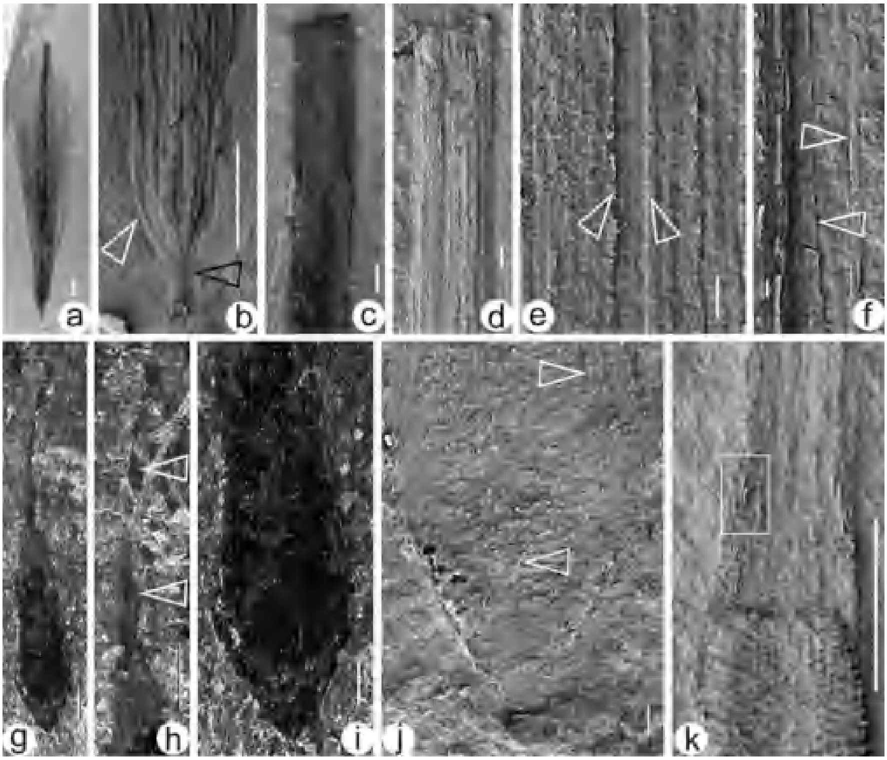

Fig. 7.8 Problematospermum ovale. Details of three seeds. PB21108 (a–f), PB20716 (n–o) from Daohugou Village, Inner Mongolia; PB21118 (g–m) from Sanjiaocheng Village, Liaoning. a, c, g–i are stereomicrographs, others are SEM micrographs. (a) A complete seed with filamentous appendages, rigid straight projection, and stalk at base. Bar = 1 mm. (b) Detailed view of seed base in a. Note stalk (black arrow) and arrangement of filamentous appendages (white arrow). Bar = 1 mm. (c) Detailed view of truncated tip of rigid straight projection of seed in a. Bar = 0.2 mm. (d) Truncated tip of rigid straight projection of seed in a, under SEM. Bar = 0.1 mm. (e) The canal (between arrows) within projection of seed in a. Bar = 0.5 mm. (f) Ultimate filamentous elements (arrows). Bar = 20 μm. (g) Seed lacking filamentous appendages. Bar = 1 mm. (h) Distal projection (arrows) of seed in g. Bar = 1 mm. (i) Details of seed body in g. Bar = 0.5 mm. (j) Detail of seed body in g, under SEM. Note remains of filamentous appendages (arrow). Bar = 0.2 mm. (k) Details of the terminal of seed body in g. Bar = 50 μm. Courtesy of International Journal of Plant Sciences

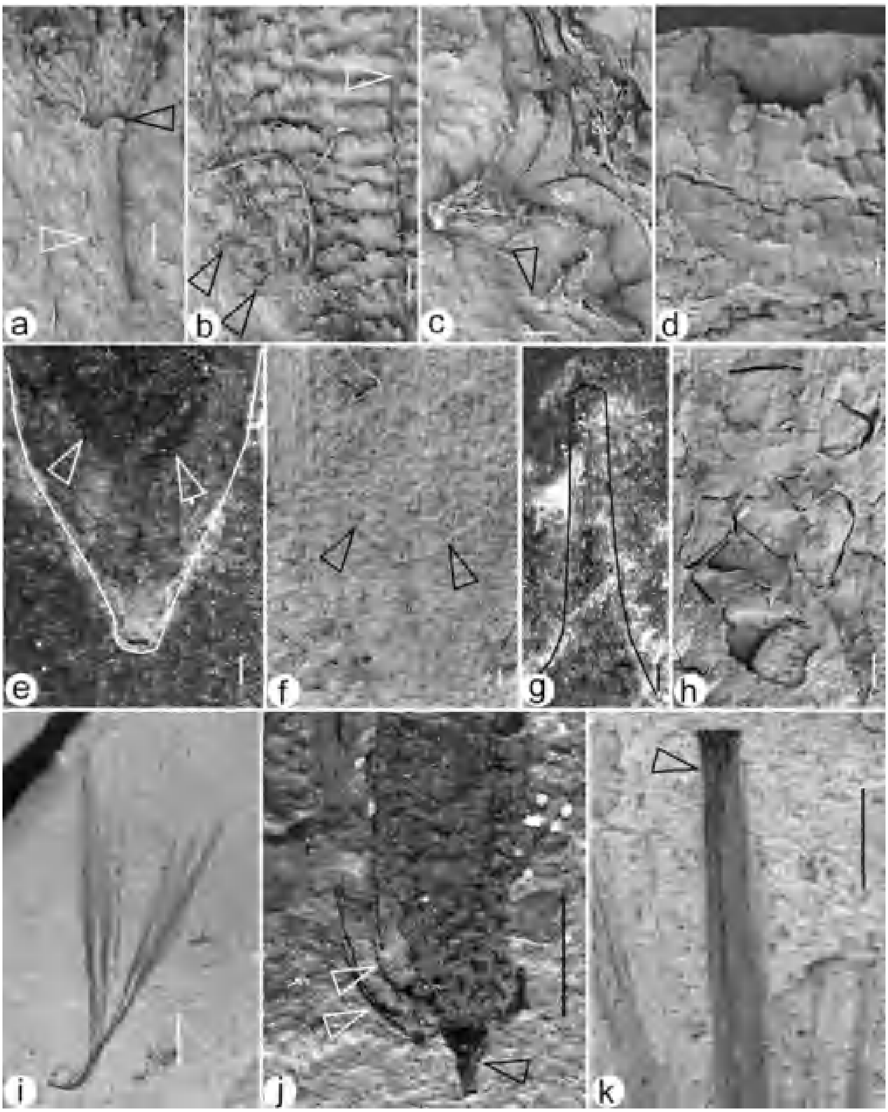

Fig. 7.9 Problematospermum ovale. Details of seeds and detached filamentous appendage. PB21176 (a–d), PB21111 (i), and PB21109 (j–k), from Daohugou Village, Inner Mongolia; PB21116 (e–h), from Haifanggou Village, Liaoning. e, g, i–k are stereomicrographs, others are SEM micrographs. (a) Details of bottom portion of seed shown in Fig. 7.7f. Note stalk (white arrow) at base and stubs (black arrow) left by fallen filamentous appendages. Bar = 0.2 mm. (b) Details of seed body of seed in Fig. 7.7f, showing longitudinal ridge (white arrow) and small processes (black arrow) on seed coat. Bar = 0.2 mm. (c) Detail of lower left corner of Fig. 7.9b. Note processes of Layer I (Sa), Layer II (Sc), and short hair on spike tip (arrow). Bar = 50 μm. (d) Layer I at joint between seed body and projection of seed in Fig. 7.7f, showing rectangular cells. Bar = 50 μm. (e) Bottom portion of seed in Fig. 7.7e, showing outline (white line) of seed body and parenchyma content (arrows) in seed. Bar = 0.2 mm. (f) The same region as in Fig. 7.9e, under

c). All cells in the seed coat are elongated and arranged parallel to the long axis of the seed body (Fig. 7.9b, c). Layer I includes two layers of cells, 20–40 × 22–53 × 40–175 μm, with a hair attached to each spike (Fig. 7.9b, c). Layer II consists of 2–3 layers of sclereids, highly compressed, about 13.5 × 160 μm (Fig. 7.9b, c). The inner part of the seed body is about 5.8 mm long, 1.25 mm wide, composed of parenchyma enclosed in the seed coat (Fig. 7.9e, f, h). The parenchymatous cells are polygonal, 6–14 × 15–26 μm and separated each other by a thin cell wall (Fig. 7.9h).

Twenty-seven specimens have apical projections at the seed apices. They are straight or slightly curved, and tapering slightly towards the apex. Each projection is composed of a central canal and peripheral wall, truncated at the tip (Figs. 7.7c, d, i, 7.8a, c–e, g, and 7.9k). The central canal is 0.2–0.4 mm wide, surrounded by a wall of 5–7 layers of cells that are oriented parallel to the length of the projection (Fig. 7.9a–e). These cells may be sclerified or lignified (Fig. 7.9c–e), 79–120 μm long and 25–30 μm wide (Fig. 7.9c–e).

Filamentous appendages are attached to the base of the seed body and terminate slightly below the tip of the projection. In a few specimens, the appendages converge just above the seed body (Fig. 7.7a). In most specimens, they are more divergent (Figs. 7.7b–d, g–h and 7.8a). Individual filamentous elements are probably one cell wide, straight, about 10–16 μm in diameter (Fig. 7.9i, k).

7.3.3 Nomenclature and Structure

Two species of *Problematospermum* recognized by Turutanova-Ketova (1930) based on nine specimens from the Upper Jurassic in Karatau, Kazakhstan. Krassilov (1973a, b) combined the two species into a single species, *P. ovale*. The specimens from the Middle Jurassic in northeastern China support the recognition of only a single species (Fig. 7.7a–i), as the statistics of morphology indicates that previously reported specimens and those reported by Wang et al. (2010) are hard to distinguish from each other.

Krassilov (1973a, b) interpreted *Problematospermum* as an ancestral angiosperm or angiosperm-like plant related to extant Compositae based on what he

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Fig. 7.9 (continued) SEM. Note border (*arrows*) of seed content. Bar = 0.1 m. (g) Projection of seed in Fig. 7.7e. Note outline of projection (*black line*). Bar = 0.2 mm. (h) Seed content in F. Note parenchymatous cells delimited by cell walls and gaps between cells and cell walls. Bar = 10 μm. (i) Detached ramifying filamentous appendage. Bar = 2 mm. (j) *Bottom* portion of seed in Fig. 7.7d. Note basally-fixed appendages (*white arrows*) and stalk (*black arrow*). Bar = 1 mm. (k) Detailed view of *top* portion of seed in Fig. 7.7d. Note rigid straight projection (*arrow*) with truncated tip, and divergent filamentous elements around. Bar = 1 μm. Courtesy of International Journal of Plant Sciences called an apical pappus. However, the filamentous appendages are attached to the base rather than to the apex of the seed (Turutanova-Ketova 1930, Plate 4, Fig. 30, 30a). This is further confirmed by the observation on Chinese materials (Wang et al. 2010). Krassilov (1973a, b) described both the apical projections and basal stalk as a tube, without showing the related figures. But the observations on Chinese materials (Wang et al. 2010) indicate that the apical projection is tubular while the stalk is not tubular (Fig. 7.8a–e).

7.3.4 Developmental Series

It is possible that the specimen originally called *P. elongatum* (Turutanova-Ketova 1930) may represent an early stage of *P. ovale* (Krassilov 1973a, b). The filamentous appendages are grouped together into a bundle and appear more or less constricted toward the seed apex (Krassilov 1973a, b). It appears that the filamentous appendages were not fully developed, and stuck together or were pressed together during early development (Fig. 7.7a), and thus looking different from the diverging arrangement in more mature ones (Figs. 7.7b–d and 7.8a). As the development progressed, the filamentous appendages expanded and diverged (Fig. 7.7g, h; Sun et al. 2001, Plate 25, Figs. 1–2, Plate 66, Figs. 1–2, Plate 75, Figs. 1–6). Each fully-developed individual filament is 10–16 μm in diameter. The filamentous appendages form a tuft of hairs around the seed body (Fig. 7.7d), which may help in seed dispersal. A seed may lose its filamentous appendages at maturity, and only a naked seed body, with or without an apical tubular projection, was preserved (Fig. 7.7e–i). Detached filamentous appendage bundles are frequently seen in the sediments (Fig. 7.9i).

7.3.5 Phylogenetic Relationships

Although treated as *incertae sedis*, *Problematospermum* is likely related to Bennettitales, Erdtmanithecales, Gnetales (“BEG group” *sensu* Friis et al. 2009) and their relatives.

In Gnetales, a micropylar tube exserts the outer integument and may help to capture pollen grains during pollination (Chamberlain 1957; Bierhorst 1971; Biswas and Johri 1997). A pollination drop draws the pollen grain down to the ovule during fertilization (Friedman 1990a, b; Yang 2004, 2007). The projection in *Problematospermum* resembles the micropylar tube in Gnetales in its apical position and tubular configuration (Fig. 7.8a–e), implying that the pollination in *Problematospermum* may be similar to that in BEG clade. Furthermore, multicellular hairs resembling the filamentous appendages of *Problematospermum* in position and morphology have been seen between ovuliferous units in Gnetum (Gnetaceae) (Arber and Parkin 1908; Martens 1971) and Bennettitales (see below). The seeds in Gnetales that have been well documented recently (Rydin et al. 2004, 2006a, b) are usually enveloped by a hard outer layer, however, such layer is missing in Problematospermum.

Certain similarities are shared between seeds of Problematospermum and Bennettitales, including apical projections connected with the seed body and a central canal surrounded by layers of cells (Stopes 1918; Pedersen et al. 1989a; Rothwell and Stockey 2002; Friis et al. 2009; Crane and Herendeen 2009; Rothwell et al. 2009). Additional similarities shared with bennettialean seeds include basal trichomes or hairs (or tubular cells) attached to the “sporophyll” stalk and trichomes extended to the upper portion of the seeds (Wieland 1906; Stopes 1918; Rothwell et al. 2009). The bottom of the micropylar tube of probable Williamsoniella coronata in Fig. 14 of Crane and Herendeen (2009) is eclipsed by some filament-like structures. If such trichomes/tubular cells are homologous to the filamentous appendages in Problematospermum, then, at least in this respect, Problematospermum resembles Bennettitales and its seed is homologous to that in Bennettitales (Friis et al. 2009). The filamentous appendages converging just above the seed body in Fig. 7.7a are reminiscent of the hairs/trichomes in Bennettitales that are pressed against the micropylar tube by the surrounding interseminal scales (Wieland 1906; Stopes 1918; Rothwell et al. 2009). The whole plant of Problematospermum is unknown and further comparison is impossible. The leaves of Bennettitales are frequently seen in the Jiulongshan Formation, making relationship between Problematospermum and Bennettitales not an impossibility.

Seeds of Erdtmanithecales have been intensively studied recently (Pedersen et al. 1989b; Friis and Pedersen 1996; Friis et al. 2007, 2009; Mendes et al. 2008). All of these seeds share a similar construction, and they are related to Erdtmanithecales, Gnetales and perhaps also Bennettitales (the “BEG group”) (Friis et al. 2007, 2009), the validity of which, however, was suspected by Rothwell et al. (2009). Problematospermum is similar to Rugonella and the square seeds in apical projection (micropylar tube) although the projections in the latters are much shorter. Its further resemblance to Rugonella includes horizontally merged short blunt processes (irregular transverse ridges) (Friis et al. 2009, Figs. 125, 127). The square seeds are distinguished from Problematospermum by their tepal-like apical extensions, lack or loss of tuft of filamentous appendages, non-sclerified micropylar tube with a 1–2 cell-thick wall (Friis et al. 2007, 2009). Similarly, Rugonella is distinguished from Problematospermum by lateral wings, lack or loss of tuft of filamentous appendages, and non-sclerified micropylar tube with 1–2 cell-thick wall (Friis et al. 2009). Eoantha from the Early Cretaceous in Baisa, Lake Baikal Area (Krassilov 1986) has no evident apical projection and its linear-lanceolate bracts looks different from the filamentous appendages of Problematospermum. Problematospermum lacks a well-preserved megaspore membrane and evident additional envelope (diagnostic features for Erdtmanithecaceae, Friis and Pedersen 1996), and thus cannot be ascribed to Erdtmanithecaceae.

New observations on Chinese materials do not support Krassilov′s comparison between *Problematospermum* and fruits of angiosperm family Compositae. Despite the superficial similarities between apical projection and basal filamentous appendages in *Problematospermum* and style and dispersal hairs in some angiosperms (e.g. *Platanus*), there is little evidence supporting this relationship. The combination of features indicates that *P. ovale* may have certain relationship with Bennettitales, Erdtmanithecales, and Gnetales.

7.4 Nubilora

7.4.1 Introduction

A key problem in studies on early angiosperms is that the carpels of angiosperms are not comparable with any single part in gymnosperms. So far there is little consensus on the origin and homology of carpels. Several authors (Taylor and Kirchner 1996; Wang et al. 2015; Doyle 2011) have repeatedly theoretically compared a carpel in angiosperms with a leaf and its axillary fertile shoot. These proposals remain tentative due to lack of favoring fossil evidence hitherto. Here a fossil fertile organ, *Nubilora triassica* gen et sp. nov., from the Late Triassic is reported, which have seeds/ovules enveloped in its lateral units. The longitudinal enveloping of ovules in *Nubilora* conjures to the way of seed/ovule-enclosing in carpels of angiosperms. Considering the early age (Late Triassic) of *Nubilora*, the implications of *Nubilora* for the origin of angiosperm carpels and its phylogenetic position in seed plants is explored. Despite its affinity open to question, *Nubilora* appears to be one of the few badly wanted stepstones between gymnosperms and angiosperms, favoring the gradualistic Darwinism.

7.4.2 Geological Background

The fossil plant material examined here was obtained from the Ganhaizi Formation in Yangqiaoqing Coal Mine (25°09′22″N, 101°55′29″E) of the Yipinglang Coal Field in Lufeng County, Yunnan Province, China. The site has yielded abundant fossil plants from the Upper Triassic Pujiacun, Ganhaizi and Shezi formations (Feng et al. 2014).

The fossil plants from Yipinglang Coal Field were briefly discussed and assigned a Late Triassic age by Hsü (1946, 1950). The Yipinglang Flora has been geographically constrained, floristically characterized, and defined as a biostratigraphic unit by Lee et al. (1976) based on their systematic study on the macroflora.

The Yipinglang flora includes 42 genera, >90 species, including elements of the Filicales and Bennettitales as the dominating groups. Yipinglang Flora includes Selaginellites yunnanensis, Equisetites lufengensis, E. (cf. platyodon) sp., Neocalamites carrerei, N. hoerensis, N. spp., Danaeopsis fecunda, D. marantacea, Marattia asiatica, M. paucicostata, Bernoullia zeillerii, Asterotheca phaenonerva, Osmundopsis plectrophora, Todites goeppertianus, T. microphylla, T. scoresbyensis, T. shensiensis, Reteophlebis simplex, Phlebopteris xiangyunensis, Gleichenites yipinglangensis, Coniopteris tiehshanensis, Thaumatopteris contracta, Th. remauryi, Geoppertella memeria-watanabei, G. kwangyuanensis, Dictyophyllum nathorstii, Di. serratum, Di. sp., Clathropteris meniscioides, C. mongugaica, C. obovata, C. platyphylla, C. tenuinerivs, C. sp., Cladophlebis foliolata, Cl. grabauiana, Cl. integra, Cl. scariosa, Cl. raciborskii, Cl. sp., Cl. (Gleichenites?) sp., Pecopteris sp., Doratophyllum hsuchiahoense, Ptilozamites chinensis, P. nilssonii, Hyrcanopteris sinensis, H. sevanensis, H. spp., Pterophyllum aequale, Pt. angustum, Pt. exhibens, Pt. magnificum, Pt. minutum, Pt. ptilum, Pt. sinense, Pt. schenkii, Anomozamites densinervis, A. inconstans, A. loezyi, A. pachylomus, A. cf. minor, A. sp., Otozamites spp., Nilssoniopteris immersa, Ni. jourdyi, Sinoctenis calophylla, S. yunnanensis, S. sp., Ctenozamites sarranii, Ct. sp., Drepanozamites nilssonii, Anthrophyopsis cf. crassinervis, Ctenis sp., Baiera elegans, B. sp., Glossophyllum? sp., Ferganiella paucinervis, F. podozamioides, F. spp., Podozamites ex gr. lanceolatus, Pod. distans, Pod. schenkii, Pod. (?) subovalis, Pod. spp., Cycadocarpidum swabii, Cy. spp., cf. Pityophyllum longifolium, Ptilophyllum sp., Taeniopteris leclerei, Ta. cf. stenophylla, Ta. spp., Carpolithus spp., Strobilites sp., Conites spp. The taxonomic composition of the macroflora indicates a Norian–Rhaetian age (the Late Triassic) (Lee et al. 1976). These parautochthonous plant fossils in the Yipinglang Coal Field are preserved as compressions or impressions in a matrix ranging from medium-grained siltstone to claystone. Massive occurrences of Euestheriidae conchostracans (including Euestheria dazuensis, E. yipinglangensis, and E. lata) associated with the fossil plants also suggest a Late Triassic age (Chen 1977).

7.4.3 Nubilora

Generic diagnosis: Female organ with lateral units. Lateral unit enveloping one or two ovules/seeds inside. Ovule orthotropous, inserted on central axis.

Type species: Nubilora triassica gen. et sp. nov.

Etymology: Nubilora from Latin word nubilorum, meaning “of cloud”, for the fossil locality in Yunnan, which is usually abbreviated as Yun (cloud) in Chinese.

Horizon: The Ganhaizi Formation, Norian–Rhaetian, Late Triassic.

Locality: Yipinglang Coal Field in Lufeng County, Yunnan Province, China (25°09′22″N, 101°55′29″E).

Remarks: The new genus is similar to *Caytonia* (Thomas 1925; Harris 1933, 1940; Reymanowna 1970; Nixon et al. 1994) and *Petriellaea* (Taylor et al. 1994) in term of ovules/seeds inside lateral units. However, the new genus can be distinguished from these two genera by its lack of basal opening for the lateral unit, no transverse folding of the lateral unit wall, and only one or two ovules/seeds per unit. These differences justify a new genus for this fossil organ.

7.4.4 Nubilora triassica gen. et sp. nov.

Specific diagnosis: The same as the genus.

Description: The organ is preserved as a coaly compression embedded in gray siltstone (Fig. 7.10a–d). It is 28 mm long and 7 mm wide, cylindrical in form, including a central axis and numerous lateral units (Fig. 7.10a). The central axis is about 1.1 mm in diameter, running from the bottom to the top, connecting and bearing at least 17 lateral units (Fig. 7.10a). A couple of lateral unit pairs are concentrated on the central axis at about the same level, leaving the central axis free between the tufts of lateral units (see lateral unit 1 and 2, 5 and 6 in Figs. 7.10a and 7.11f). The basal lateral units are more mature than the distal ones (Fig. 7.10a). Each lateral unit is 4.2–5 mm long, 1.3–1.4 mm wide, 1.3–1.5 mm thick, with a decurrent base and a pointed tip, departing from the central axis at angles between 45° and 50° (Fig. 7.10a). The surface of lateral units is smooth, with longitudinal texture (Fig. 7.12a, c). There appear to be several longitudinal striations along the ventral margins (Fig. 7.11d). Within each lateral unit there are two or one seed/ovule (Figs. 7.10a–c and 7.11a–c). There is additional space above the top of the ovules/seeds (Fig. 7.11a–c). The seeds/ovules are not attached to the wall of lateral unit, but directly connected to the central axis of the organ (Fig. 7.10b–d and 7.11a–c). The seeds/ovules are 2.3–2.8 mm long, 1.3 mm wide, 0.5–0.7 mm thick (Figs. 7.10b, c and 7.11a–c). A small (aborted?) ovule about 1.1 mm long and 0.5 mm wide is seen in a lateral unit (Fig. 7.12b). The seeds are present in the basal lateral units, with smooth coats 80–100 μm thick, arcate and independent of adaxial wall, straight and fused with the abaxial wall (Figs. 7.10c and 7.11b). In an opened lateral unit, an ovule is broken through the middle, revealing the anatomy of the ovule (Figs. 7.10b and 7.11a, e). The ovule is orthotropous, directly connected to the central axis (Figs. 7.10b–d and 7.11a–c). The nucellus is 2.6 mm long and 1.4 mm wide, surrounded by an integument (Figs. 7.10b and 7.11a, e). The integument is about 0.36 mm thick, covering up the nucellus almost completely, free from the nucellus to the bottom, and meeting above the tip of the nucellus (Figs. 7.10b and 7.11a, e).

Etymology: *Triassica* for the Triassic, the age of fossil.

Holotype: YKLP20014.

Depository: the palaeobotanical collection, Yunnan Key Laboratory for Palaeobiology, Yunnan University, Kunming, China.

Fig. 7.10 Nubilora triassica and its details. LM. (a) The organ embedded in the sediments as three dimensionally preserved coalified compression. Bar = 10 mm. (b) Lateral unit 6 in a. Note the outline of the split lateral unit and ovule (ov) inside. Refer to Fig. 7.11a, e. Bar = 1 mm. (c) Lateral unit 1 in a. Note the outline of the lateral unit, one seed (s) inside, and their relationship to the central axis (ca). Refer to Fig. 7.11b. Bar = 1 mm. (d) Detailed view of basal portion of the lateral unit in b. Note the margins of nucellus (red arrows), ovule (blue arrow), and lateral unit (white arrow). Bar = 0.5 mm

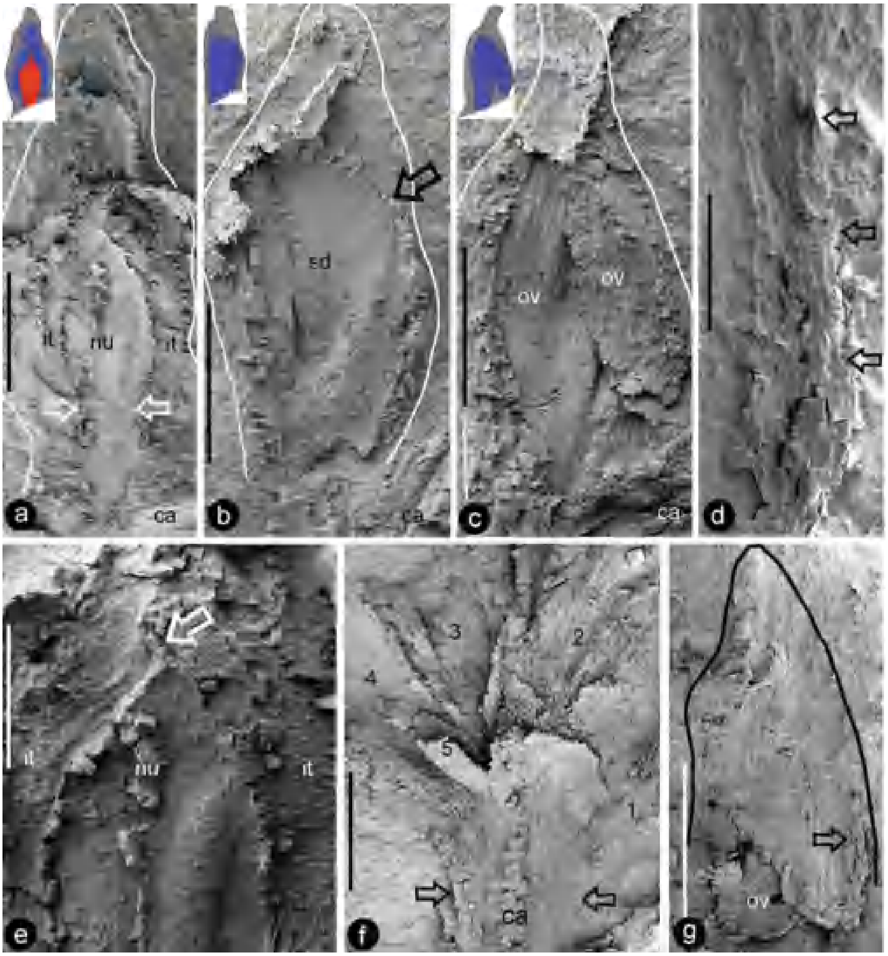

Fig. 7.11 Details of lateral units and ovules/seeds of Nubilora triassica. SEM. (a) The lateral unit shown in Fig. 7.10b. Note the outline (white line) of the lateral unit, ovule [including nucellus (nu) and integument (it)], and their relationship to the central axis (ca). The sketch is shown in upper-left. Bar = 1 mm. (b) Lateral unit shown in Fig. 7.10c. Note the outline of the lateral unit (white line), one seed (sd) inside, and their relationship to the central axis (ca). The sketch is shown in upper-left. Bar = 1 mm. (c) Lateral unit 7 in Fig. 7.10a. Note the outline of the lateral unit (white line), two ovules (ov) inside. The sketch is shown in upper-left. Bar = 1 mm. (d) Longitudinal striations (arrows) along the ventral margin of a lateral unit, enlarged from arrowed region in g. Bar = 0.2 mm. (e) Detailed view of the distal portion of the ovule in a. Note the integument (it) bracketing the nucellus (nu), and the micropyle (arrow). Bar = 0.5 mm. (f) The portion of the organ labeled as 8 in Fig. 7.10a, showing at least five lateral units (1–5) concentrated at almost the same level on the central axis (ca), which otherwise has smooth margins (arrows). Bar = 1 mm. (g) Lateral unit 9 Fig. 7.10a. Note the outline of the lateral unit that is broken at the bottom, an ovule (ov) formerly covered but now exposed. The ventral margin (arrow) is to the right. Bar = 1 mm

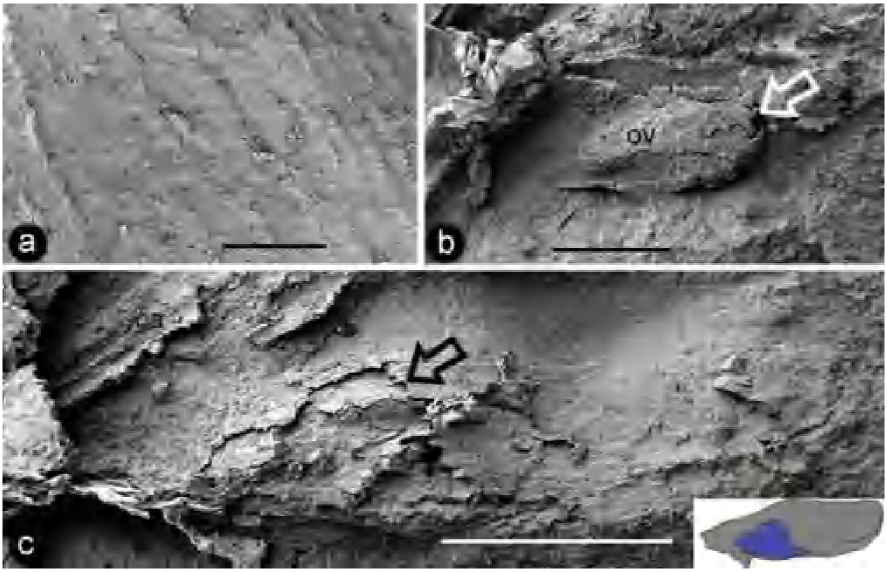

Fig. 7.12 Details of lateral units and ovules/seeds of *Nubilora triassica*. SEM. (a) Longitudinal texture on the surface of a lateral unit. Bar = 0.1 mm. (b) One aborted (?) ovule (ov, *arrow*) inside the lateral unit 3 in Fig. 7.10a. Bar = 0.5 mm. (c) The lateral unit 2 in Fig. 7.10a. Note the longitudinal texture on its surface (*upper right*), broken enclosing layer, exposed seed (*arrow*) inside, and their relationship to the central axis (ca). The sketch is shown in the *lower-right*. Bar = 1 mm

7.4.5 Discussions

Lack of any trace of pollen and millimetric size of the ovules/seeds in the lateral units imply that *Nubilora* is a female organ (Figs. 7.10b, c and 7.11a–c). Thanks to the physically connection among lateral units of various stages, the development from ovules to seeds in *Nubilora* may be revealed (Fig. 7.10a). A seed in one of the basalmost lateral units (Figs. 7.10c and 7.11b) appears to have a seed coat, thus distinct from its precursor (ovule) in early development (Figs. 7.10b and 7.11a, c, e). The difference between them implies these structures (ovules and seeds) in the lateral units of *Nubilora* are the same parts in different developmental stages (Fig. 7.13).

The ovules/seeds of *Nubilora* are enveloped by the wall of the lateral units (Figs. 7.10b, c and 7.11a–c). This feature distinguishes *Nubilora* from all fertile fossil organs that have their ovules/seeds naked or exposed to the exterior. There have been some previous records of fossil plants with seeds enveloped from the Mesozoic. For examples, *Caytonia* and *Petriellaea* from the Mesozoic have their seeds surrounded in cupules, and one of them was once interpreted as angiosperms (Thomas 1925) until refuted later by more careful studies (Harris 1933, 1940). The transversal folding of the cupules in these groups are hard to correlate with the

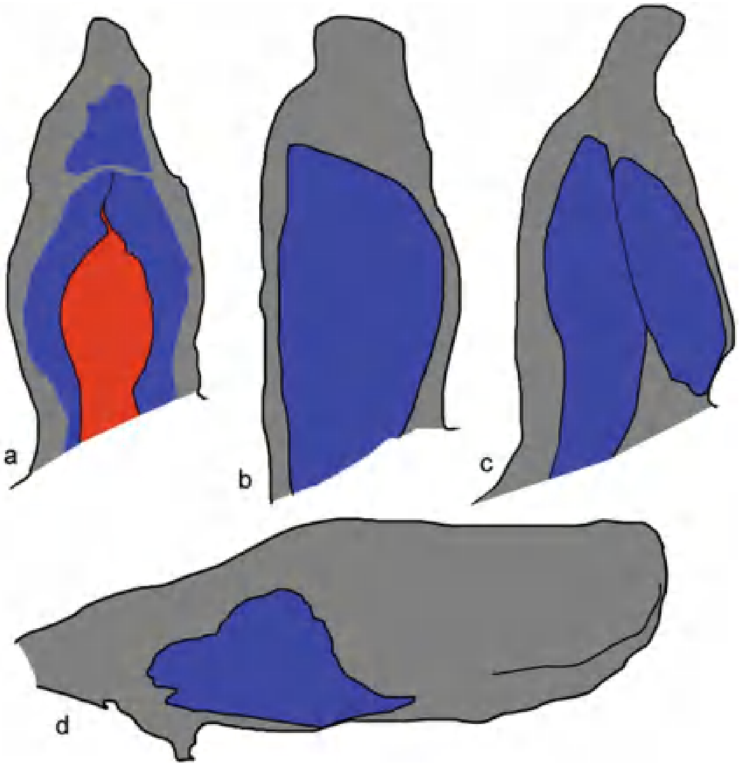

Fig. 7.13 Sketches of lateral units and ovules/seeds of Nubilora triassica. Gray for wall of lateral unit, blue for ovule/seed, red for nucellus. (a) Lateral unit shown in Figs. 7.10b and 7.11a, e. (b) Lateral unit shown in Figs. 7.10c and 7.11b. (c) Lateral unit shown in Fig. 7.11c. (d) Lateral unit shown in Fig. 7.12c

longitudinal folding of angiosperm carpels (Doyle 2006). Although similar to Caytonia (Thomas 1925; Harris 1933, 1940; Reymanowna 1970; Nixon et al. 1994) and Petriellaea (Taylor et al. 1994) in terms of enveloped/surrounded seeds, Nubilora is distinguished from these two genera in its longitudinally folded envelope, and only one or two ovules/seeds per unit. Dirhopalostachys, another interesting plant from the Late Jurassic—Early Cretaceous of Russia (Krassilov 1975), may be the only fossil organ that demonstrates the greatest resemblance to Nubilora because of its cylindrical form, paired capsules arranged along an axis, enclosed basal orthotropous seed. However, its differences from Nubilora are also equally obvious, namely, single seed in capsule and apical beak of Dirhopalostachys contrast strongly against one or two seeds per lateral unit and lack of distal extension in Nubilora. These differences justify a new genus for the fossil organ, Nubilora gen. et nov. This new fossil taxon brings unique hints on the origin and evolution of angiosperm carpels.

The extent to which the ovules and seeds are enclosed cannot be determined accurately in *Nubilora* now. This uncertainty opens two possible alternative scenarios for the evolution leading to angiospermy starting from *Nubilora*. I will discuss both scenarios, focusing on the derivation of angiosperm carpels.

Scenario One The seeds, especially the ovules, of *Nubilora triassica* are assumed physically and completely enclosed by the wall of the lateral units. Then the pollination in *Nubilora* has to be completed by sending sperms to ovules through pollen tubes, which have to penetrate ovule-enclosing tissues (wall of the lateral units). This kind of pollination is restricted to angiosperms and is never seen in any gymnosperms (Endress and Igersheim 2000a, b; Tomlinson and Takaso 2002). Under such assumption, *Nubilora triassica* could be regarded as the earliest angiosperm although it is from the Late Triassic, in which no unequivocal angiosperm has been reported before. It is noteworthy that this conclusion is in line with the recent discovery of angiosperm-like pollen grains from the Middle Triassic (Hochuli and Feist-Burkhardt 2004, 2013) and the fossil-calibrated BEAST analysis (Prasad et al. 2011).

Scenario Two The seeds are assumed not completely enclosed by the wall of the lateral units in *Nubilora*, namely, there is an unknown opening somewhere on the lateral unit. This assumption is more acceptable for many considering the Triassic age of *Nubilora*, in which gymnosperms are highly diversified and angiosperms are at most sparse. Then pollen grains may enter lateral units and fertilize ovules within the lateral units of *Nubilora*, as in *Caytonia* (Harris 1933, 1940; Reymanowna 1970, 1973). However, *Nubilora* is distinct from *Caytonia* in several aspects. *Nubilora* has only one or two ovules per lateral unit, ovules inserted directly onto central axis, longitudinally folded envelope, and no basal opening for pollen entrance, while *Caytonia* has more than two ovules per cupule, ovules not related to the organ axis, transversally folded cupules, and a basal opening for pollen entrance (Nixon et al. 1994). It is well known that some extant angiosperms have their ovules not physically completely enclosed (Eames 1961; Hill and Crane 1982; Cronquist 1988). Taking this into consideration, *Nubilora* may still be an angiosperm in spite of its possibly incomplete enclosure of ovules/seeds. In this term, *Nubilora*, though not a full-fledged angiosperm, may well be just one step before full angio-ovuly. According to the strict criterion of angiosperms (angio-ovuly) suggested by various authors (Tomlinson and Takaso 2002; Wang 2009), *Nubilora* under this scenario cannot be placed in *bona fide* angiosperms. However, such non-angiospermous placement does not reduce the evolutionary significance of *Nubilora*. *Nubilora* with such in-between, almost-complete, critical status is exactly the long wanted fossil bridging the gap between angiosperms and gymnosperms. If this interpretation is correct, then the lateral unit of *Nubilora* should be comparable to and homologous with an angiosperm carpel. The here-assumed partial enclosure of ovule in *Nubilora* might be completed in later evolution, giving birth to *bona fide* angiosperm carpels.

Nubilora′s implications for the origin and evolution of carpels are insusceptible to variations of the above speculations. Carpels of angiosperms have been interpreted as composite organ derived from a subtending leaf and its axillary fertile branch (Taylor and Kirchner 1996; Skinner et al. 2004; Mathews and Kramer 2012; Wang et al. 2015). Although this hypothesis has been favored by various independent evidence (Rounsley et al. 1995; Roe et al. 1997; Skinner et al. 2004; Zheng et al. 2010; Guo et al. 2013; Liu et al. 2014; Zhang et al. 2017), fossil evidence (especially earlier one) favoring this hypothesis has been lacking hitherto. The presence of two seeds/ovules in a single fructification of Nubilora implies that the situation in Nubilora is distinct from those seen in Gnetales and Bennettitales, in which each seed alone is surrounded by adjacent structures, and that the ovules/seeds of Nubilora are borne on a branch (equivalent to placenta in angiosperms). If Nubilora shares a common ancestor with angiosperms, orthotropous ovules inserted directly onto the central axis in Nubilora imply that placenta/ovule is independent of enclosing carpel wall, and that orthotropous ovules and basal placentation may be ancestral features in angiosperms. Similar arrangement of orthotropous ovules in a structure has also been seen in Dirhopalostachys (Krassilov 1975) of a relatively younger age. In the meantime, the arrangement of orthotropous ovules in Archaefructus on the assumed dorsal (not ventral) bundle of carpel wall (Ji et al. 2004; Wang and Zheng 2012) could be taken as a consequence of coalescence and transposition. Such a placentation of Archaefructus is unexpected for early angiosperms by the classical theories, but it does offer a good explanation for the insertion of ovules on the dorsal in Brasenia (Endress 2005), which otherwise appears out of place among the assumed basal angiosperms that were supposed to have marginal placentation (Eames 1961; Cronquist 1988). Intriguingly, basal placentation and one or two ovules per carpel have been theoretically predicted for early angiosperms by Taylor and Kirchner (1996) in their Fig. 6.3e. Recently Liu et al. (2014) made similar prediction of ancestral carpels based on their studies on morphology and anatomy of Magnolia flowers. According to their conclusion, placenta is an ovule-bearing fertile branch that has been undergoing reduction and finally got enclosed and protected by its subtending bract. This conclusion is in line with and favored by Rounsley et al. (1995) based on developmental genetic studies of living model plants [reviewed by Skinner et al. (2004) and Mathews and Kramer (2012)], Wang et al. (2015) based on a Jurassic fossil plant with free central placentation, and Guo et al. (2013) based on analyses of flower anatomy and development of kiwi fruits. Thus the organization of ovules in lateral units of Nubilora from the Triassic appears to match perfectly with the seek-image for the carpel precursor proposed by these authors (Rounsley et al. 1995; Taylor and Kirchner 1996; Skinner et al. 2004; Wang 2009; Doyle 2011; Mathews and Kramer 2012; Guo et al. 2013; Liu et al. 2014; Wang et al. 2015), underscoring the predictive power and rationality of these hypotheses. The lack of outer integument in Nubilora makes its ovule more like that in gymnosperms and unlike that in most extant angiosperms that usually have bitegmic ovules, suggesting its in-between evolutionary status. Maybe Nubilora, from the so-called Gymnosperm Age (Late Triassic), is exactly the fossil that has been sought by palaeobotanists for centuries. Extrapolating based on current information, the evolutionary precursor of Nubilora should have naked axillary ovule(s) subtended by foliar parts. Apparently, this prediction will face critical tests in the future. It seems intriguing that *Palissya* or its relatives are in the reach and ready to fit in and complete the picture. It seems that there appears to be no saltation in seed plant evolution, or at least the formerly assumed unnegotiable gap between angiosperms and gymnosperms is becoming narrower. After over-century-long unease in the heaven, it appears that Charles Darwin could relax a bit now.

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Chapter 8

The Making of Flowers

8.1 Major Events in the History of Plants

Angiosperms are a subset of seed plants, and seed plants are a subset of land plants. Therefore angiosperms should share more or less some common features (including reproductive ones) with other peer plants. It is a pity that such a uniformity was not revealed in the previous studies. Here I try to summarize briefly the history of plants, with a focus on reproductive organs, and give a general picture before addressing the origin of angiosperms.

8.1.1 Before the Landing

Initially, the organisms on the earth are unicellular. Being diploid or haploid, these individual cells live independently, and they may frequently perform mitosis. When two haloid cells fuse, they form one single diploid cell. When the diploid cell performs meiosis, it gives rise to two haploid cells. Only under stressed conditions, the cells may suspend their normal activities and form cysts, which revive under favorable conditions and divide into cells that continue their biological activities. In this way the diploid and halploid phases alternate each other, although the proportions of each phase in the life cycle may vary among different groups. Compared to the later derived ones, the major feature for these organisms is that there is no differentiation between reproductive and vegetative tissues.

The differentiation between reproductive and vegetative tissues is not possible until after multicellularization. Multicellularization is the first step for organisms stepping forward to complicated forms. The first step of such differentiation may be the development of hyphae-like structure, which performs photosynthesis and mineral absorption. Probably the hyphae-like morphology may be more likely playing a role in the absorption function, which prefers maximal surface area.

X. Wang, *The Dawn Angiosperms*, Springer Geology,
DOI 10.1007/978-3-319-58325-9_8

The multicellularization of such primitive vegetative tissue gives rise to more complicated ones, which require canalized arrangement of cells in three dimensions to fulfil their functions in different environments. At the same time, multicellularization of the (diploid or haploid) reproductive tissues gives rise to multicellular cysts. Cysts, due to their protecting function, are usually of spherical forms. The spherical forms of cysts may subject to changes due to variation in number of cysts, their relative spatial relationship, and their spatial relationship with the vegetative parts.

The occurrence of the differentiation between reproductive and vegetative parts before landing implies that sporangium (equivalent to the above cyst) occurred before the plant landing so there is no question on origin of sporangium in land plants because it is already present in the ancestors of land plants and this is a perquisite for land plants. This inference is compatible with the historical fact that crypt spores are seen in the Middle Cambrian (>510 Ma) (Strother et al. 2004; Yin et al. 2013; Strother 2016) while the vegetative parts (branches with tracheids) of typical land plants are missing until the Silurian.

8.1.2 The Landing

Before the landing, the plants had to provide solutions for new problems they would face on the land: loss of water, more variable ambient temperature, lack of buoyancy, usage of atmospheric CO2 from the air, lack of anchorage, and greater vertical water gradient. To cope with the loss of water content, cuticle with stomata in addition to cell wall (extracellular matrix) is necessary and developed. Exposing to aerial environment in which temperature varies diurnally requires the plants to have some mechanism to stabilize the internal temperature within certain tolerable range. Plants cope this challenge with transpiration, during which water becomes vaporized due to heat from the sun and environment and thus keeps the amplitude of temperature fluctuation within the tolerance scope of plants. The occurrence of stomata cuticle is conducive to efficient transpiration, temperature maintaining, and gas exchange. Unlike in water, a major challenge for land plants is retaining their configuration against the gravity. The plants′ solution for this challenge is developing vascular bundles composed of tracheids that have stronger (relative to the tissues such as parenchyma) mechanical property to hold the morphology of the plants. The additional function of these tracheids includes that, taking advantage of the vertical water gradient, they allow more efficient transportation of water throughout the plant tissues, conducive to stabilization of temperature within the plants. Roots are parts of vegetative parts specialized for anchoring and water-mineral absorption. The former multicellular cysts (sporangia) are borne on the terminals of branches, conducive to the dispersal of spores. The branches and roots are results of diverted development of former multicellular vegetative tissues that are elongated extensions of vegetative tissues in their aquatic ancestors. Two dimensionally expanded leaves are not necessary for land plants until later stages of evolution.

8.1.3 After Landing

Now plants are exposed to environments that are much more heterogeneous than in aquatic environments. Such differentiated environmental forcing not only drives the adaptation of plants living in different niches but also drives the differentiation among the parts of land plants. In the early stages, this is more embodied in the differentiations between different vegetative parts, e.g. between shoot and root as well as leaf and branch.

As said above, shoot and root should be the result of differentiation of former vegetative parts in the ancestors of land plants. Adapted to absorption and anchoring functions, roots are different from its peer shoot in presence of specialized root cap, fine root hairs with increased absorbing surface area, and lack of photosynthesis. In contrary, the shoot plays more important role in supporting the plants, controlling the forms, raising the sporangia to higher positions for more efficient spore dispersal, and photosynthesis. One of the major trends in shoot evolution is enhancing its mechanical support by various mechanisms, including secondary growth. A major evolutionary trend of shoot is enhancing the photosynthetic efficiency through various metamorphoses of shoot, in term of branching pattern, relative spatial deployment of shoots, forming various two-dimensional expanded structures (leaves).

The evolution of reproductive parts may be the most important story of plant evolution, although the counterpart of vegetative parts is indispensable and more meaningful for lower plants. Such importance is mainly and convincingly demonstrated in the diversity of various reproductive structures, including sporangium, spore/pollen, ovules, seeds, fruits, especially flowers, and various parts later recruited for the successful dispersal of the diaspores. Thus it is quite natural and rational that deciphering the evolutionary history of plants is largely done in term of the reproductive organs, especially the female ones. To tell this amazing evolutionary story of plants, finding a common framework shared by all plants is of crucial importance to stitch piecemeal evolution stories of different groups.

8.1.4 Sexual Reproductive Cycle (SRC)

As mentioned above, the occurrence of sex precedes the landing of plants. This fact implies that SRC is a common framework for the life cycle shared by all land plants. SRC comprises two crucial points (zygote and spore) and two intervals in between [zygote to spore is diploid generation (sporophyte), and spore to zygote is haploid generation (gametophyte)]. These two points are conservative and

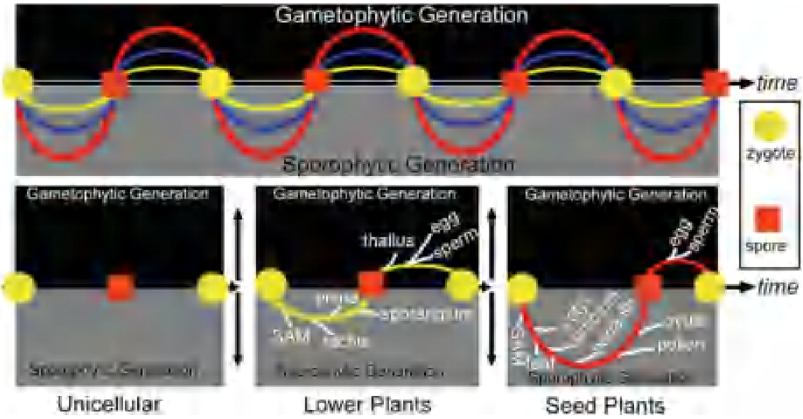

Fig. 8.1 Life histories of plants comprise sporophytic and gametophytic generations, which are delimited by spore and zygote. The diversity of plants is mostly embodied in the variety of sterile parts that tend to vary while reproductive core process remains relatively conservative throughout almost the whole plant kingdom. The evolution of plants mostly is embodied in their vegetative morphology, dominance and length of one of two generations. Unicellular organisms demonstrate little morphological variations while seed plants have developed highly diversified vegetative morphological variations. The deviation from the core reproductive process may be taken as a proxy of evolution grade

invariable for all land plants, while all variations of plants (including multicellularization, lengths and dominance of certain generation, differentiations of organs, etc.) occur in these two intervals. And these points and intervals alternate each other, forming a life cycle and defining the generations of plants (Fig. 8.1). Such a cycle continues the preceding one and is continued by the next one, forming endless life lineages unless extinctions occur. For the convenience of communication, it is artificially designated that a SRC starts from a zygote, and stops just before the formation of the zygote of next generation (Bai 2015).

For unicellular organisms, a SRC starts from a zygote, which is an endproduct of a fusion between two haploid cells (fertilization). This is the beginning of the diploid generation and sporophyte of the taxon. The zygote may or not undergo mitosis and form colonies, depending on taxon. Under certain condition, such zygote undergoes meiosis, giving rise to halploid cells (spores). This is the beginning of the haploid generation and gametophyte of the taxon. The haploid cells may or not undergo mitosis and form colonies, depending on taxon. Under certain condition, two of these haploid cells may fuse and form a zygote, concluding a SRC of the taxon. The lengths, proportions, and dominance of diploid and haploid generations in the whole cycle is taxon specific (Fig. 8.1). One good example for this phase of evolution is Chlamydomonas.

For multicellular organisms, a SRC is basically the same as that of unicellular organisms except the following new variations are introduced into the two intervals. In addition to the program seen in unicellulars, multicellularization is a major innovation that may occur either in the haploid, diploid or both generations of the taxon. The zygote may undergo mitosis and the products of such mitosis (daughter cells) may not be separated from each other as before. Instead the daughter cells are more or less organized together in various canalized ways. The organizing of these cells in three dimensions and their position relative to the meristematic cells determine the morphology of the sporophyte of the concerned taxon. The haploid gametophyte may also undergo mitosis, yielding cells that may be aggregated and organizing in certain canalized ways. Again, if multicellular, the organizing of these cells in three dimensions and the relative position of the meristematic cells determine the morphology of the gametophyte of the taxon. It is clear that multicellularity is introduced to the two intervals between two conservative points (zygotes and spores). The introduction of multicellularity in sporophyte, gametophyte, or both makes the diversification of plant body plan possible, and places the foundation for the innovations and evolution in later derived plant groups. An example for this phase of evolution is Volvox.

8.1.5 Generation Alternation

SRC comprises two phases, diploid sporophytic one and haploploid gametophytic one. Initially such alternation is between isomorphic sporophytes and gametophytes, as seen in Ulva, Palaeoblastocladia (Remy et al. 1994; Figs. 4.2, 3.23 of Taylor et al. 2009). In the later evolution one of the phases becomes increasingly extended and gains dominance morphologically, while the other becomes increasingly reduced and dependent on the dominant one. Two extreme examples are seen in bryophytes and angiosperms. In bryophytes the gametophytes are dominant and sporophytes are dependent. The situation is reversed in angiosperms, namely, the gametophytes are extremely reduced and dependent on the sporophytes that are much more developed and dominant.

8.1.6 Sexual Modes

The occurrence of sex is symbolized by the fusion of two gametes. Initially, there is no difference in shape and size between two fusing gametes. The fusion of such two isomorphic gametes is called isogamy. During the later stage of evolution, one gamete becomes smaller than the other. The fusion between such gametes is called anisogamy. Further evolution brings up enhanced differentiation between the gametes, namely, morphologically there are obvious differences, a female gamete is non-flagellate, non-motile and much larger while a male one is flagellate, motile and much smaller. A fusion between such two gametes is called oogamy. The evolution usually is directional, from isogamy to oogamy (Fig. 8.2).

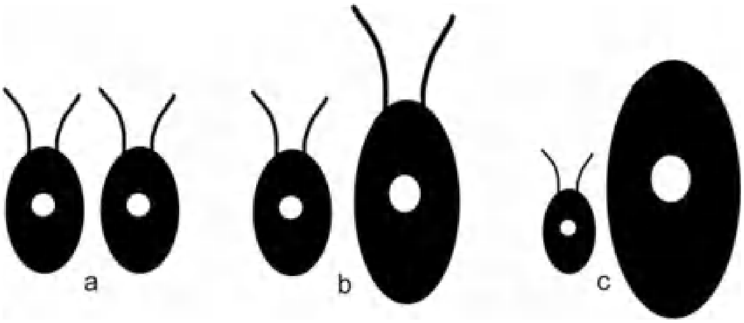

Fig. 8.2 Three sexual modes, isogamy (a), anisogamy (b), and oogamy (c). Note the changes in relative size and mobility of the gametes

8.1.7 Tissue Differentiation

Tissue differentiation is the next major innovation in plant history. Initially, all cells in multicellular cells are functionally and morphologically equal, as in Volvox. Due to whatever reason, functional and morphological differences occur among the cells. The separation of germ cells from other somatic cells may be the earliest tissue differentiation. Cells committed to somatic growth lose their potential to give rise to eggs, sperms or spores, and evolve to perform better photosynthesis and other vegetative functions. The separation of meristematic cells from other cells defines a new growth pattern and directs the morphogenesis of plants. This is the functioning mechanisms behind the great plant morphological diversity, including the unprecedented amazing diversity of flowers in angiosperms. The trace of such differentiation can be dated back at least back to the Ediacara (600 Ma ago) (Fig. 8.3; Chen et al. 2014).

8.1.8 Organ Differentiation

Shoot and root are parts of vegetative part of a plant, and their differentiation is an adaptation to the habitat and vertical growth form of plants (Fig. 8.4). In aquatic habitat the absorption is performed by the surface of the extended vegetative parts, and water buoyance reduces the demand for a mechanical support. Terrestrial habitat is quite different from the aquatic in that the absorption can only be performed by the bottom part, and gravity requires a stronger mechanical support for plants. Such new habitat and requirement induce the differentiation between shoot and root. A root is the lower part of a plant, and it performs two major functions, anchoring and water/mineral absorption. The characteristic features of

Fig. 8.3 Differentiation of tissue in an about 600 Ma old fossil recovered from China. Courtesy of Lei Chen

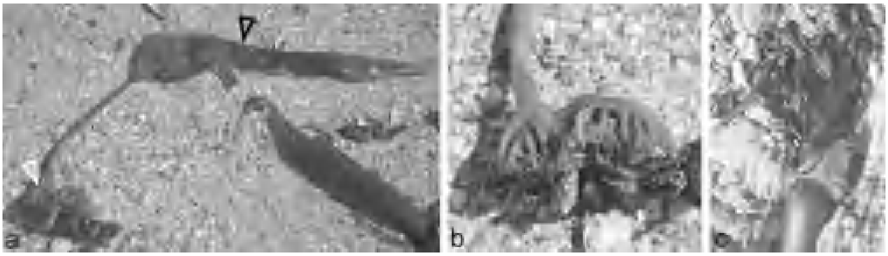

Fig. 8.4 Differentiation of organs in Laminaria. (a) whole plant with "root" (white arrow), "leaf" (black arrow), and "stem" in between. (b) "root". (c) "leaves" on the distal of the plant

root are root hairs (which increase the absorbing surface area of root for enhanced absorption) and root cap (which protects root meristematic cell from abrasion during root growth). A shoot is the upper part of plants and defines the morphology of most land plants. The variation and modification of the shoot give birth to branch, leaf, and reproductive organs, and they play an important role in plant morphogenesis.

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8.1.9 Leaf

Leaf and branch are parts of a shoot, and their differentiation is a major event in the history of land plants. Shoots in early land plants are homogeneous, namely, all shoot parts (telomes) are all equivalent in morphology (bifurcating telome) and function, and there is a sporangium on the terminal of each shoot. But the organization of shoot parts undergoes a series change and some of them lose their sporangia and are organized in a special way and give rise to leaves. At first some of the formerly fertile branches become sterile and intermingle with the fertile ones (for example, Pseudosporochnus and Stauropteris, Figs. 11.12 and 11.41 of Taylor et al. 2009). In the meantime some of the branches become elongated and stronger than others, and the latter become laterals organs attached to the former (overtopping) (Stauropteris, Fig. 11.41 of Taylor et al. 2009). Then to intercept as much as possible sunshine, the three dimensionally arranged branches become increasingly arranged in a plane (planation). Finally, as the laminar tissue expand and fill up the space between branches (webbing) with parenchyma or chlorenchyma, megaphylls are derived in such a way from their precursor branches (Zimmermann 1959). Megaphylls can be traced at least back to the Early Devonian (>392 Ma) (Hao and Xue 2013a), and the transition from branches to pinnae has been seen in the Devonian (Li and Hsü 1987). Such megaphylls are frequently seen in early fossil ferns such as Ellesmeris sphenopteroides (Fig. 11.38 of Taylor et al. 2009) and Ankyropteris (Fig. 11.168 of Taylor et al. 2009) and others. For examples pinnae of Archaeopteris and Proteokalon appear more like aggregations of several branches in almost the same plan (Figs. 11.5, 12.4, 12.7, 12.35 of Taylor et al. 2009). Such morphological changes are accompanied by anatomical changes, such as spatial arrangement of vascular bundles and organization of vascular bundle (from amphicribral to collateral). It is noteworthy that all these changes are not synchronous and do not proceed at the same rate. The birth of leaves signifies the subfunctionalization of former homogeneous shoot parts, enabling plants to perform photosynthesis more efficiently. In the meantime, the non-foliar parts become branches and are committed to the function of mechanical support, which is achieved by various modifications including secondary growth.

8.1.10 Heterospory

Heterospory is a major event in the history of land plants, in which the spores differentiate into two types of different morphologies, namely, megaspores and microspores. This event marks the occurrence of two genders although sexuality has its existence before landing. Before heterospory, all spores in the sporangia are of the same size and morphology. Since this event the difference in energy and nutrition allocations between two genders becomes increasingly great. Megaspores are allocated more energy and nutrition, which are shared among fewer number of peers, while limited amount of energy and nutrition are allocated among greater number of microspores. In this way the development of the zygote is assured with enough initiating nutrition supply and becomes more advantageous against those with limited nutrition supply. The nutrition supply to the megaspores is limited by the biomass of the megaspore themselves because after maturation megaspores (just like microspores) leave their mother plants, germinates on site with favorable condition, mainly relying on the nutrition deposited in the megaspores themselves. Heterospory may be intrasporangial (*Barionphyton*, Fig. 13.4 of Taylor et al. 2009) or intersporangial (*Selaginella*, Fig. 13.9 of Taylor et al. 2009). At least some of the fossil evidence indicates that a single megaspore per sporangium (monomegaspory) is a result of sterilization of three other tetrads (*Cystosporites devonicus*, Fig. 13.7 of Taylor et al. 2009). The origin and mechanism behind heterospory are not fully understood, although its occurrence is seen in Selaginellales, ferns, and seed plants. Heterospory can be traced back at least back to the Early Devonian (>392 Ma ago).

8.1.11 Endospory

Dispersed spores, micro- or macro-, have to face harsh environmental stresses after leaving their mother plants. To avoid such stresses and enhance the survival rate, some of the megaspores delay their leaving from the mother plants and are retained in the sporangia on the mother plants, namely, endospory. The megaspore may reach its maturity and develop its gametophyte before falling off from the mother plants. Endospory paves the road for the later occurrence of ovules/seeds, in which the megaspores are retained in the sporangia until the embryos have developed to certain extent before leaving the mother plants.

8.1.12 Ovule

Ovules are special megasporangia that remain attached to their mother plants (sporophytes) even after fertilization. Such a tight bond in nutrition supply between megaspores and mother plant guarantees not only enough nutrition supply for sporogenesis but also enough nutrition supply for the development of gametophytes and the formation of embryo, which are highly reduced and retained in the former sporangia. Besides nutrition supply, an ovule comprises both nucellus (former megasporangium) and surrounding protective integument (derived from the sterilized peers of the nucellus) (Fig. 13.12 of Taylor et al. 2009). Therefore an ovule is morphologically equivalent to an aggregation of several sporangium-bearing branches among which only the central one remain reproductive while its surrounding peers divert from their former development and metamorphose collectively into an integument. An integument initially comprises several individual unfused sterilized branches, which may coalescent in later development and gives rise to the cup-like single-layered tissue surrounding the nucellus, as seen in most seed plants. Accompanying the occurrence of ovules, the contrast between dominance of sporophyte and reduction of gametophyte is greatly enhanced. Corresponding to this change in female part, the microspores (pollen grains) are highly enhanced in their numbers and much more reduced to adapt to the new pollination strategies adopted by the plants. This interpretation is supported by detailed anatomic study (Fagerlind 1946; Johri and Ambegaokar 1984; Herr 1995), 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 bearing megasporangium.

8.1.13 Diverted Development

From the earliest land plants with homogeneous telomes to angiosperms with various organs and parts, the changes involved include continuous differentiation among former the same or similar parts. The above differentiations between macrospore and microspore, between nucellus and its integument are good examples of diverted development. Additional examples are the differentiations between ovules and interseminal scales in Bennettitales (Crane and Kenrick 1997), between disc flowers and ray flowers in Helianthus, as well as sterile and fertile flowers in the same inflorescence of Viburnum (Lu et al. 2017). Apparently, diverted development is a universal mechanism behind the long-going evolution and diversity of land plants.

8.1.14 Outer Integument

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). However, the trace of outer integument may have been present in Cordaianthus duquesnensis (Cordaitales, Figs. 8.18c, 8.31a; Rothwell 1982). 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 quite different from that of the inner one. The outer integument, like other lateral organs such as sepal, tepal, petal requires YABBY gene expression to grow, implying that it is foliar (phyllome) in nature (Skinner et al. 2004). This conclusion is substantiated by the morphological difference between the outer and inner integuments. Stomata on the outer

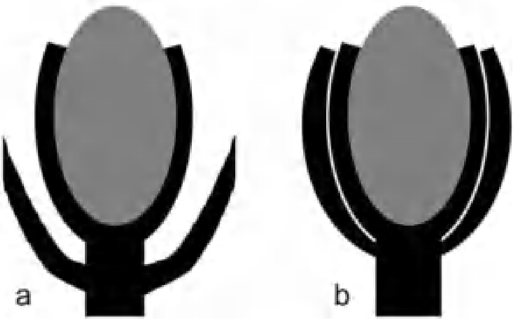

Fig. 8.5 Outer integument may be derived from the foliar structures attached on the funiculus of an ovule

integuments (Eames 1961; Zhang 2013) suggest a foliar nature for their bearers. As there are bracteoles along the ovular stalk in Cordaitales (Bertrand 1911; Florin 1944; Rothwell 1982) and some of them even take a position similar to that of an outer integument (Figs. 8.5, 8.18c, 8.31a), it requires little imagination to conceive that the outer integument in angiosperms may be derived from the bracteoles attached to ovular stalk as in Cordaitales, as reproductive structures of plants frequently become more elaborated through recruiting nearby vegetative organs (Frohlich 2003). The additional protective layers seen in the ovules of Gnetales may similarly involve recruiting former foliar parts.

8.1.15 Angio-Ovuly

The protection for ovules start from the earliest known seeds in which ovules are barely protected by the structure named cupules (Gerrienne et al. 2004). Such cupules are derived from adjacent branches, and the connation of these branches provides increasing protection for the ovules throughout the history of plants. If the evolution from megasporangium to ovule involves recruiting more peripheral parts for protection, such protection is further enhanced by another innovation, angio-ovuly, in angiosperms in which ovules are enclosed by ovarian wall before pollination. This innovation brings several advantages to angiosperms. First, enhanced physical protection for ovules by ovarian wall makes formerly vulnerable ovules free from animal attacks. In gymnosperms, the ovules are naked and exposed to the interior space, and thus they as most fragile parts are frequently targets for herbivorous animals, especially insects. The introducing of ovarian wall for the first time provides a complete protection for ovules, although similar protecting tendency has been demonstrated in Czekanowskiales, Bennettitales, and Caytoniales to various extent. Second, accompanying such physical protection, secluding ovules inside ovary stabilizes the growing environment for ovule development. Unlike ovules in gymnosperms that are subject to various harsh environmental stress (e.g. desiccation) and animal attacks, ovules in angiosperms at least most times grow in a stabilized and controlled environment. Apparently, this is conducive to the successful development of ovules. Third, self-incompatibility is for the first time introduced into plants due to the enclosure of ovary. In gymnosperms, pollen grains approach the micropyles before pollination. In angiosperms, pollen grains do not have such a chance. Instead they perch on the stigma, which exudes some proteins that prevent pollen grains of the same plant from germinating and thus enhances cross-breeding and encourages hybridizing. This unprecedented genetic advantage plays an important role in the diversification of angiosperms. Fourth, the distance between micropyles and stigma functions like a racing track on the track for the pollen grains, which have to demonstrate their superiority through their racing from the stigma to the micropyles. In this way, the pollen grains with better fitness are selected to improve the fitness of the offsprings.

8.1.16 Vivipary

In term of nutritional relationship vivipary is an innovation one step further than ovules, in which seeds germinate and develop into seedlings while attached to the mother plants. This strategy extends the nutritional connection between two generations of sporophytes, and thus ensures the nutrition supply to and well-being of the new sporophyte. This phenomenon is well-adopted in mangroves (Fig. 8.6), and similar trend is sometimes also seen in other plants including *Triticum* (angiosperms) and *Podocarpus* (Coniferales).

8.1.17 Angio-Carpy

Enclosed fruit (angio-carpy) is an innovation that provides further physical protection for plant offsprings, in addition to above ovarian protection. Such protections frequently occur as fleshy or spiny coverings that are conducive to the dispersal of the fruits of plants. Such examples are seen in various extant taxa, including Siparunaceae, Atherospermaceae, Monimiaceae, Solanaceae, Fagaceae, etc., in which one or more fruits are protected by additional layer of plant tissue. Similar structure is also seen in some early angiosperms, such as *Chaoyangia liangii* (Chap. 5), *Callianthus dilae* (Chap. 5), *Physalis* (He and Saedler 2005; Wilf et al. 2017).

8.1.18 Differentiation of Flowers in Inflorescence

Besides the above mentioned example of diverted development in evolution, flowers may differentiate from each other in morphology and function. The most

Fig. 8.6 Vivipary of mangrove plant, note the seeds have germinated while still on their mother plants

obvious example is the capitate inflorescences in Compositae, in which the peripheral ray flowers and central disc flowers in the same inflorescence have different symmetries and morphologies. The latest reported example is seen in *Viburnum* (Adoxaceae), in which the flower morphology, fertility, gender, and function vary according to their different positions in the inflorescence (Lu et al. 2017).

8.1.19 Stamens

Pollen organs in all seed plants are aggregations of microsporangia in various ways. This is exemplified in various taxa, including Palaeozoic seed ferns (*Paracalathiops* and *Schuetzia*, Millay and Taylor 1976), Ginkgoales, Coniferales, Glossopertidales, Caytoniales, etc. (Taylor et al. 2009; Schulz et al. 2014). This is especially obvious in Medullosales. Parallel to these, male parts of *Hypericum quadrangulum* (angiosperms), *Rhacophyton ceratangum* (ferns?), and *Psilophyton crenulatum* (Psilophytales) have clustered sporangia on the termini of branches (Taylor et al. 2009), suggestive of their derivation of stamen from former clusters of sporangia borne on branches. The major evolutionary trend in stamens is timed protection and exposure for success and efficiency in gene passing to next generations.

8.2 Basic Units of Reproductive Organs in Land Plants

The most characteristic feature of angiosperms is their flower, which distinguishes them from all other seed plants. Theoretically, flowers of angiosperms must have their counterparts in gymnosperms. Therefore before we can address the issue of origin of angiosperms it is necessary to elucidate the evolution of reproductive organs in non-angiosperm groups. Understanding this background makes the understanding of gynoecia in angiosperms much easier.

To avoid unnecessary misunderstanding, it is necessary to clarify the definitions of two categories of plant organs, leaf and branch, before we start examine the validity of sporophyll in each individual group. Leaf ideally designates more or less two dimensionally expanded parts that are traversed by collateral vascular bundles, and it usually has a bilateral symmetrical cross view and demonstrates no secondary thickening. Branch ideally designates one dimensionally extended parts that are traversed by amphicribral vascular bundles or vascular bundles arranged in a concentric pattern, and it usually has a radial cross view and demonstrates certain secondary thickening. Considering that all leaves are derived from branches in early land plants that had no leaves, it is expected that there are certain transitional stages between these two typical parts. For example, the leaves of *Pinus monophylla* are not two dimensionally expanded, they are one dimensionally extended and is round in cross-view. But, like all typical leaves, they have collateral vascular bundles in the center. Therefore although their morphology appears branch-like, their identity is revealed by their vascular bundles. In the meantime, pinnae in some ferns may have amphicribral bundles, which imply that the transition from branch to leaf is not completed in these groups yet. Otherwise, the distinction between leaf and branch in higher plants is quite obvious.

8.2.1 Early Land Plants

It is obvious that there is no leaf in Psilophytes, which are characterized by their simple organization, namely, their shoots comprise only branches and sporangia on their termini [Cooksonia caledonica (Fig. 8.12 of Taylor et al. 2009); Horneophyton lignieri (Fig. 8.40, Taylor et al. 2009); Uskiella spargens (Fig. 8.60 of Taylor et al. 2009)]. The vascular bundle in the branch is protostele, namely, an amphicribral bundle of radial symmetry (Agalophyton major (Fig. 8.19b of Taylor et al. 2009); Fig. 8.7). The later evolution introduces differentiation between branches, and the sporangia are apparently still attached to the termini of branches [Renalia hueberi (Fig. 8.67 of Taylor et al. 2009); Psilophyton forbesii, P. dapsile (Figs. 8.82 and 8.83 of Taylor et al. 2009); Trimerophyton robustius (Fig. 8.85, Taylor et al. 2009); Oocampsa catheta (Fig. 8.86, Taylor et al. 2009)]. Since there is no leaf at all, it is ridiculous to call any part or the whole plant "sporophyll".

8.2.2 Sphenopsida

There are clearly leaves in Sphenopsida. However, these leaves are vegetative and have nothing to do with sporangia, therefore there is no ground for the valid existence of "sporophyll" in Sphenopsida. Instead the sporangia in sphenopsids

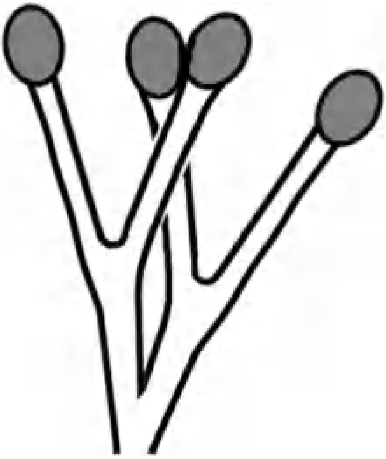

Fig. 8.7 Sporangia on the termini of branches in earliest land plants

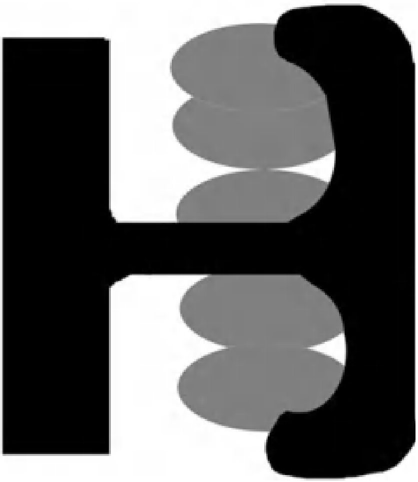

Fig. 8.8 Peltate sporangiophore bearing sporgania (gray) on its adaxial side in Sphenopsids

are borne on a stalk called sporangiophore (Equisetum, Fig. 85c of Ogura 1972), implying that the formerly assumed “sporophylls” are actually clusters of aggregated sporangia (Fig. 8.8). Similar configuration is clearly seen in fossil sphenopsids such as Eviostachya hoegii (Fig. 232 of Ogura 1972; Fig. 10.6 of Taylor et al. 2009), Peltastrobus reeda (Fig. 10.22 of Taylor et al. 2009), Protocalamostachys pettycurensis (Fig. 10.29 of Taylor et al. 2009), Calamostachys (Fig. 85f of Ogura 1972; Fig. 10.69 of Taylor et al. 2009), and Equisetites arenaceus (Fig. 10.97 of Taylor et al. 2009). Frequently cones of sphenoposids comprise alternating whorls of bracts and sporangiophores, but bracts may be missing in some (Fig. 85 of Ogura 1972). In an unnamed fossil Sphenophyllales of the Early Permian, sporangiophore is especially elongated and directly attached to the cone axis (Cúneo et al. 2015). This lax fossil cone indicates that typical compact cones in sphenopsids are result of long time evolution through condensation and reduction of sporangiophores. Apparently, there is no trace of “sporophyll” in Sphenoposida. Almost all sphenopsids have their sporangiophores in axils of the bracts, no matter whether these two parts fuse each other or not and bract are present (Calamostachys) or not (Archaeocalamites) (Figs. 85f, 242b, 265 of Ogura 1972).

8.2.3 Lycophytales

Modern lycophytes are rare and relics of once highly-diversified fossil antecedents. In fossil lycophytes there are clearly typical leaves (Lepidophylloides), and again these leaves are only seen in the vegetative parts (Ogura 1972). In the less-developed taxa of lycophytes, the sporangium is attached to the adaxial of a lateral branch where there is no trace a leaf (Haskinsia sagittata, H. hastata, Fig. 8.9a; Fig. 9.6 of Taylor et al. (2009); Leclercqia complexa, Fig. 8.9b; Fig. 9.24 of Taylor

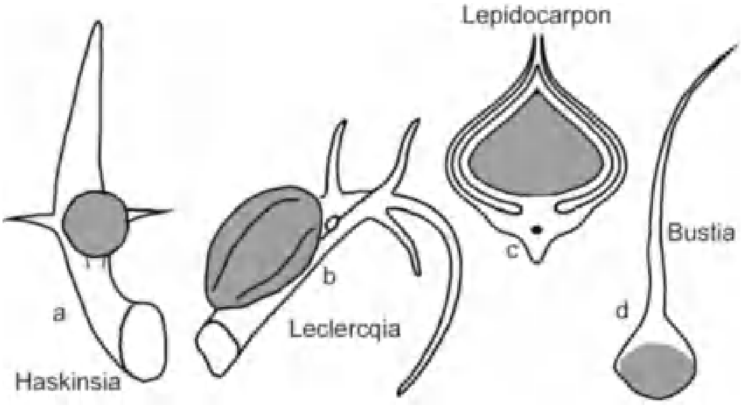

Fig. 8.9 Four different lateral appendages bearing sporangia in Lycophytes. Note the adaxial position of the sporangia and the trend of increased sporangium-protection in Lepidocarpon. Redrawn after Taylor et al. (2009)

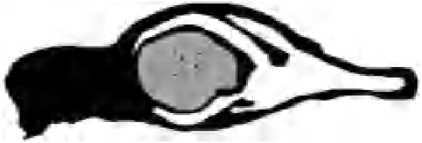

Fig. 8.10 Sporangium of Miadesmia membranacea protected by layers of tissues. Redrawn after Benson (1908)

et al. (2009)). In slightly developed taxon, the lateral branches in the above taxa are arranged in a plane, with two sporangia on the adaxial (Estinnophyton yunnanense, Fig. 9.13 of Taylor et al. (2009)). Further modification in the reproductive organs of lycophytes is seen in Minarodendron cathaysiense, in which the megasporangium is subtended by a more or less foliar-like structure that still has a branch at the tip [Fig. 9.11 of Taylor et al. (2009)]. Similar situation is seen in Flemingites schopfii, and only difference is that the former terminal branch is lost [Fig. 9.63 of Taylor et al. (2009)]. Barinophyton citrulliforme may have sporangia on the abaxial of a foliar part [Fig. 9.123 of Taylor et al. (2009)]. Bustia ludovici has a megasporangium on the adaxial of a foliar part [Fig. 8.9d; Fig. 9.125 of Taylor et al. (2009)]. In more derived taxon, the axillary megasporangium becomes more protected and wrapped by the foliar-appearing parts that are apparently derived from formerly furcated branches [Lepidocarpon lomaxi, Fig. 8.9c; Fig. 9.70 of Taylor et al. (2009)]. The wrapping and protection of megasporangium culminates in Miadesmia membranacea (Fig. 8.10; Benson 1908). The ligules in the so-called sporophylls may well be interpreted as highly reduced shoot apices sandwiched between the sporangia and the other parts of the organs [Figs. 194, 197 of Ogura (1972)]. This series of modification in lycophytes indicates that the foliar-appearing structure is derived through fusion and flattening of the former branches, and there is no real “megasporophyll” in lycophytes.

8.2.4 Ferns

There are two major types sporangial development in ferns, euaporangiate and leptosporangiate types. Eusporagniate type is seen in Ophioglossales and Marattiales, in which the spores are embedded inside sessile sporangia. Leptosporangia are stalked, and usually aggregated into sori [Fig. 11.1 of Taylor et al. (2009)]. Such a type is thought more primitive than the eusporangiate type (Bierhorst 1971). The sporangia aggregate into sori through fusion of their stalks [Corynepteris and Biscalitheca, Figs. 11.68 and 11.69 of Taylor et al. (2009)], and sori are frequently covered and protected by indusia, as frequently are seen in Filicales. Thus sori and their indusia together form complexes that have nothing comparable to typical foliar structures [Figs. 11.1 and 11.100 of Taylor et al. (2009)]. Sori are arranged in at least four ways in term of their position relative to the foliar structures in Filicales. First, sori are attached to the abaxial side of the foliar structures (pinnae) (Fig. 8.11a, b). In this case, the sori are usually supplied by vascular bundles connected with the veins in the foliar structures. Such pattern is exemplified in Woodsia. Second, sori are attached to the margins of the pinnae and on the points where the veins terminate. Such pattern is exemplified by Dicksonia, Dicksonites (Galtier and Béthoux 2002), Eophyllogonium (Mei et al. 1992), Gigantonomia (Li and Yao 1983), Sobernheimia (Kerp 1983), Ovulepteris (Pšenička et al. 2017). Although some of these organs are thought bearing ovules, detailed information on integument, micropyle, and seed coat is lacking, therefore they are at most interpreted as megasporangia. A more derived form can be formed if the pinnae are reduced to nil and only sporangia are seen along the termini of reduced branches. Such pattern is exemplified by Onoclea. Third, the sporangia are in the axils of subtending foliar structures (bracts). This pattern is demonstrated in Ophioglossum [Fig. 228b of Ogura (1972)]. Fourth, micro- and mega-sporangia are clustered on branch termini and surrounded by foliar-like structures (sporocarp), with the megasporangia situated in the center. This pattern is exemplified in Marsileaceae.

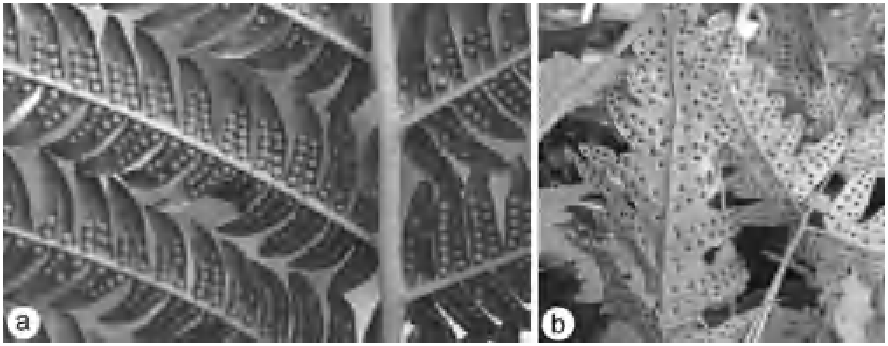

Fig. 8.11 Fern pinnae with sporangia attached to the abaxial side of the pinnae

Vascular bundles in pinnae of ferns may be bicollateral, amphicribral (concentric), or enclosed by endodermis [P129 of Ogura (1972)]. This implies that the evolution levels vary among different taxa in Filicales although the sporangia are consistently supplied by vascular bundles that are more or less different from those in the pinnae in term of organization.

8.2.5 Archaeopteridales and Aneurophytales

These two typical progymnosperms that demonstrate secondary growth typical of gymnosperms but have no seeds. Their basic reproductive units are aggregations of sporangia that are more or less concentrated to the adaxial side of the unit. The terminal sporangia may have been sterilized and appear like a branch [Fig. 8.12; Figs. 12.8, 12.9 and 12.10 of Taylor et al. (2009)]. The configuration and organization of such basic reproductive units conjure to a cluster of sporangia. Such units cannot be comparable to any known foliar structures.

Cecropsis luculentum (Late Carboniferous) is a heterosporous pteriphyte that is thought related to progymnosperms. Their clusters of micro- and megasporangia are borne on the adaxial of foliar structures [Fig. 12.38 of Taylor et al. (2009)].

8.2.6 Cycadales

Cycadales are the most primitive among living seed plants, therefore they are of crucial importance in plant systematics. The fossil evidence indicates that Cycadales can be dated at least back to the Permian (Zhu and Du 1981). Various fossils were related to the Cycadales, including *Archaeocycas*, *Phasmatocycas*, and *Primocycas* (*Crossozamia*). But later studies indicate that at least some of them may represent a lineage independent of Cycadales and the ovules are inserted on the midrib rather than leaf lamina as assumed previously (Axsmith et al. 2003).

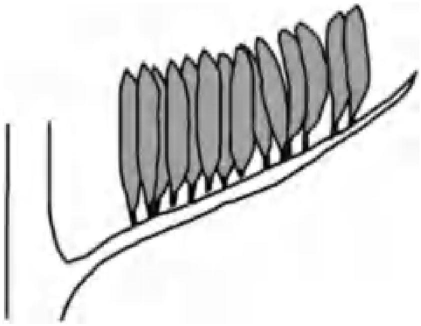

Fig. 8.12 Reproductive organs of *Archaeopteris*, showing sporangia borne on the adaxial of the axis

Cycadales became dominant during the Mesozoic and declined since the Cretaceous.

Cycas is of special interest in plant morphology in that their female units demonstrate especial resemblance to a leaf, seeming to suggest that there do be sporophylls, which, however, do not resemble leaves (foliar structures) at all in other taxa. Therefore *Cycas* seems to be the only evidence favoring the validity of "sporophylls". However, this only evidence and the conclusion drawn from it are now facing more challenges from recent studies.

1. The ovules in female units of naturally grown *Cycas rumphii* and *C. pectinata* tend to be inserted adaxially laterally and with their micropyles pointing adaxially, not along the laterals or margins of the assumed leaves or foliar structures (Fig. 8.13a, b). This new information makes the comparison between reproductive units of *Cycas* and *Archaeopteris* more rational and conceivable.
2. Developmental experiment of *Cycas sexseminifera* indicates that, in the same cone, normally grown female units are leaf-like with ovules attached to the laterals, while those units without pressure from peers have their ovules turning to the adaxial (Wang and Luo 2013). Such comparison suggests that the leaf-like appearance of female units in *Cycas* is a consequence of reaction to external stress (mechanical pressure) rather than a consistent feature due to inherent factors (genetics).
3. Under extreme situation, *Encephalartos cerinus* not only have bisexual cone but also have bisexual "sporophylls", in which both the pollen and ovules occur on the abaxial side of a single "sporophyll" (Rousseau et al. 2015). The sporophyll

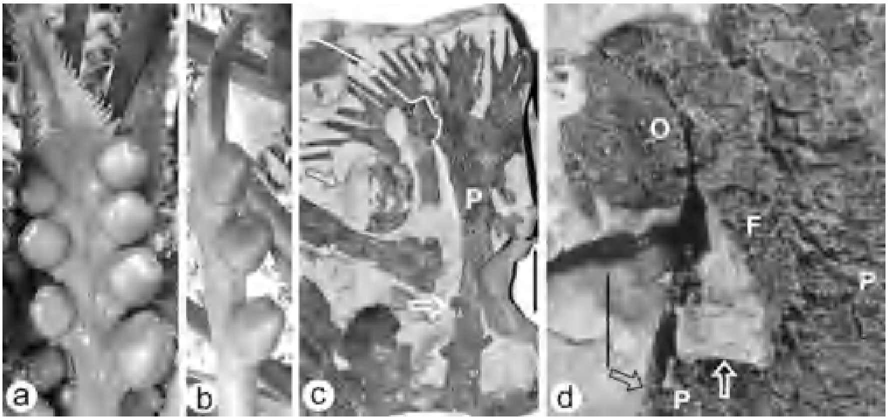

Fig. 8.13 Living and fossil reproductive female parts of cycads. (a) Adaxial surface view of a female part showing ovules inserted on the adaxial and lateral. (b) Side view of the same female part in a showing the micropyle pointing to the adaxial. (c) Female parts of *Primocycas* showing an attached seed (*black arrow*) and an immature ovule (*white arrow*). (d) Detailed view of the immature ovule (o) in c, note the pedicel of the female part (p), funiculus (f) of the ovule (o), and sediment between the ovule funiculus and female part pedicel

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Fig. 8.14 Teratological "megasporophyll" of *Zamia furfuracea*. Note several bracts helically arranged in the place of a former "megasporophyll"

in this case would be more rationally interpreted as an aggregation of microsporangia (pollen sacs) and megasporangia (ovules).

4. Sometimes a "megasporophyll" of *Zamia furfuracea* may metamorphose into a shoot comprising helically arranged bracts (Fig. 8.14), implying that the assumed sporophyll is equivalent to a branch rather than a leaf.
5. Arrangement of ovules in some *Zamia* is not on the laterals of assumed megasporophyll [Fig. 25 of Worsdell (1898)], implying that these ovules are borne on a branch.
6. Amphicribral vascular bundle with secondary growth seen in the assumed "megasporophylls" of *Cycas revoluta* (Fig. 4 of Worsdell 1898) are something frequently seen in the branches but not expected for any typical foliar structures, undermining the foliar nature of the "megasporophyll" in Cycadales.
7. Recent study on an assumed cycad fossil, *Bernettia* (Kustatscher et al. 2016; Fig. 8.15), indicates that the ovules are borne on the adaxial (not abaxial) of the scales. If the affinity assigning is correct, this discovery is an aggregation of sporangia in line with my observation in point 1), suggesting the assumed megasporophyll is an aggregation of sporangia. However, if this assigning is not correct, *Bernettia* appears to be more comparable with some conifers in which the ovules are borne adaxially.
8. Ovules are inserted adaxially on the "megasporophylls" in *Primocycas* (Fig. 8.13c, d)

In short, various evidence from fossil as well as living cycads converge to the same conclusion that there is no faithful foliar "megasporophyll" in cycads.

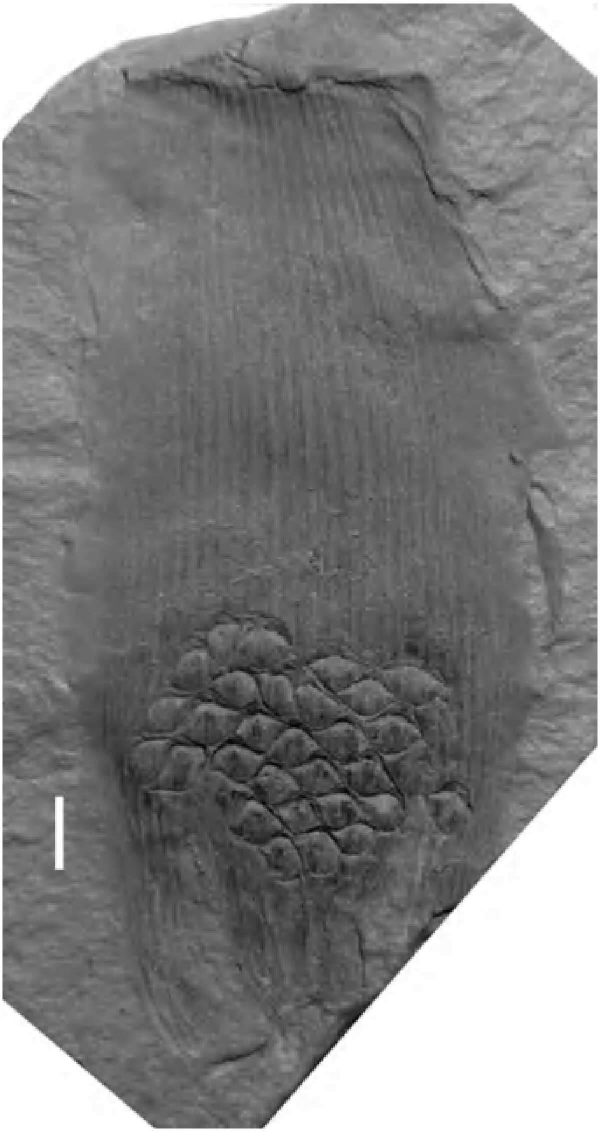

Fig. 8.15 Female part of *Bernattia* with ovules on the basal adaxial

8.2.7 Ginkgoales

Ginkgoales are the second most primitive group among the living seed plants, and they share axillary branching pattern with the remaining seed plants, therefore their significance for plant systematics is no less than Cycadales. Ginkgoales can be traced back to the Permian (Florin 1949), and their diversity culminated during the

Mesozoic. In term of the nature of “megasporophyll”, living and fossil Ginkgoales present much more convincing signals than Cycadales.

Among the living Ginkgoales, Ginkgo biloba, normally there are two or one ovule/seed on each pedicel. Under such situation, there in no way to convincingly demonstrate the non-foliar nature of the assumed “megasporophyll” in Ginkgo. However, when there are more than two ovules/seeds in each fertile unit, it is much easier to convince people of the non-foliar nature of megasporophyll as in tetratology of some Ginkgo, Yimaia, Trichopitys (Fig. 18.2, Taylor et al. 2009).

As early as back to 1950s, a teratology of Ginkgo has been reported, in which several ovules are seen clustered (Florin 1949; Zheng and Zhou 2004; Shi et al. 2016). The arrangement of these ovules are not in a plane, as expected for a foliar structure, but in three dimensions (Fig. 8.16). The three dimensional arrangement indicates that what we face are branches or a shoot rather than a foliar structure.

Parallel to this extant example, fossil reproductive organs of Ginkgoales shed similar light on the nature of megasporophyll. Yimaia is a fossil Ginkgoales recovered from the Jurassic of Henan, China, in which there are several ovules clustered on the terminal of a branch (Fig. 6c of Zhou et al. 2007; Zhou and Zheng 2003; Fig. 8.17). Apparently, these ovules are not arranged along the laterals of assumed leaf and the ovules are on termini of branches that may be highly reduced, making the ovules as if clustered on the terminal of a branch. Although such arrangement appears surprising for many, it becomes rational when the earliest record of Ginkgoales is taken into consideration.

Trichopitys represent the earliest fossil that may be related to Ginkgoales. As depicted by Florin (1949), the ovules are attached to slender branches that are in the axils of leaves. The branch nature of female units of Trichopitys is suggested not only by the configuration of the female units, arrangement of ovules, but also by the axillary position of the female units relative to the subtending bracts.

Taking all together, there is no evidence favoring the assumed foliar nature of female organs in Ginkgoales, as mentioned by Florin (1949).

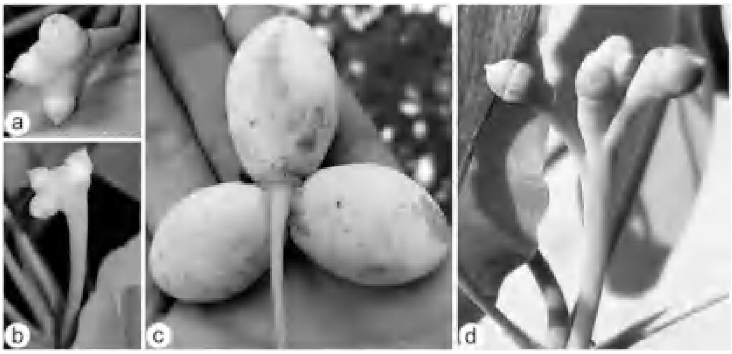

Fig. 8.16 Three dimensionally deployed ovules/seeds of living Ginkgo biloba refuting foliar nature of the so-called “megasporophyll”

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Fig. 8.17 Several ovules clustered on the terminals of *Ginkgo* female organs

8.2.8 Cordaitales

Cordaitales are the dominating and prolific seed plants in the late Palaeozoic, and they are thought related to Coniferales (Florin 1949). The organization and configuration of reproductive organs in Cordaitales are of especial importance because they provide crucial evidence on the organization and provenance of cones in, at least most, Coniferales. It is therefore noteworthy mentioning them here.

In the previous record, the pollen sacs are interpreted are on the termini and *Florinites*-type pollen grains are found in situ in the pollen sacs. However, this picture should be complemented with additional information here. As seen in Fig. 8.18a, d, e, pollen sacs with *Florinites* pollen grains may be sandwiched between the two adjacent bracts and the pollen sac may be attached to the abaxial of the bract in *Cordaixylon dumusum*. Taking all together, it is more rational to state that the pollen sacs are either between two bracts or situated on the terminal of the secondary shoot in Coradaitales.

Ovules in gymnosperms were thought unitegmic, in contrast to the bitegmic ovules frequently seen in angiosperms. This difference is frequently taken as one of the major differences between gymnosperms and angiosperms. However, this assumed difference is not always realistic. For example, at least in some *C. dumusum* there is an additional layer outside the integument (Fig. 8.18c). Although the origin and homology of this part is still mysterious, it is apparent that additional part besides integument is not something unique of angiosperms.

The ovule and its pedicel are called “fertile scales”, in contrast to scales that are sterile and called “sterile scales” in literature. Such term usage implies that parts of both categories are all of foliar nature, as said Goethe “Alles ist Blatt”. However, this thinking may be gratuitous and can be easily disillusioned by careful comparison of the morphologies of these two parts. As seen in Fig. 8.19, the cross section of sterile scales are dorsiventrally flattened, just like typical leaves. However, the

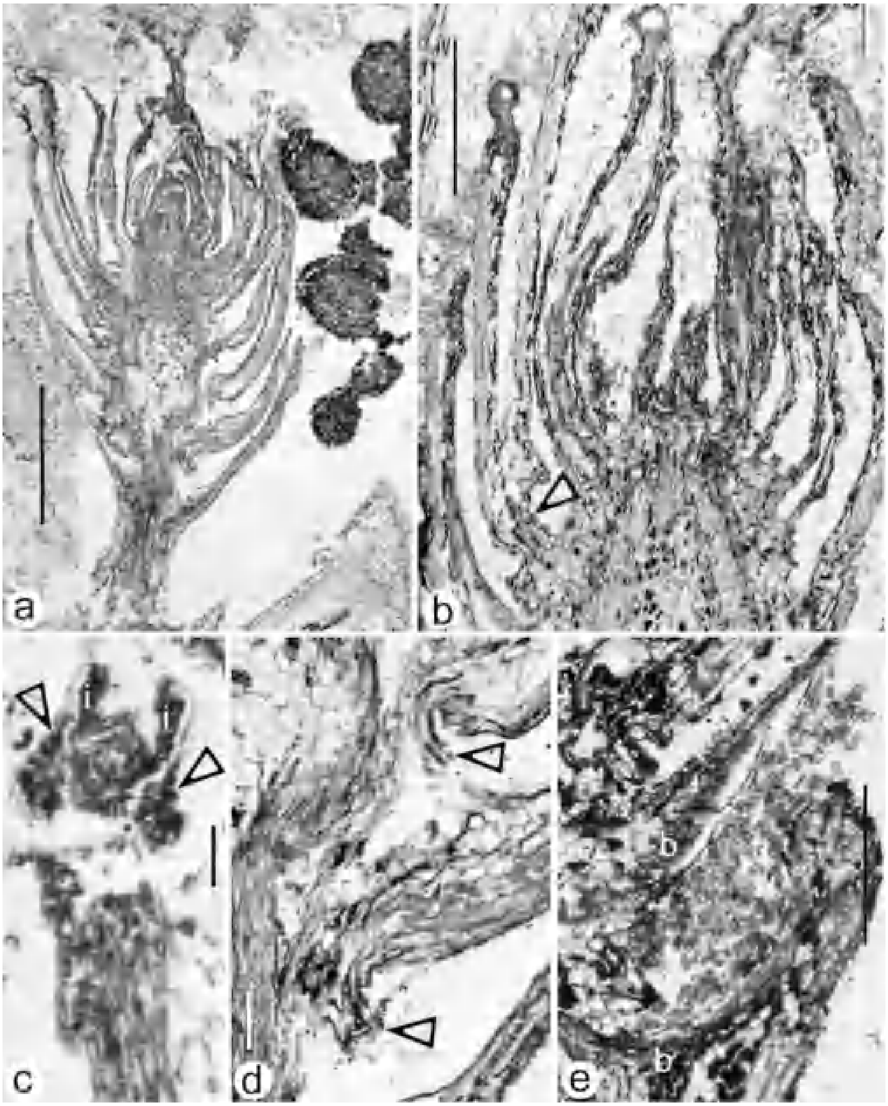

Fig. 8.18 Reproductive organs of Cordaitales. (a) Reproductive organ of Cordaixylon dumusum. (b) Female organ of Cordaianthus duquesnensis. Note the furcated pedicel (arrow) of two ovules. (c) An ovule of Cordaianthus duquesnensis, showing additional parts (arrows) outside the integument (i). (d) Detailed view of the organ in a, showing abaxial stub (arrow) of possible pollen sac. (e) In situ pollen grains in pollen sac sandwiched between two bracts (b)

cross section of the ovule pedicel is quite different and has a dorsal ridge (Fig. 8.19). The contrast between sterile scales and ovule pedicels suggests that ovule is borne on a branch, not on a leaf. In addition, two ovules borne on branched funiculi (Fig. 8.18b) also suggest that they are not on leaves.

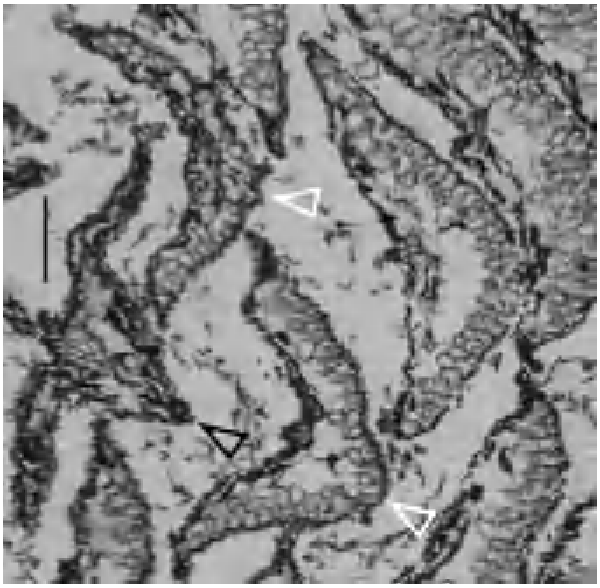

Fig. 8.19 Cross views of ovule pedicel (black arrow) and sterile scales (white arrows), showing different configurations. Bar ¼ 0.1 mm

Florin (1944) thinks that the ovular stalks tend to change from elongated branched into short unbranched during the evolution (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. 8.5a, b, which paves the way leading to bitegmic ovules in angiosperms.

8.2.9 Coniferales

Coniferales are the most diversified group in living gymnosperms, and they play important roles in the vegetation during the Mesozoic. Phylogenetically, Coniferales are related to Cordaitales through Palaeozoic and Mesozoic fossil taxa including Walchiostrobus, Thuringostrobus, Ernestiodendron, Voltzia, Pseudovoltzia, Tricranolepis, Schizolepis, Aethophyllum (Florin 1951; Schweitzer 1963). Therefore the scales in cones of at least Coniferales are thought homological and comparable to the secondary fertile shoots in Cordaitales. This relationship provides a rational explanation for the female cones in Pinaceae, Aucariaceae, and some other families, but very problematic in Podocarpaceae, Taxaceae, and some Cupressaceae (Fig. 8.20).

Fig. 8.20 Female parts of Coniferales. (a) *Taxus* showing fleshy part around the seed. (b) Fleshy fruit of *Juniperus macrocarpa* completely enclosing seeds. (c) Sketch showing seed-bearing scale (s) in the axil of a bract (b)

Judging by the general morphology, it is hard to distinguish bract and scale in Podocarpaceae. This led to Tomlinson et al. (1989) to say that there is no ovuliferous scale in some Podocarpaceae. Vazquez-Lobo et al.′s function genetic study (2007) started to shed light on this issue. In their study, the genes restricted to scales in other conifer families are expressed in the vascular bundle that are wrapped by the bract, suggesting that the scale is surrounded by the longitudinally enrolled bract in Podocarpaceae. This inference is favored by the tissue organization in *Nageia nagi*, in cross section of the female unit of which the tissue of bract surrounds that of the ovule (Wang et al. 2008). This is further reinforced by anatomical study on a fossil taxon related to Podocarpaceae, in which serial paraffin sections indicate that the ovule and its pedicel are highly reduced and enrolled by a longitudinally folding bract. Similar situation may have been seen in another fossil taxon, *Stachytaxus* (Arndt 2002; Axsmith et al. 2004), in which the several ovules appear to be inserted on the distal adaxial portion of the lateral appendage. Currently available information does not allow to distinguish between two scenarios, (1) the ovule-bearing part is wrapped by the subtending bract proximally, (2) the ovule-bearing part simply adnates to the adaxial of the bract. However, it becomes clear that the modes proposed by Florin (1949) is also workable for Podocarpaceae, although the spatial relationship between bract and scale in Podocarpaceae is different from other families.

Taxaceae is troublesome in term of cone structure, which is hard to compare with cones in other families and those in Cordaitales (Fig. 8.20a). This trouble is partially due to the misleading morphology of the cone. According to Dupler (1920), the ovule terminating the cone in *Taxus* is actually on the terminal of a lateral branch that is equivalent to a secondary shoot in Cordaitales. Due to overgrowth of this branch and underdevelopment of the truthful terminal shoot and other lateral appendages of the original cone, this branch appears as if a cone axis and its ovule as if on the terminal of the cone axis. This illusion can be easily expelled if the development of taxaceous cones is taken into consideration. The weird cone organization in Taxaceae may be interpreted as a result of heteroblasty in development. Thus Taxaceae, although irregular in appearance, does not constitute an exception to the model advanced by Florin (1949).

Following the pattern seen in Pinaceae and other families, lateral appendages in cones in Cupressaceae are interpreted as the result of fusion between scales and their subtending bracts. But it is noteworthy that there are exceptions to such generalization. For example, the ovule in Platycladus orientalis is attached to the cone axis and surrounded by subapical bracts (Zhang et al. 2000). In Juniperus macrocarpa (Fig. 8.20b), there are three ovules/seeds fully covered by only one whorl of three bracts. Instead arranged in the same radius as the bracts, three seeds alternate the bracts, suggestive of ovules independent of bracts. Although such situations defy Florin′s pattern for Coniferales, it is clear that ovules/seeds are not borne on any leaves, and sporophylls are non-existing in Coniferales.

8.2.10 Palissya

Palissya is an enigmatic taxon from the Mesozoic (Schweitzer 1963; Schweitzer and Kirchner 1998). The lateral unit of the cone comprises a subtending bract and a branch bearing ovules in the axil of the bract. Like in Stachytaxus (Arndt 2002), there are two rivaling interpretations on the spatial relationship between the bract and its axillary branch in Palissya. In one of them, these two parts are separated from each other, like the situation seen in Pinaceae. In the other, the axillary branch sinks into the bract and probably at least partially wrapped by the bract. The latter scenario appears more similar to that seen in Taxoidaceae. In either of the scenarios, it is clear that ovules are borne on a branch, not a leaf.

Normally, the cones in Coniferales are unisexual, either male or female. The segregation between two genders makes it hard to interpret the homology of female and male cone parts in Coniferales. For example, the female cones in Pinaceae are interpreted as compound, while the male ones are interpreted as simple. It has been perplexing to compare these two types of cones. What is the reason behind the different organizations has been a mystery. However, the door is not completely closed for plant morphologists. The occurrence of bisexual cone in Pinus maritima [Fig. 2f of Rudall et al. (2011)] provides a unique window through which some insight may be obtained. In this cone, since the female and male parts occur in the same cone, the similarities and differences between the female and male parts become obvious. First, in both female and male cones, the female and male parts are all lateral appendages. Second, all so-called “sporophylls” are aggregations of sporangia, and the difference lies in being either micro- or megasporangia. The major difference between these two lies in the organization of their lateral appendages. The ovulate scales, equivalent to the secondary shoots in Cordaitales, are in axils of bracts, and they together form the so-called seed-scale-bract complexes. The ovulate scales were originally branches bearing multiple ovules, but the ovules are reduced to a few in number and reflex adaxially in extant Coniferales. Similarly, the so-called microsporophylls are clusters of multiple microsporangia, and they are reduced in number of pollen sacs and reflex abaxially in extant Coniferales. Their major difference from the female counterparts is that they have no subtending bracts. This lack of subtending bracts makes the male cone simple, in contrast to the compound female ones. It is interesting to note that the arrangement of the male below female parts in such bisexual cones resembles that of “flowers” in angiosperms, in which male parts lack subtending foliar parts (probably except Nothodichocarpum in Chap. 5) and are below the female parts, and ovular parts are usually subtended and enclosed by the subtending foliar parts. We will come back to this point later.

8.2.11 Gnetales

Gnetales are a very interesting plant group that is at least formerly frequently related to angiosperms, partially due to the great morphological resemblance between *Gnetum* and eudicot angiosperms. Gnetales are unique among extant plant groups in term of occurrence of micropylar tubes. Their very regular decussate arrangement of parts along axes makes them distinct in gymnosperms. According to Eames′ hypothesis that is favored by recent study on fossils related to Ephedraceae (Rothwell and Stockey 2013), the ovules in Ephedraceae are borne on the termini of branches, not leaves. Parallel to this, gene expression pattern in the male units of *Ephedra* (Stützel 2010) suggests that the male parts of Gnetales and Coniferales are branches in nature, having little to do with leaves. It is interesting to note that, at least in some fossil more or less related to *Ephedra* (*Pseudoephedra*), the assumed micropylar tubes are not hollow but rather solid, secluding the nucellus from the exterior space. This features seems to suggest that the pollination in this fossil taxon is angiospermous rather than gymnosperms (See Chap. 7 for details).

8.2.12 Caytoniales

Caytoniales are one of the important Mesozoic seed ferns. *Caytonia* (Fig. 2.6) is one of the representatives of this group. The common feature of this group is that all seeds are covered inside a structure that may be called cupule, and their ovules are not fully secluded from the exterior space at the time of pollination. The cupule bends adaxially in *Caytonia*. Formerly the arrangement of cupules was thought in two ranks in *Caytonia*, but this thinking is facing challenge from a recently found fossil from the Early Cretaceous of China, in which the cupules are apparently arranged helically along an axis (Wang 2010). The provenance of cupule is interpreted as ovules/seeds wrapped by adaxially transversely folding foliar structure, which implies that the cupule is a composite organ. Similar conclusion has been reached by an independent study on so-called “*Umkomasia*”, in which the ovules/seeds are thought borne on branches and covered up by foliar structures on the sides (Shi et al. 2016).

8.2.13 Peltaspermales

Peltaspermales are another group of the Mesozoic "seed ferns". The seeds in this group are hang on the adaxial side of a peltate shield (Taylor et al. 2009). It is obvious that such peltate structure has little to do with typical leaves, and it may be better interpreted as fused ovule/seed pedicels, just as seen in Sphenopsids.

8.2.14 Glossopteridales

Glossopteridales are most important plant group in the southern hemisphere during the Palaeozoic. The reproductive organs in this group is characterized by a cluster of ovules/seeds are inserted on the midrib of a subtending leaf. Such an organization appears to favor the term "sporophyll", but it should be taken as a composite organ comprising a subtending foliar structure and an axillary branch bearing several ovules/seeds that adnates to the subtending foliar structure (Fig. 2.3). This structure was once related to carpels in angiosperms (Retallack and Dilcher 1981b).

8.2.15 Bennettitales

Bennettitales are an important group in gymnosperms that were thought related to angiosperms, at least partially due to their bisexual reproductive organs in which the female parts, male parts, and bracts are arranged from center to the periphery in the order. Such arrangement resembles closely to that in Magnoliaceae, and thus constitutes the excuse connecting Bennettitales and angiosperms (Arber and Parkin 1907). However, this connection appears rushing and whimsical because botanical research in the past century could not find any structure intermediate between magnoliaceous carpel and female parts of Bennettitales. Recently Bennettitales were related to Gnetales and Erdtmanithecales due to one shared feature, micropylar tube. The female part of reproductive organs in Bennettitales is characterized by ovules and interseminal scales arranged helically along the central receptacle, and the ovules are almost covered by the surrounding interseminal scales except their micropylar tubes (Fig. 17.80 of Taylor et al. 2009). It is said that the interseminal scales are homologous to the ovules and get sterilized during the evolution (Kenrick and Crane 1997). If this interpretation is correct, it can be inferred that the ancestral status in Bennettitales is that there are numerous ovules helically arranged along the central axis, a situation seen in the Pentoxylales (see below).

8.2.16 Pentoxylales

Pentoxylales are a mysterious group among gymnosperms that are restricted to the southern hemisphere. This group is characterized by five steles with secondary growth in the stem. Although not clearly understood, the organization of the female cone in Pentoxylales has been demonstrated well enough. The female cone comprises numerous orthotropous ovules/seeds helically arranged along and around the central axis (Fig. 8.21).

8.2.17 Vojnovskales

Vojnovskales are widely distributed in the Carboniferous and Permian of North America, South America, Africa and Asia. Their leaves have parallel venation. Cones are axillary. Seeds are flattened dispersed among the sterile bracts in the distal of the cone, and free of bracts in the lower part of the cone (Fig. 8.22).

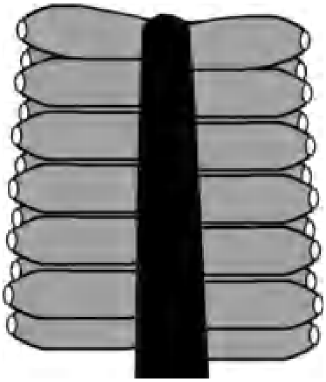

Fig. 8.21 Longitudinal section of female cone of Pentoxylales, showing ovules/seeds arranged around the cone axis

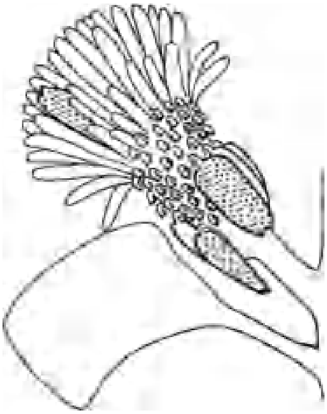

Fig. 8.22 Reproductive organ of *Vojnovskya paradoxa*. Note the seeds (dotted) dispersed among bracts. Redrawn after Meyen (1988b)

Summary of Non-angiospermous Plants
The above descriptions of the female parts in various taxa in non-angiospermous taxa indicate that ovules and sporangia in land plants are always borne on branches, not on leaves, thus the so-called "megasporophyll" is actually a misnomer and should be eliminated in plant morphology. Similar proposals had been made by various authors, including Fagerlind (1946), Florin (1949), Meeuse (1963), Melville (1964), and others. Elimination of "megasporophyll" has direct influence on plant systematics, especially that of angiosperms, in which a carpel had been accepted gratuitously as an equivalent of a leaf for more than a century.

Actually, interpreting a carpel as a leaf has met troubles in the past decades. The persistence of such interpretation is not due to rationality but rather lack of sound competing hypothesis. Now with more information about ancient fossil plants and extant plants, we are allowed to interpret the homology and provenance of carpels in more realistic way. Before that, I will go over some features of several basic types of gynoecia in angiosperms.

8.2.18 Caryophyllales

The ovules are inserted on the lateral of the floral axis, completely independent of the surrounding enclosing foliar ovarian walls that are supplied by independent vascular bundles (Fig. 8.23). This is especially obvious during the early development of the gynoecium (Lister 1884; Zheng et al. 2010).

8.2.19 Myrtaceae

The ovules are borne on an axis (placenta) enclosed by the surrounding ovarian walls. These ovules are, at least most times, supplied by amphicribral vascular bundles derived from the placenta (Schmid 1984).

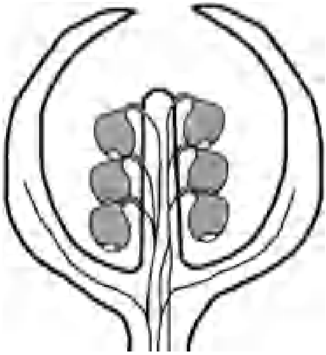

Fig. 8.23 Free central placentation in which the ovules are attached to the extended floral axis

8.2.20 Actinidiaceae

The ovules in this family are arranged in an axile placentation, namely, the ovules are borne on an axis inside the ovary. The vascular bundles supplying the ovules are amphicribral in organization (Guo et al. 2013).

8.2.21 Amborella

The vascular bundle in the base of the carpel furcates into two vascular bundles, each entering the adaxial placenta and abaxial carpel wall, respectively (Buzgo et al. 2004). The vascular bundle supplying the ovule is amphicribral in organization while the one supplying the carpel wall is collateral (Fig. 8.24).

8.2.22 Magnoliaceae

Magnolia was once thought the most primitive taxon among living angiosperms. The vascular system divides into two subsystems at the base of the flower, namely, stellar system and cortical system. The vascular bundles in the stellar subsystem are collateral in organization, forming contrast to the cortical subsystem in which the vascular bundles are amphicribral in organization. Recent study indicates that the so-called carpel in Magnolia comprises adaxial placenta and abaxial carpel wall, each derived from a primordium distinct from the other (Liu et al. 2014). The ovules are supplied by the amphicribral bundles connected to the cortical subsystem, while the carpel wall is supplied by collateral bundles connected to the stellar subsystem (Liu et al. 2014). Recently it is shown that the placenta and carpel wall in Michelia are of distinct nature and separated from each other originally (Zhang et al. 2017).

8.2.23 Brassicaeae

This family may be the best-studied one among all angiosperms. The typical gynoecium, as seen in Arabidopsis, comprises two carpel walls and two placentae, each alternating the other. The carpel wall and placenta are controlled by exclusively different gene sets, and the ovules may well be borne a branch that could have been recruited onto the carpel during the evolution (Roe et al. 1997; Rounsley et al. 1995; Skinner et al. 2004; Mathews and Kramer 2012). The number of carpels sometimes may increase to three or four in other genera in the families.

Fig. 8.24 Longitudinal section of a carpel of Amborella, showing the carpel wall (cw) and placenta (p) together secluded the ovule (o) on the curved tip of the placenta. The vascular bundles in the carpel wall and placenta are fused in the base of the carpel

8.2.24 Solanaceae

The ovules are inserted on the floral axis, surrounded and enclosed by the carpel walls. Sometimes a pepper can be seen developed within another pepper (Fig. 8.25a). Since a pepper (fruit) is not expected to be borne on a leaf or leaf margin, the pepper-in-pepper appears to reject the carpel margin interpretation of

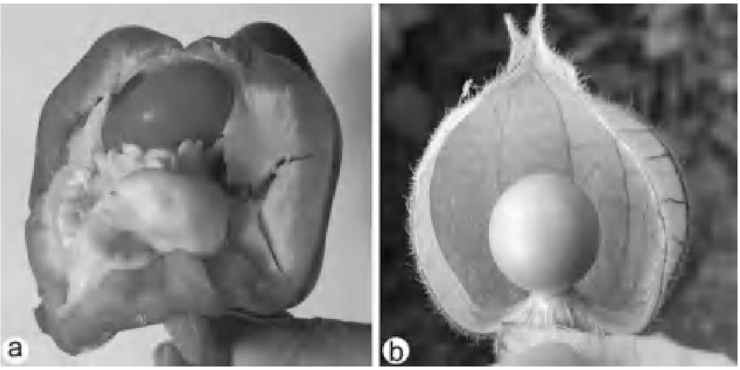

Fig. 8.25 Weird fruits. (a) An opened fruit of *Capsicum* showing numerous seeds and a fruit developed on the placenta inside another fruit. (b) A fruit of *Physalis* showing a fruit enclosed by connate sepals

the placenta in *Capsicum annuum*, favoring and consistent with that ovules are borne on the distal of floral axis in other families.

8.2.25 Basellaceae

A single ovule is inserted on the floral axis, and surrounded and enclosed by three carpel walls from the above. The vascular bundle of the ovule is equally independent from each of those supplying three carpel walls, implying that the ovule belongs to none of the so-called "carpel" (Sattler and Lacroix 1988).

Summary: No megasporophyll
"Megasporophyll" is a term frequently used in plant morphology. At least partially this term is accepted due to the influence of a celebrity, Johann Wolfgang von Goethe (1749–1832). One of his famous words is "Alles ist Blatt", which occurred first time in his brochure titled "Versuch die Metamorphose der Pflanzen zu erklären" (Goethe 1790). Since then the fundamental units of female and male reproductive organs are called "megasporophylls" and "microsporophylls", respectively. The term "megasporophyll" became much widely used after Arber and Parkin (1907) took "megasporophyll" as precursor of the carpel of the assumed primitive angiosperms Magnoliaceae. Arber and Parkin (1907) thought the female units of *Cycas* is a good example of "megasporophyll". Actually, this may be the only case where the term "megasporophyll" appears applicable because no trace leaf morphology is seen in other taxa. The usage of this term and its implications are directly hinged with the deciphering the nature of basic units of gynoecium in angiosperms (so-called "carpel"). Since the above survey indicates that both gymnosperms and angiosperms do not have "megasporophyll" and "megasporophyll" is a term deep-rooted in plant morphology, it is necessary to remove it from any further usage before we can rationally address the issue about the origin of carpels in angiosperms.

8.3 Definition of a Carpel

8.3.1 Defining a Carpel

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" cannot reach a consensus on the definition of a carpel. 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) as well as fossil evidence (Retallack and Dilcher 1981a; Crane and Dilcher 1984; Dilcher and Crane 1984; Dilcher and Kovach 1986; Sun et al. 1998, 2001, 2002; 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) (Fig. 8.26a, c). According to detailed morphological and anatomic observations, this definition is not applicable for flowers in many families (Puri 1952; Boke 1964; 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 Lacroix (1988) 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

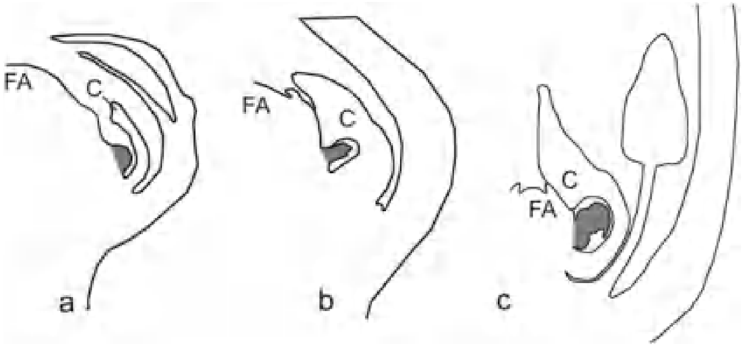

Fig. 8.26 Enclosing ovules fulfilled by floral apex and carpel wall together in Gyrostemonaceae (a, b) and Phytolaccaeceae (c). Note the ovule (gray) and its spatial relationship relative to the floral apex (FA) and enclosing carpel wall (c). (a) and (b) are redrawn after Hufford (1996), (c) drawn after Decraene et al. (1997)

families (Sattler and Lacroix 1988). This confliction in concept forces botanists to search for a more applicable definition for carpels.

8.3.2 Converging on a New Definition

According to the developmental genetic studies of Arabidopsis, a carpel comprises foliar ovarian wall and placenta (Bowman et al. 1999; Skinner et al. 2004). Based on gene expression pattern, Skinner et al. (2004) reach the conclusion that the placenta is a secondary shoot independent of the foliar carpel wall. 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 Magnoliaceae (Liu et al. 2014; Zhang et al. 2017), Ranunculaceae (Thompson 1934) and other families (Laubengayer 1937; Puri 1952; Sattler and Lacroix 1988; Nuraliev et al. 2011; Guo et al. 2013). Fagerlind (1946), Taylor (1991), and Doyle (2008) 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 Perlin redefined a carpel as “a gynoecial appendage that encloses the ovule(s) but does not necessarily bear them” (Sattler and Perlin 1982). 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. 2007a, b; Wang and Zheng 2009; Wang and Wang 2010), ovules and their bearers apparently should have a much longer history than that of carpels and their bearers, and should be separated from the latter (Bowman et al. 1999) (Fig. 8.27).

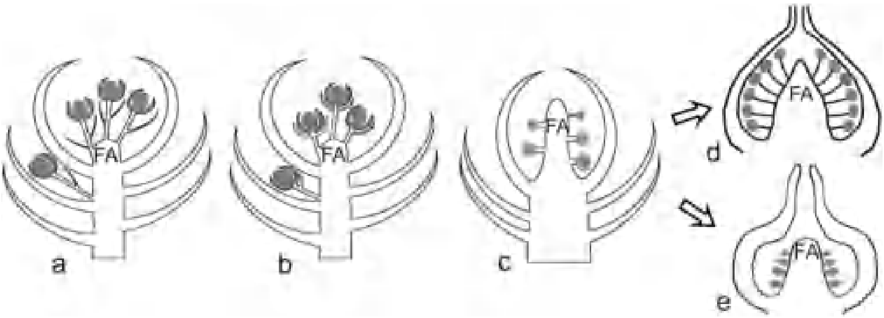

Fig. 8.27 Diagrams of Cordaitales (a, b) and their derivatives (c–e). (a) A reproductive shoot of Cordaitales. Note the ovules interspersed with sterile scales, and ovular stalks with bracteoles. (b) A more derived reproductive of Cordaitales. The bracteoles on the ovular stalks aggregate to the ovule as the ovular stalks become shorter than in a. (c) Female reproductive organ derived from Cordaitales. The ovules have two integuments and are concentrated at the floral apex. The scales are covering the floral apex bearing ovules. (d and e) More reproductive organs possibly derived from Cordaitales-like plants. Note the arrangement of the ovules on the floral apex and ovular stalks of various lengths

The enclosure of ovules in angiosperms is accomplished by the ovary wall, which consists of either the carpel wall alone (Eames 1931, 1961) or both carpel wall and the floral apex (Boke 1964; Sattler and Lacroix 1988; Hufford 1996; Decraene et al. 1997). According to Sattler and Perlin (1982) and Sattler and Lacroix (1988), the function of the carpel is only to protect the ovules, which are cauline. For example, the Basellaceae do 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. 8.30c). In the Gyrostemonaceae, the ovules are borne on the periphery of the floral apex and covered by the carpel walls that initially only subtend the ovules but later arch over and surround the ovules (Hufford 1996; Fig. 8.26a, b). In the Cactaceae, numerous ovules inserted on the floral apex are under the coverage of several carpel walls that converge over the floral apex secluding the ovary (Boke 1964; Fig. 8.28b–e), which is simply a hollow under the carpel walls. Similarly, ovules borne on the central column are gradually covered and later enclosed by carpel walls from the bottom up in Caryophyllaceae (Lister 1884; Thomson 1942). In Ranunculus, the carpel wall initially subtends rather than encloses the ovules (Fig. 321d of Haupt 1953). Similar situation is also seen in Adonis (Foster and Gifford 1974) and, importantly, Magnolia (Liu et al. 2014; Zhang et al. 2017). This partially explains why Thompson (1934) completely rejects the existence of carpels in traditional sense.

If there is only one ovule to be enclosed, the carpel wall may surround the ovule from its abaxial and lateral sides (Figs. 8.26a–c, 8.29d, f), as in Illiciaceae, Ranunculaceae, Gyrostemonaceae, and Phytolaccaceae (Figs. 30–31, Thompson 1934; Figs. 16–22, Hufford 1996; Figs. 6g, 7a–b, Decraene et al. 1997; Wang et al. 2015). When there are numerous ovules to be enclosed by a single carpel and these ovules may be borne on the floral apex, an ovary with free placentation may come to form, as in Delphinium consolida as described by Baillon in 1880 (Thompson 1934; Puri 1952; Fig. 8.29a). When the floral axis is appressed to and fuse with the ventral margins of the only carpel wall, it may form placentation as seen in Michelia

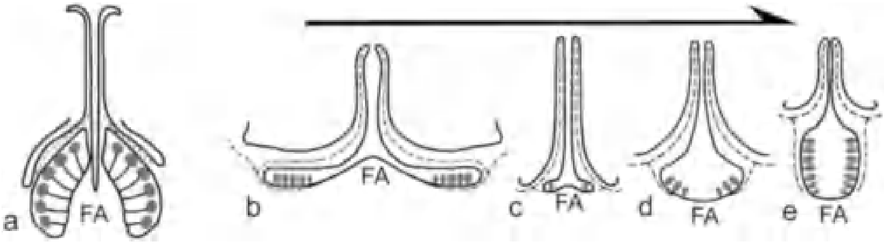

Fig. 8.28 Flowers of the Portulacaceae (a) and Cactaceae (b–e). (a) Gynoecium with free central placentation in the Portulacaceae. Note its similarity to Fig. 8.27d. (b–e) Flowers in Cactaceae. Note the reduction and recession of the floral apex in the series, ovules on the floral apex, as well as little change in the carpels in these longitudinal sections. (b) Pereskia pititache. Note its similarity to Fig. 8.27e. (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

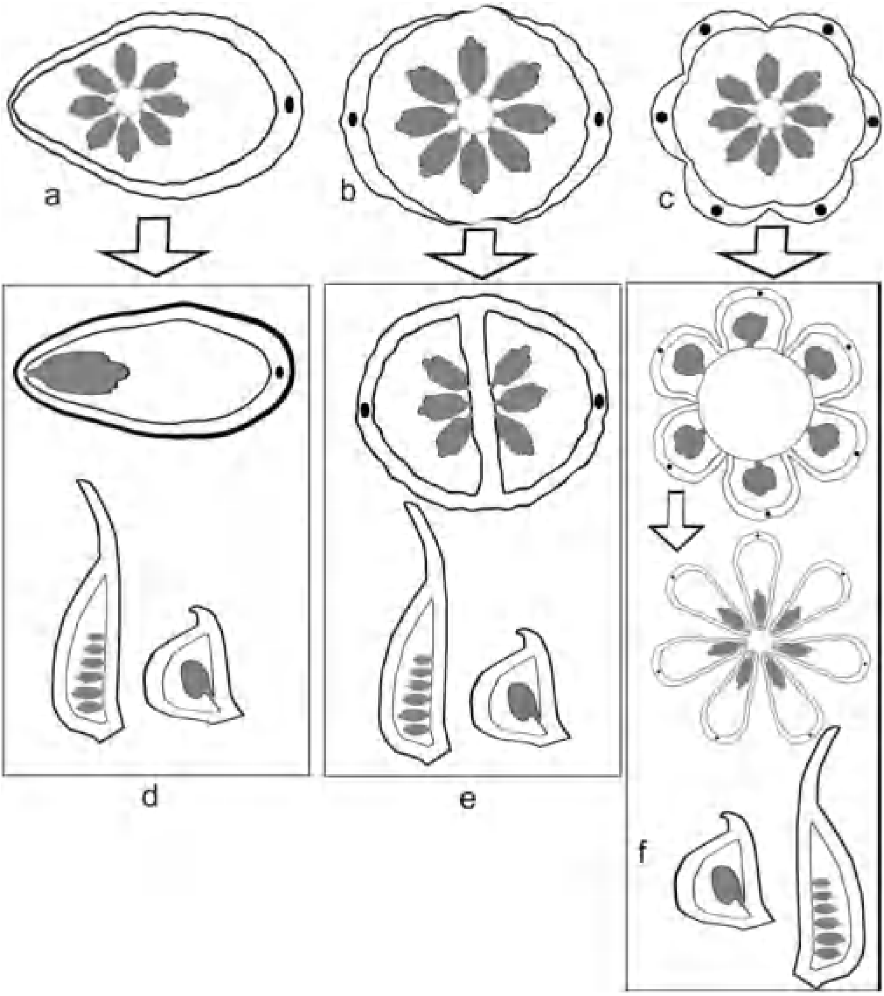

Fig. 8.29 Possible relationship among different placentations. Note the variable number of carpels surrounding the placenta in a–c. Each of them may give rise to other types of placentations (d–f) through metamorphoses, following the direction of the arrows. All ovules are in gray

(Magnoliaceae, Wang et al. 2015; Zhang et al. 2017), Aquilegia, Aconitum, Delphinium (Ranunculaceae) [Fig. 8 of Baillon (1871)], Fumariaceae (Payer 1857; Judd et al. 1999), and Fig. 8.29d. When there are numerous ovules to be enclosed by multiple carpel walls and these ovules are borne on the periphery of the floral apex, these carpel walls may either collectively converge and cover the floral apex (as in Cactaceae, Boke 1964; Figs. 8.28b–e and 8.29c), forming free central placentation, or each carpel contains an ovule or a file of ovules on the floral apex, forming axile placentation. When there are two placentae and two carpel walls arranged in the same whorl, the typical gynoecium of Brassicaceae can be formed. 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. 8.28c). Papillae on the carpel walls may fill up the space between carpel walls and form the transmitting tissue (Boke 1964; Decraene et al. 1997; Bowman et al. 1999).

Despite the above interpretation, many botanists tend to stay with the classic definition of carpels. 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 many angiosperms including 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" (¼ carpel wall) has an obvious border with the floral apex at its base (Fig. 7b of Decraene et al. 1997), which is suggested by the spatial arrangement and orientation of the cells. The same can be said of situations in the Amborellaceae, Ranunculaceae, Cactaceae, Basellaceae, Gyrostemonaceae, Cactaceae, Brassicaceae, Basellaceae, 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 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 is also undermined by free central placentation in Amarathaceae, 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; Sect. 6.2), has flowers that have ovaries each with free central placentation (Fig. 8.31c). 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 nature of placenta. Maybe future research will bring more similar cases into light.

Even though the traditional axial theory has gained support from living and fossil angiosperms, it is true that it cannot explain everything. The dominance of the appendicular theory is not a random event. The latter can account for many phenomena in angiosperms. Actually, both theories emphasize different aspects and parts of carpels and both of them are right in certain aspects. If carpel wall and placenta are separated, it becomes clear that each school of thought is correct about the part it emphasizes. Since every organ in plants was originally derived from dichotomous branches, every plant part is axial in nature, and thus differentiating between axial and foliar nature of plant organ in earliest land plants would be meaningless. What the present author wants to emphasize is that the immediate precursor for the carpel wall was a foliar organ, and the immediate precursor of placenta was a branch bearing ovule(s). 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:

> A carpel comprises carpel wall and placenta, and the carpel wall is a foliar organ that encloses the placenta. A carpel wall *per se* does not bear ovules.

8.3.3 Derivation of the Carpel

8.3.3.1 The Making of Carpels

The carpels in angiosperms may be derived from the ovulate cone of Cordaitales-like plants or other plants with axillary branching with the least modifications for the following reasons.

1. The scales in Cordaitales tend to cover, surround, or enclose ovules (Florin 1939; Rothwell 1982, 1993; Costanza 1985; Wang and Tian 1993; Wang 1997; Wang et al. 2003; Hilton et al. 2009a, b). This tendency appears to be a common rule in seed plants, as it has been seen in the evolution of Coniferales (Schweitzer 1963; Tomlinson and Takaso 2002; Wang et al. 2008) and Gnetales (Fagerlind 1946; Liu and Wang 2016), suggesting that it may well happen in the ancestors of angiosperms. This trend is further extended in the so-called “Chinese Lantern” effect or Inflated-Calyx Syndrome (ICS) seen in Solanaceae (Angiosperms), namely, connate sepals encapsulating the mature fruit (He et al. 2004; He and Saedler 2005) and angiocarpy in Monimiaceae (Lorence 1985) (Fig. 8.30).
2. Female organ of Cordaitales has tens of scales that can be categorized in three types (Wang 2009). These scales may have the potential to evolve into different organs or floral parts. Some of them may turn into carpel walls, and others into 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 Figs. 8.18c and 8.27a–c. This appears already materialized in some Cordaitales (Rothwell 1982; Figs. 8.18c and 8.31a). 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 difficulty deriving extra integuments in angiosperms (Eames 1961) can also be overcome in this way. Furthermore, the presence of stomata on outer integument (Eames 1961; Zhang 2013) supports the derivation of integument from a foliar part, which is also frequently suggested by molecular studies (Skinner et al. 2004).
4. The aggregation in point 3 has parallel examples in Coniferales and Gnetales (Florin 1939, 1944, 1951; Fagerlind 1946; Schweitzer 1963). These two latter

groups are thought related to or derived from Cordaitales. It is not surprising but rather expected that similar evolutionary trends are applicable in Cordaitales-like plants and their other derivatives.

5. Developmental genetics indicates that carpel wall and placenta are floral parts of different natures and controlled by different sets of genes (Bowman et al. 1999; Frohlich 2003; Skinner et al. 2004; Mathews and Kramer 2012). The carpel wall is equivalent to a leaf, while the placenta is equivalent to an ovule-bearing shoot.
6. The organization of flowers in Cactaceae is closely comparable to that in Cordaitales. The floral structure in Fig. 8.28b–e shows a smooth transition from Fig. 8.28b to e. And Fig. 8.28b shows little difference from Fig. 8.27d, which is an imaginative 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 carpel walls. Note that in the series from Fig. 8.27b to e, there is little change in the configuration of the carpel walls. 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. 8.27d 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, Basellaceae, Amarathaceae, and Juglandaceae, have free central or basal placentation in their ovaries, in which the floral apex bears numerous or one ovule and is independent from the surrounding ovarian wall (Judd et al. 1999).
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 (Fagerlind 1946; Retallack and Dilcher 1981b; Taylor 1991; Doyle 2008). 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). At the end of his paper, 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 are not elaborated on or well-evidenced by fossils.
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 theory advanced in this book. When the number of ovules in the free central placentation is reduced to one, the basal ovule in an ovary, as in Basellaceae (Sattler and Lacroix 1988), may be derived (Fig. 8.30a–c). Asymmetrical growth may turn an ascidiate carpel into an ascido-plicate and further conduplicate (Taylor 1991).

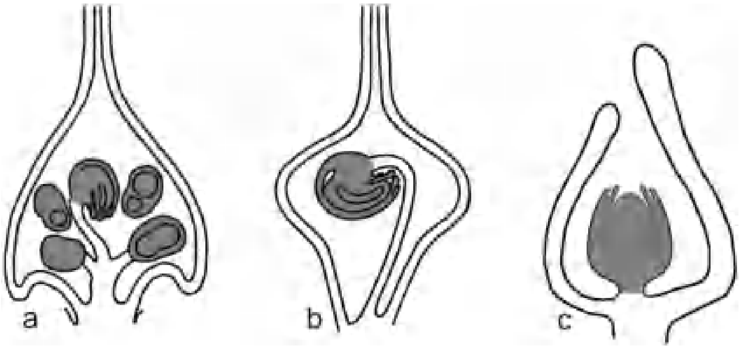

Fig. 8.30 Derivation of basal placentation from free central placentation. Note the number of ovules is reduced from many to one in the series from (a) to (c). (a) and (b) are redrawn after the figures of Amarathaceae in Joshi (1938). (c) shows the ovary with a basal ovule in Basellaceae, after Sattler and Lacroix (1988). All ovules are in gray

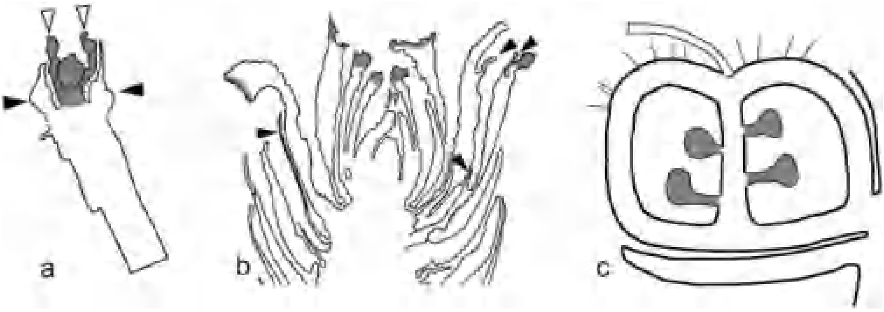

Fig. 8.31 Fossil evidence from the Permian and Jurassic. (a) Ovule of *Cordaianthus duquesnensis* from the Permian. Note the ovule with additional appendages (black triangles), equivalent to outer integument, outside integument (arrows). (b) Secondary shoot of *Cordaianthus duquesnensis* with apical ovules. Note bracteoles (black triangles) on the ovular stalks. (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

This transition is supported by fossil evidence of a possible ascido-plicate carpel in *A. eoflora* (Ji et al. 2004), *Sinocarpus* (Leng and Friis 2003, 2006; Dilcher et al. 2007), *Liaoningfructus* (Wang and Han 2011), and living angiosperms (Taylor 1991). Deriving carpels with free central placentation from a Cordaitean counterparts appears not contradicting this conclusion and has the potential give rise to various types of placentation (Figs. 8.29a–f and 8.37).

Based on the above comparison, the author thinks that it **more plausible to derive angiospermous carpels from the sterile bracts attached to the reproductive secondary shoot**, as in Cordaitales, than from the cupule-subtending leaf in *Glossopteris* (Retallack and Dilcher 1981b) or the rachis in *Caytonia* (Doyle 2008).

8.4 Placenta

8.4.1 Isolation of Placenta from Carpel Wall

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

1. Frequently placentae have vascular bundles separated from those of carpel walls (Thompson 1934; Laubengayer 1937; Puri 1952; Sattler and Lacroix 1988; Hufford 1996; Nuraliev et al. 2011; Guo et al. 2013; Liu et al. 2014; Zhang et al. 2017, among many) (Fig. 8.28b–e). Since the vascular skeleton is conservative and may be more informative about the history of organs (Eames 1926), placentae at floral apex with one or more vascular bundles independent of other parts strongly favor a cauline/axial interpretation of placentae (Sattler and Lacroix 1988; Decraene et al. 1997). Such independent vascular bundles of placentae suggest that the so-called cauline origin of placentae (or “acarpellate” gynoecium) may exist at least in the Nyctaginaceae, Illiciaceae, Piperaceae, Solanaceae, Magnoliaceae, Phytolaccaceae, Actinidiaceae, Chenopodiaceae, Polygonaceae, Malvaceae, Urticaceae, Scyphostegiaceae, Salicaceae, Primulales, Juglandaceae, Myricaceae, Santalaceae, Cactaceae, Amaryllidaceae, Berberidaceae, Basellaceae, Asteraceae, Cyperaceae, Poaceae, and Amarathaceae (Engler and Prantl 1889; Laubengayer 1937; Joshi 1938; Puri 1952; Boke 1964; Sattler and Perlin 1982; Sattler and Lacroix 1988; Heywood et al. 2007; Zheng et al. 2010; Guo et al. 2013; Liu et al. 2014; Zhang et al. 2017). The placentae in these families are either enclosed by carpel walls 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 (Amarathaceae, Fig. 8.30a) and a single ovule on a long stalk in Pupalia lappacea (Amarathaceae, Fig. 8.30b). These two examples from the same family at the very least confirm the existence of placenta independent of carpels in Amarathaceae.
2. Developmental genetics also supports treating carpel and placenta separately (Bowman et al. 1999; Frohlich 2003; Skinner et al. 2004; Mathews and Kramer 2012). Study of the model plant, Arabidopsis, indicates that the juxtaposition of expression of adaxial (REV) and meristem (STM) factors, a characteristic for axillary meristem formation, is also seen in a placenta, implying that a 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 during its early development, but the shoot apical meristem (SAM) and its gene expression are detectable during this stage.
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

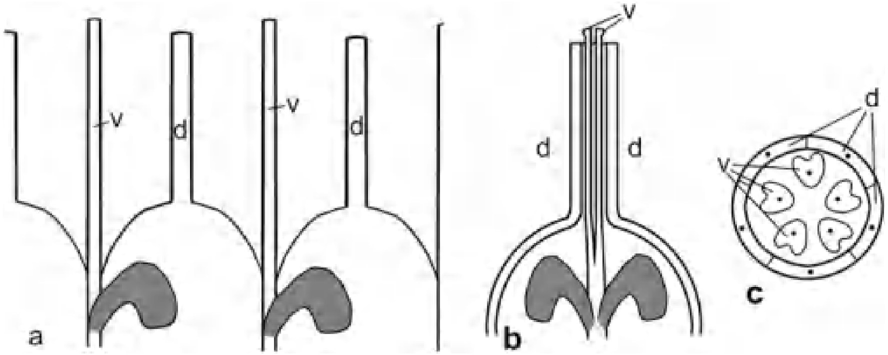

Fig. 8.32 Floral diagrams of *Pyrola elliptica* (Pyrolaceae) (Hunt 1937). (a) Opened gynoecium, according to the classic theory. Note the ovules (gray in color) in the ovary. The so-called “ventral bundle” (v) of the carpel is longer than its “dorsal part” (d) and almost isolated from the rest of the 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)

carpels merely roofing the ovular chamber and forming the styles and stigmas”. The situation in Cactaceae is almost exactly what the axial theory predicts: the ovules in *Pereskia* are inserted on free receptacular tissue (¼ floral apex) that is covered by a roof composed of multiple foliar parts, forming an ovary (Boke 1964; also seen Fig. 8.28b–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; also see Fig. 8.30a, 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. 8.32) 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 upper ends of the carpels. This configuration makes them more likely parts of the independent placenta rather than ventral margin of the carpels (Fig. 8.32). 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. The formerly assumed ancestral angiosperm *Magnolia* demonstrates similar pattern, namely, two primordia give rise to placenta and carpel wall, respectively (Liu et al. 2014). Although not clearly seen, the carpel in *Amborella* seems to comprise an adaxial ovule-yielding part and an abaxial ovule-enclosing part (Buzgo et al. 2004; Yamada et al. 2004). It is more likely the ovules are attached to the floral axis and independent from the ovary wall (¼ carpel wall).

4. Flower development indicates that all primordia of ovules, like those of 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, 35, 36 of Thompson (1934)]. In addition, floral axis bearing clusters of ovules in the ovary (free central placentation) has been seen in Portulaceae (Payer 1857; Judd et al. 1999), Polygonaceae, Chenopodiaceae, Primulaceae (Payer 1857; Puri 1952), Amaranthaceae (Joshi 1938), Actinidiaceae (Guo et al. 2013), and others. Furthermore, although interpreted otherwise, the placentation in Gyrostemonaceae (Hufford 1996) and Phytolaccaceae [Figs. 6g and 7a, b of Decraene et al. (1997); Fig. 1a, b of Zheng et al. (2010)] can be, at least equally plausibly, interpreted as floral axes bearing ovules enclosed by the subapical foliar parts.
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 have an independent history and should be separated from the carpel wall (Bowman et al. 1999). Those taxa with axillary branches bearing ovules, such as in Ginkgoales, Coniferales, and Cordaitales, on one hand, confirm the longer history of ovules, on the other hand, suggest the axillary ovules seen in angiosperms should not be exceptional among seed plants.
6. This is a suggestion supported by the recent discovery of Xingxueanthus from the Middle Jurassic, an inflorescence bearing female flowers with free central placentation. The ovules are borne on a central column and have nothing to do with ovarian wall (see Chap. 6 for details). Euanthus from the same age, although without free central placentation, demonstrates parietal placentation, in which the ovules can be interpreted as inserted on the lateral of invaginated floral axes and covered and enclosed by hairy tissues from the above.
7. All these concurrently point to the independence of placenta from carpel wall.

8.5 Origin of Placenta

The appendicular theory states that placentae are derivation of leaf margin (Eames 1961). This theory has led many botanists to search for such prototypes of carpels, which would have ovules/seeds borne along the leaf margins. For example, megasporophylls of Cycas once were a target of interest (Arber and Parkin 1907; Thomas 1931). To derive a marginal placentation out of the cupules of Caytonia, Doyle (1978, 2006, 2008) (and other scholars) tried to expand the assumed rachis of Caytonia. 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 and Coniferales, it is logical to correlate the ovules, secondary axillary

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

Cordaitales	Angiosperms	Coniferales	Gnetales
Sterile scale	Carpel wall	N/A	Outer integument
Bracteole on ovular stalk	Outer integument	N/A	N/A
Ovule	Ovule	Ovule	Ovule
Integument	Inner integument	Integument	Inner integument
Extra appendage	Outer integument	N/A	Outer integument
Secondary shoot apex	Placenta	N/A	N/A
Secondary shoot	Placenta	Scale	Ovuliferous unit
Bracteole on ovular stalk	Aril, obturator	N/A	N/A
Bract	Carpel wall	Bract	Bract

shoot, and sterile scales in Cordaitales-like plants with the ovules, placenta, and carpel walls in angiosperms (Figs. 8.27 and 8.28; 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 (Rothwell 1982; Wang and Tian 1993; Wang 1997; Hilton et al. 2009a; Wang et al. 2003). As frequently seen in the transverse sections of the ovulate cones of Cordaitales, there are multiple scales surrounding the central distal ovules. If these sterile scales become connated laterally and the ovules are concentrated onto the short shoot apex in Cordaitales, they can constitute something like flowers in Cactaceae of angiosperms (Fig. 8.28b). 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. Another candidate is *Juniperus macrocarpa* (Cupressaceae), in which three ovules alternate the bracts, which enclose the ovules after pollination (Fig. 8.20b). The only difference between *J. macrocarpa* and angiosperms is the time of pollination. Brockington et al. (2009) put Portulaccaceae as the sister of Cactaceae. Interestingly, the ovules of Portulaccaceae are borne on a protrusion on the base of the ovary, very similar to those in Fig. 8.27d, 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 elongate 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 (Fig. 8.27a–c), which paves the way to bitegmic ovules in angiosperms, but also helps to give rise to the placenta.
3. There is a smooth transition from secondary shoot in Cordaitales to the flowers in Cactaceae (Figs. 8.27 and 8.28). If the sterile scales in Cordaitean plants are

symmetrically arranged, their fusion and enclosure will result in a free central placentation, as in Capparales (Hufford 1996; also see Fig. 8.29c). When each individual carpel covers only one ovule on the periphery of floral apex, the placentation as that in Gyrostemonaceae, Phytolaccaceae, and Papaveraceae (Hufford 1996; Decraene et al. 1997; Fig. 8.26a–c) may be derived. Invagination of the floral axis makes the formerly lateral ovules as if on the wall of the cup-shaped floral cup, as seen in Cactaceae and Salicaceae.

4. Other types of placentation in angiosperms may be of independent origin or derived from those in point 3 through various transformations. 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. 8.29a–f).

   Marginal placentation may come into being when a subtending enclosing carpel wall surrounds a floral axis bearing numerous ovules and the floral axis becomes appressed and fused with the carpel margin (Figs. 8.29a–d and 8.37). This results in follicle, as in Ranunculaceae and Magnoliaceae (Baillon 1871; Marilaun 1894; Thompson 1934). However, if the number of the ovules on the floral axis is reduced to one, it will end in an achene as in Ranunculaceae (Baillon 1871; Thompson 1934). Axile or pseudoaxile placentation may be derived from free central placentation through the intrusion of carpel margins, as suggested by Takhtajan (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 (Fagerlind 1946; Puri 1952; Fig. 8.29c–f; Fig. 8.37).

5. Bennettitales are most frequently discussed group in study on origin of angiosperms. However, despite Arber and Parkin (1907) have proposed possible relationship between Bennettitales and angiosperms and palaeobotanists have been working hard searching for related evidence, the gap between these two groups remains as huge as it was a century before until recently. Rothwell and Stockey (2010) described Foxeoidea, a new member of Bennettitales, in which the ovules have no exserted micropylar tubes as expected for Bennettitales, instead the ovules are surrounded by interseminal scales. If these interseminal scales fused each other and complete the enclosing of ovules, a status of angio-ovuly would have been reached, making the plant an unequivocal angiosperm. Recent discovery of Zhangwuia in the Jurassic of China (Liu et al., in progress) seems to favor this guess as it may stand for a stage of evolution between Foxeoidea and angiosperms.

6. The basal ovule has been a puzzle for many botanists, at least for the proponents of the appendicular theory (Laubengayer 1937). The basic reason behind this puzzle is that the ovule is independent of the carpel walls surrounding it (Sattler and Lacroix 1988). However, according to the theory advanced 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. 8.30a–c). Therefore, a basal ovule can be taken as the only survivor of a free central placenta, as in Polygonaceae and Caryophyllaceae (Laubengayer 1937; Sporne 1974).

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 (Thomas 1931; Puri 1952). When the apex of the ovary was sealed by secretions, it may result in a carpel/ovary as in some basal angiosperms (Qiu et al. 1999; Endress and Igersheim 2000a, b; Endress and Doyle 2009). Similar phenomenon is also seen in *Caytonia* (Harris 1940).
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).
9. Amphicribral bundles is commonly present in the placenta of Myrtales and many other families. Amphicribral bundles are characterized by phloem deployed around xylem, just as in the protostele and young branches, suggestive shoot-nature of the bearing organ. It is unequivocal that free central placenta, as frequently seen in the Centrospermae, is an extension of the floral axis. Therefore it is logical to see such anatomic features of shoot or branch in such placenta in Centrospermae. The occurrence of amphicribral bundles in other families without free central placentation, such as in Magnoliaceae and Amborellaceae (among many), is more or less irrational according to the classic theory in which carpel is taken as a metamorphosed leaf that is expected to be supplied by collateral bundles. A more logical interpretation for such “irrational” phenomenon is that placentae in these families are actually branches bearing ovules (Liu et al. 2014; Zhang et al. 2017).
10. 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 bearing 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, simplified or not, protruding or invaginating, that bears ovules*. It may be derived from an ovule-bearing secondary shoot in the immediate ancestor of angiosperms, which might be comparable to Cordaitales-like plants.

8.6 Spatial Relationship Between Ovule and Adjacent Parts in Gymnosperms

Caytoniales *Caytonia* may be the most controversial gymnosperm that is frequently related to angiosperms or their origination. There are various hypotheses on the evolution and derivation of the reproductive organs of *Caytonia* (Harris 1933; Krassilov 1977; Doyle 2008). Generally, there is a consensus on the formation of the cupule in *Caytonia*, namely, the ovules got enclosed by the transversely folding subtending foliar parts. In this case, it may be interpreted as seeds/ovules borne on an axillary branch are enveloped by the subtending foliar part.

Petrielleales *Petriellea* is another Mesozoic so-called seed fern documented from the south hemisphere (Taylor et al. 2009). Like in Caytoniales, the ovules are almost completely enclosed by the cupule. Different from *Caytonia*, the cupule opening is located on the abaxial side in *Petriellea*. This opening position appears alienating Petrielleales from angiosperms, in which the ovules most times are located in the axil (adaxial) of the carpel wall, just as in the Caytoniales. However, this alienation is reduced if the reproductive organ of *Yuhania* is taken into consideration. Apparently, the ovules are located on abaxial side of the enclosing foliar parts in *Yuhania*. Although this feature makes the phylogenetic position of *Yuhania* hard to resolve among extant angiosperms, *Yuhania* and *Petriellea* seem to remind botanists that some seed plants were exploring different morphospace and spatial part-combination that is not frequently seen among extant plants. Whether such plants have left living offsprings in current ecosystem is an intriguing question awaiting answers.

Cupressaceae may be the most diversified in term of the ovule and bract relationship among extant gymnosperms. Unlike most other conifers, in which the axillant scale and the ovules on it are in bract axils in the cones (therefore the scale and its subtending bract should be aligned to the same radius), the ovules in Cupressaceae either alternate the bracts as in *Juniperus oxycedrus macrocarpa* or concentrated to the cone apex and surrounded by the bracts as in *Callitris* (Takaso and Tomlinson 1989 and *Platycladus* (Zhang et al. 2000). Although such spatial relationship between ovules and bracts is hard to account for in the Florin model, the situation can become much ameliorated if the scale and its ovules are taken as a branch independent of the adjacent bracts. Assuming so, the scale and their ovules may either alternate the bracts or be concentrated to the cone apex and surrounded by the bracts. Although such ovule (sporangium)-foliar part relationship appears weird among seed plants in which axillary branching is almost ubiquitous, sporangium does have the liberty to combine with the adjacent foliar part in any spatial combination. This is exemplified by the above mentioned Caytoniales, Petriellaeales, *Yuhania*, as well as some example from the Devonian *Dibracophyton*, the sporangium in the latter is bracketed by two bracts from the above and the below (Hao et al. 2012). The difference and diversity in term of cone organization between Cupressaceae and other conifers imply that Cupressaceae is a group of plants that deserves further investigation.

Pseudoephedra is a very special plant from the Early Cretaceous of Liaoning, China (Chap 5; Liu and Wang 2016). It is unique in that its general morphology resembles that of *Ephedra* but, instead of the expected micropylar tube, it has a solid style at the apex of its female reproductive organ. Such morphology implies that the megasporangium (nucellus) is fully enclosed by the otherwise called integument. So far this is the only case of integument fully enclosing nucellus since the origin of seed in the Devonian. Such morphology forces the pollination and fertilization to be performed in a way only seen in the angiosperms, namely, the pollen tube has to grow through the tissue enclosing the nucellus.

Podocarpaceae appears unique among conifers in term of the relationship between ovule and bract, and existence of scale or not in the family. Tomlinson et al. (1989) once questioned the existence of scale in Podocarpaceae. However, if, according to the Florin model, a scale is an originally ovule-bearing secondary branch, such a scale may exist in the Podocarpaceae. The uniqueness of Podocarpaceae may be accounted by formerly unexpected spatial relationship between scale and bract, namely, instead of only subtending the scale as in other conifers, the bract in Podocarpaceae may fold longitudinally and wrap the formerly axillary scale completely (except at the tip of the scale). This hypothesis is favored by an anatomically preserved fossil from the mid-Cretaceous of the North America and histology of the cone unit in living Podocarpaceae (Wang et al. 2008). Taking all conifers into consideration, the scale and its ovules in conifers may be free from the bracts and combine with the latters spatially in various way, the bracts may be either smaller and free from or fusing with scales, or bigger and fusing with and surrounding the smaller axillary scale, partially (as in Araucariaceae) or almost completely (as in Podocarpaceae).

8.7 Enclosing Ovules

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

8.7.1 Spatial Relationship and Ways of Ovule-Enclosing in Angiosperms

Despite the diversity of gynoecia in angiosperms, there are only limited number of ways of ovule-enclosing in angiosperms.

Type A Floral Apex and Its Lateral Appendages Together Enclose the Ovules This is seen clearly in Cactaceae and Phytolaccaceae (Boke 1964; Decraene et al. 1997; Figs. 8.26 and 8.28). In Cactaceae all of the ovules are borne on the periphery of the floral apex, and the carpel walls (foliar parts) are independently inserted on the lateral of the floral apex. These carpel walls (foliar parts) are connate laterally and eventually cover the ovule-bearing floral apex (Figs. 8.28b–e). Furthermore, Centrospermae may be called “pseudo-carpellate” (in Meeuse′s sense), in which the central columnar ovuliferous axis is encased by subapical subtending bracts (Sporne 1974). The latter case would be very similar to that in Fig. 8.27e and similar configuration has been seen in some early angiosperms such as *Xingxueanthus* (Wang and Wang 2010) and *Canrightia* (Friis et al. 2011). Septa develop much later in Cactaceae (Boke 1964), implying that septa may be 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). Parallel to this, partially developed septa have been seen in Myrtaceae (Schmid 1980).

Monetianthus is anatomically preserved fossil plant recovered from the Cretaceous sediments in Portugal (Friis et al. 2009). Applying SEM and synchrontron X-ray radiation tomography technologies, the details of the fossil are revealed. Although the claimed tepals and stamens require further effort to confirm, the ovules are almost completely enclosed by the surrounding tissues. This fossil plant was related to the basal angiosperms (Friis et al. 2009), therefore it may shed some light on the ovule-enclosing in angiosperms. The ovules in *Monetianthus* were interpreted as in a laminar placentation. The existence of a central column implies that the floral axis terminates in such a column. Thus the enclosing of the ovules in *Monetianthus* could be taken as ovules on the lateral of floral axis get enclosed by the floral axis itself and/or subapical lateral (foliar or not) appendages.

The word “almost completely enclosed” is used for above *Monetianthus* because in Fig. 2b of Friis et al. (2009), there is a ventral slit on the apex of the gynoecium. This slit makes the affinity of *Monetianthus* susceptible to various interpretations. Considering the width of the slit is big enough to allow a pollen grain to enter the gynoecium, then the possibility of gymnospermous pollination cannot be excluded completely. Considering the study history and changes about the affinity of *Caytonia* that was once erroneously placed in angiosperms, exercising extra care appears necessary to pin down the affinity of *Monetianthus*.

Type B Each Lateral Foliar Part Encloses One Ovule in Its Axil The situation in Gyrostemonaceae and Illiciaceae is slightly different (Hufford 1996). In this type each carpel wall covers one of the many axillary ovules that are borne on the floral axis. Initially the carpel walls only subtend the ovules from the bottom. During the development each carpel wall overgrows and surrounding the axillary ovule from the bottom, sides as well as above (Fig. 8.26a–c).

Type C Each Foliar Part Encloses Multiple Ovules in Its Axil Good examples of this type can be seen in the Magnoliaceae. The ovules in this type are borne on axillary branches, and these ovules are enclosed by the subtending foliar parts. The ovule-bearing branches may either be axillary and isolated from the subtending foliar parts, or fuse with the margins of the subtending foliar part and thus appearing inserted on the so-called carpel margin (Liu et al. 2014; Zhang et al. 2017).

Type D Integument Encloses the Nucellus 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). This situation in Pseudoephedra (Liu and Wang 2016) is comparable to this type.

Type E One Placenta and One Foliar Part Together Enclose the Ovule In this type, the ovule is on the tip of the placenta, which recurves and brings the ovule to the (adaxial) center of the carpel (interior of the ovary), and the associated facing foliar part joins the placenta from the above and both sides and thus completing the enclosure of the ovule. The stigma in this type comprises the distal portion of both placenta and foliar part. This situation is well exemplified by Amborella (Fig. 8.33; Endress and Igersheim 2000a, b; Buzgo et al. 2004).

Type F Multiple Placentae and Multiple Foliar Parts Arranged in the Same Whorl Together Enclose the Ovules In this type, the placentae and foliar parts alternate each other and are arranged on the lateral of floral axis terminal in a whorl. The ovules are inserted on the adaxial of and thus protected by the placenta. The foliar parts on each side of all placentae and the placentae jointly complete the ovule-enclosing. The stigma in this type mainly comprises the distal portion of the placentae. This situation is well exemplified by the well-known Arabidopsis, the

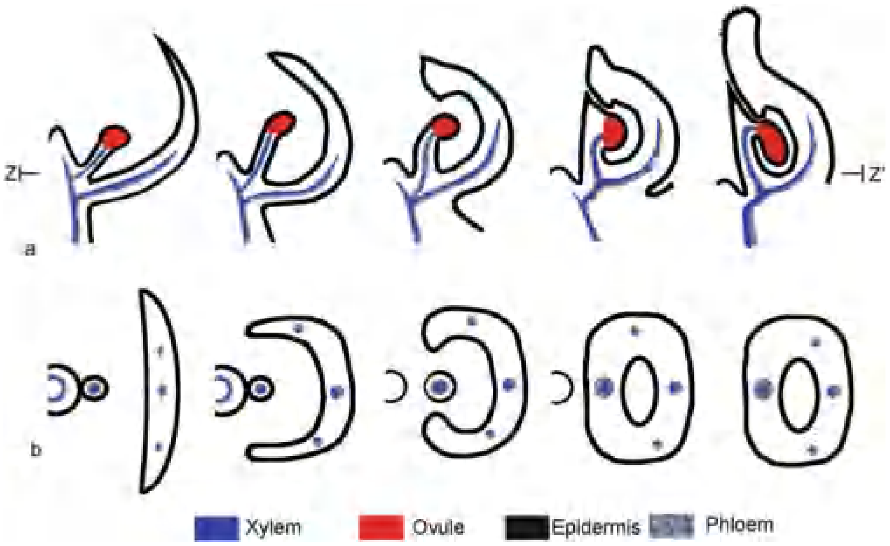

Fig. 8.33 Inferred steps from a gymnospermous ancestor to the carpel of Amborella. Note the distinction between the vascular bundle organizations in placenta and carpel wall and their changes in the process

gynoecium of which includes two placentae and two foliar parts (carpel walls). The other members of the family show similar configuration, and the only difference is that their numbers of placentae and foliar parts may increase to three or four.

Type G Ovule Is Enclosed by An Above Recurving Foliar Part The ovule inserted on the lateral of floral axis is situated just below a foliar part and gets enclosed by the latter. Such spatial relationship between ovule and enclosing foliar part is not known until recently when Liu and Wang documented a fossil from the Jurassic, Yuhania. However, this type is conceivable because ovules in abaxially recurved cupule such as Petriellea has been known in the fossil record for long time (Taylor et al. 2009). Dorsalistachya, a recently reported fossil from the Permian (Wang et al. 2017) also has microsporangia and macrosporangia hang on the abaxial of the foliar parts. However, the extant representative of such type is still missing.

Type H Ovules Are Surrounded and Fully Enclosed by the Adjacent Interseminal Scales This is rarely seen in the fossil record. A recently recovered fossil (Zhangwuia) from the northeastern China, in which the ovule is fully secluded from the exterior space by tissues (Liu et al. in progress). The general morphology of this reproductive organs resembles that of Bennettitales. Interesting, Rothwell and Stockey (2010) documented a fossil, Foxeoidea, from the Cretaceous of North America, in which the ovule appears be surrounded but not fully enclosed by the adjacent interseminal scales. Whether these two fossil demonstrate two examples in an evolutionary series is still an open question awaiting future answers.

8.7.2 Parts Involving in Ovule-Enclosing

Examining the above ways of ovule-enclosing, the parts involved in the megasporangium enclosing in angiosperms include various categories of plant organs.

1. Integument. If Pseudoephedra of Type D is taken as an angiosperm, its megasporangium is fully enclosed by its integument.
2. Adjacent foliar part. The foliar parts in Type B, C, E, F, G either take the full or partial responsibility of enclosing the ovules.
3. Interseminal scale. This can be seen in Type H, in which the ovule-enclosing is performed by the adjacent interseminal scales. These interseminal scales, according to Kenrick and Crane (1997), were originally sterilized ovules.
4. Branch. The ovules are enclosed or protected, partially or fully, by floral axis or placenta, with help of foliar parts or not, in Type A, B, C, E, F, or G.

8.8 Flower

The appendicular theory 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 recent studies. 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 and 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 seem to be 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 invaginated (Boke 1964). The flower-in-gynoecium phenomenon (Sattler and Lacroix 1988) and pepper in pepper (Fig. 8.25a) suggests that the terminal portion of the flower (gynoecium) is also a branch system, in addition to fact that other portion of flower is a branch-derived system.

According to the appendicular theory, a carpel is a leaf bearing ovules along its margins. If this is correct, the vascular bundles supplying the ovules should be collateral as in foliage leaves. Actually, the vascular bundles supplying the ovules are usually amphicribral (Guo et al. 2013; Liu et al. 2014; Zhang et al. 2017), casting doubt over the validity of the appendicular theory. In addition, anatomy of magnoliaceous flower indicates that the vascular bundles supplying sepals, petals, stamens and ovules are derived from the bundles in the cortex, not stellar bundles, quite different from those supplying foliage leaves, implying that at least the ovules are not equivalent to leaves or parts of typical leaves.

Taking all together, the author thinks that since ovules, ovary, and gynoecium were originally branch-derived organs, a flower should be taken as a poly-order reproductive branch system.

8.9 Favoring Evidence

The above hypothesis is in agreement with various evidence of extant and fossil plants. Although the evidence is not exhaustive and further testing is still needed before wide acceptance, it seems that the following evidence at least can help to focus attention from botanists onto the points that can be used to test the validity of the hypothesis.

8.9.1 Extant Plants

Anatomy Amphicribral and collateral bundles are two easily distinguishable types. The former is frequently seen in small branches and occurs among the branches of the early land plants. While the latter is much derived and is, according to the theory of megaphyll origination, a result of flattening of former shoot system. The presence of amphicribral organization in bundles supplying ovules in various angiospermous taxa (Worsdell 1898; Schmid 1980; Guo et al. 2013; Liu et al. 2014) indicates that ovules, as megasporangia retained on mother plants, are borne on shoot terminals, not on leaf margins. The ovules and ovarian wall (carpel wall) are supplied by bundles of a different organization, implying two different provenances for these two parts in gynoecium. This information assemblage makes a simple foliar nature and single origin of so-called carpel impractical in botanical studies.

Morphology It is true that a carpel appears unitary in morphology. But this appearance-based unitary carpel inference cannot stand examining. It is well-known that, at least in many taxa including *Amborella*, *Adonis*, *Magnolia*, *Illicium*, and *Gyrostemon*, there are two primordia, one for placenta and one for carpel wall, in the early development of carpels. The unitary integral carpel morphology is a result of coalescence and connation, rather than a reflection of its essence (Foster and Gifford 1974; Herr 1995; Hufford 1996; Buzgo et al. 2004; Liu et al. 2014).

So-called leaf-like appearance of so-called “megasporophyll” in *Cycas* is a result of compaction rather than genetic controlling. The so-called megasporophyll may well be a branch bearing ovules on its lateral and adaxial (Wang and Luo 2013).

Function Genes As molecular biology flourishes, more and more is understood about the molecular mechanism and networks behind the morphology and development of carpels. The reciprocally exclusive expression of some genes, such as STK, REV, and YABBY etc, in placenta and ovarian wall in various model plants including *Arabidopsis*, *Oryza*, and *Petunia* demonstrates clearly that placenta and its bearing ovules are controlled by gene sets that are quite different from those for carpel walls (Rounsley et al. 1995; Roe et al. 1997; Skinner et al. 2004; Mathews and Kramer 2012).

8.9.2 Fossil Plants

Sporangia have a history much longer than that of leaves (Taylor et al. 2009; Hao and Xue 2013b). Palaeobotanical practice in the past centuries has proven that the early land plants have no leaves and their sporangia are borne on the terminals of branches. Leaves, at least megaphylls, are derived through flattening and webbing of former branch systems (Hao and Xue 2013a). This fact makes sporangium borne on leaf margin a much derived, not plesiomorphic, status in plant evolution. Ovules as megasporangia retained on the mother plants are logically borne on branch terminals, not leaves (Fig. 8.34).

The initial development of pinnae frequently shows intermediate or chimeric combination of characters. For example, Shougangia bella (Wang et al. 2015; Fig. 8.35) has both basal pinnae and a distal cluster of sporangia in a single leaf. This case cannot be simply interpreted as sporangia borne on foliar structure, but rather some proximal portion of the lateral appendage has sterilized and flattened into pinnae, a rather primitive initial stage of pinnae development. This interpretation is in line with independent research on the origin of fern pinnae based on Chinese fossil material (Li and Hsü 1987).

Shoots only have amphicribral, not collateral, bundles in the early land plants. The occurrence of collateral bundles is closely correlated with that of megaphylls and probably a character restricted to megaphylls. The rare occurrence of

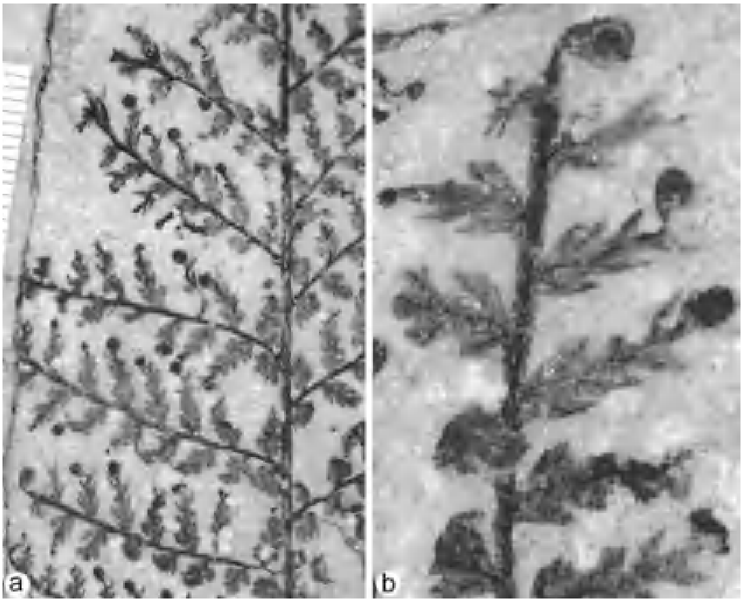

Fig. 8.34 A Palaeozoic Sphenopteris with possible seed/ovule/megasporangium on the terminal of the branched. Although appearing on a leaf, the seed-like structures are actually borne on branches. Courtesy of Dr. Jun Wang

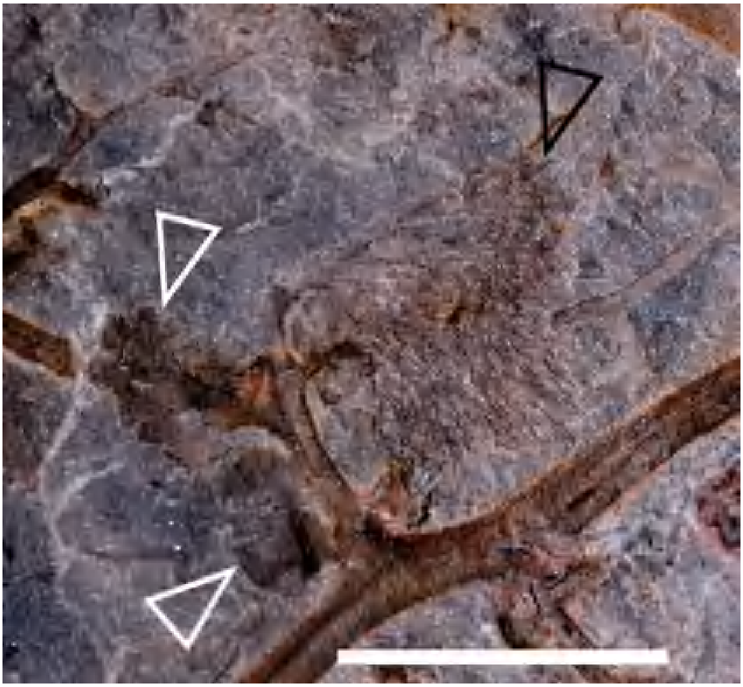

Fig. 8.35 A lateral appendage of *Shougangia bella* showing proximal pinnae (white arrows) and distal cluster of sporangia (black arrow). Courtesy Dr. Deming Wang

amphicribral bundles in leaves of ferns is a sign of lower level pre-foliage evolution and is almost completely absent in the seed plants.

Re-examining the specimen of *Primocycas* from the Permian of China indicates that at least some of the ovules are borne on the adaxial of the so-called "megasporophylls" (Fig. 8.13d), suggestive of a three dimensional configuration rather than an assumed two dimensional leaf. Combining with above mentioned observation of living *Cycas*, it is clear that the assumed "megasporophyll" is a misnomer in botany, and the ovules in all seed plants are borne on branches (metamorphosed into leaf-like or not).

8.10 Angiosperm Prototype and Its Relationship to Other Seed Plants

The bract-scale complex theory advanced by Florin (1939, 1951, 1954) has been used to interpret Cordaitales and the derivation of Coniferales from Cordaitales (Florin 1939, 1954; Schweitzer 1963; Rothwell 1982, 1993; Wang and Tian 1993; Wang 1997). This runs into trouble when interpreting the female cone of

Podocarpaceae (Tomlinson et al. 1991; Tomlinson 1992; Tomlinson and Takaso 2002; Mill et al. 2001) and Taxaceae (Wilson 1953; Florin 1954), 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” of 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 although their spatial relationship is unexpected. In addition, work on a coniferous fossil female cone of Stachyotaxus (Fagerlind 1946; Arndt 2002; Axsmith et al. 2004) suggests that the spatial relationship between bract and scale in this taxon may be similar to that in Podocarpaceae. Furthermore, 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 is 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 to one, overgrowing and suppressing the development of the main shoot. In this way, using the bract-scale complex theory can unite all Cordaitales and almost all Coniferales seamlessly (Fig. 8.36; 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 bracteoles on ovular stalks in Cordaitales-like plants. This interpretation parallels that of Coniferales, although different terms are used, and seems to be favored by the study on a fossil of Ephedraceae (Rothwell and Stockey 2013). Thus these three groups can be linked to each other based on a similar organization in their reproductive organs (Fig. 8.36; Table 8.1).

As mentioned above, a flower in angiosperms may be taken as a poly-order reproductive branch system or its derivative. If a flower is correlated to a reproductive shoot in Cordaitales-like plants, it is not hard to infer that the Cordaitales, Angiospermae, Ginkgoales, 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 groups Pinaceae and Gnetales together (Chaw et al. 1997, 2000; Bowe et al. 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 the

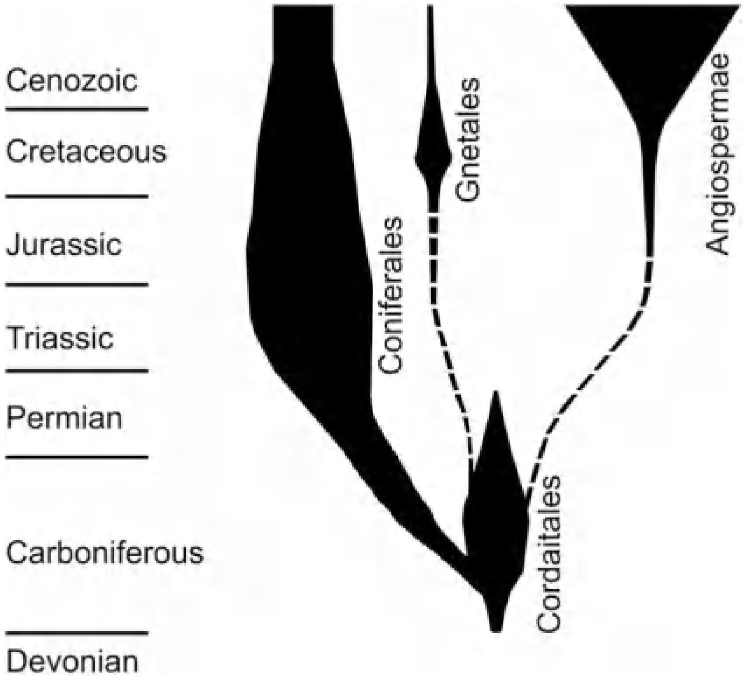

Fig. 8.36 Possible relationships among Cordaitales, Coniferales, Gnetales, and Angiospermae

new theory presented here, there are at least 8 different ways to constitute a gynoecium or "carpel", and Caryophyllales should be among the most primitive angiosperm groups. This is supported by the presence of crassinucellar instead of tenuinucellar ovules, diploid perisperm instead of triploid endosperm, hollow style, poorly defined stigma, intergradation among leaves, bracts, sepals, and petals, highly diversified wood anatomy, small vessel diameter, rayless xylem, and diverse palynomorphology in Caryophyllales, all of which are signs of primitiveness in angiosperms according to the theories of angiosperm evolution (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 are related to each other. Vuillemin 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) and Doyle (2008) also mentioned the possible homology between angiosperm flowers and bract-bracteole-terminal ovule system in gymnosperms. However, these hypotheses were neither elaborated on nor well-evidenced, at least by fossils. The major difference between the current argument and previous ones lies in stronger support from a Jurassic and Triassic fossils including the aforementioned *Xingxueanthus* (Fig. 8.31c; also see Chap. 6), besides the support from function gene studies, morphology, and anatomy. *Xingxueanthus* provides a crucial support and reinforces the author′s

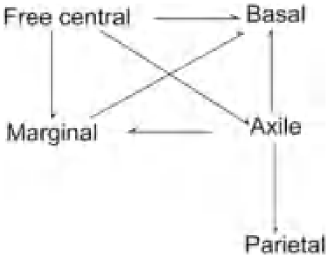

Fig. 8.37 Major evolutionary relationships among various placentations. The arrows mark the directions of the general evolutionary trends, which, however, may be reversed sometimes

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.

Despite increasing favoring evidence, it should be stated clearly that this theory needs more data to test its effectiveness and applicable scope (Fig. 8.37).

8.11 Merits of the Unifying Theory

8.11.1 Simplicity and Directness

Deriving carpel walls from sterile scales or bracts 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 the forming of ovule-protecting structures in Coniferales, Bennettitales, and Gnetales, (3) the spatial relationship between the bracts and ovule-bearing secondary shoot in Cordaitales requires little transformation or assumptions to give rise to carpel wall and placenta in angiosperms.

8.11.2 Support from Various Fields

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

8.11.3 Difficulties Negotiated

8.11.3.1 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 and thus makes the latter possibility close to nil. Now it appears that the derivation of angiosperm gynoecia from reproductive organs of Cordaitales, Coniferales, Gnetales, Bennettitales, or their derivatives is more plausible.

8.11.3.2 Derivation of Outer Integument

The outer integument is another bottleneck in previous studies on the origin of angiosperms. Efforts have been made to show that it was derived from the cupule in Glossopteridales or Caytoniales (Retallack and Dilcher 1981b; Doyle 1978, 2008). Not infrequently more than two integuments have been seen in angiosperms (Eames 1961). If the outer integument was taken as derived from a cupule, then provenance of these extra integuments, not mention carpel wall, constitutes a new road block. There are already outer-integument-like structures outside the integument of *Cordaianthus duquesnensis* (Figs. 8.18c, 8.31a) that can give rise to outer integument in angiosperms. In addition, prophylls 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).

8.11.3.3 Clear Definitions of Carpel Wall and Placenta

The classic definition of a carpel is hard to apply at least in Phytolaccaceae, Basellaceae, Gyrostemonaceae, Cactaceae, Primulaceae, and probably other families. The forming of carpels even in Illiciaceae, Magnoliaceae, Ranunculaceae, and Amborellaceae is not consistent with the pattern assumed in the classic theory. These persisting headache problems vaporize when the new theory is applied. For example, Boke (1964) has experienced difficulty telling which ovule belonged to which carpel in Cactaceae, because some 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 (placenta) and carpel walls because these two are independent parts in flowers and may have any spatial combination. In addition, using the classic definition of carpels, Decraene et al. (1997) separated 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, namely, carpel does not bear ovules, the above separation between adaxial and abaxial parts of a carpel becomes superfluous and unnecessary.

8.11.3.4 Diversity of Gynoecia vs. Multiple Candidates, Pathways, and Combinations

Angiosperms are greatly diversified and their diversity is at least partially attributed to their great diversity in gynoecium. As seen in previous sections, the diversity of angiosperm gynoecia can be characterized by the way their ovules get encloses, the nature of parts involving in ovule-enclosing, the number of these parts, spatial relationship among these parts and their position relative to the floral axis, the morphology of the floral axis, etc. Variation in either of these features may give rise to a new type of gynoecium. Among these features, floral axis morphology is rarely addressed previously, as other features have been well and easily recognized. I will spend a little more space on this feature.

Floral axis, as a subset of typical axis, is usually an elongated protruding structure. This configuration is most frequently seen in many groups including angiosperms. Axis morphology other than this typical configuration occurs in angiosperm flowers. Due to the function of ovule-protection or others, the shoot apex development pattern alters by earlier initiation of subapical lateral primordial and arresting of apical meristem, giving rise to a concave or invaginated configuration for the shoot apex. Such invaginated floral axis is clearly seen in those taxa with inferior ovary and hypanthium (e.g. Cactaceae, Cucurbitaceae, Myrtaceae, Saxifragales) and the Moraceae, in which the flowers are protected by the enlarged invaginated shoot apex. So far invaginated floral axis is only seen in angiosperms, and it may be taken as character helpful to pin down an angiospermous affinity for a plant in future studies.

As discussed in Sect. 8.7, there are at least eight different ways of ovule-enclosing in angiosperms, and the parts involved in the enclosing range from integument, foliar parts to branches. Such a diversity of parts involved in and their spatial combination contribute to the great diversity of angiosperm gynoecium. The great diversity of angiosperm gynoecium implies multiple derivations of angiosperm gynoecia from various ancestors, and challenges the formerly assumed single provenance of angiosperm carpels, for example, from a conduplicate carpel with marginal placentation as in Magnoliaceae. Although the latter idea appeared to be supported by some evidence including *Archaefructus* (Sun et al. 1998, 2002), this support vaporized when more detailed studies on better preserved specimen (Ji et al. 2004) and more materials (including the holotype of *Archaefructus liaoningensis*) (Wang and Zheng 2012) revealed that the ovules in *Archaefructus* are actually inserted on the dorsal vein of the carpel wall. Actually, recently discovered *Nothodichocarpum* from the Early Cretaceous Yixian Formation reinforces that ovules inserted on the dorsal vein (Han et al. 2017) is a rather common phenomenon among early angiosperms in the Formation. Also the various types of gynoecia in the fossil angiosperms of the Yixian Formation (see Chap. 5) suggest that (1) these gynoecia cannot be the most ancestral ones because the differences among them are too great, and (2) a common ancestor, if existing, should be much earlier than the Early Cretaceous.

The evolutionary history of reproductive organs in land plants may be briefed as a history and fate of sporangia in land plants. Assuming so, the homology of angiosperm gynoecia becomes much easier to understand and appreciate. Sporangia and branches are the elementary parts of land plants. Leaves are a derived product of metamorphosis of former fertile branches. The occurrence of leaves and their spatial combination with branches in space provides more alternatives for reproductive as well as vegetative organs possible. Those fertile-remaining sporangia may shift in space, diversify in morphology and function, and combine and fuse with adjacent branches and leaves to give rise new morphology of reproductive organs for plants. As discussed in above, spatial position of sporangia relative to the adjacent sterile parts define the gynoecium in angiosperms. Technically, the ovules (megasporangia, here we focus on female ones only) may be shifted, fused, and thus positioned on the adaxial, margin, abaxial side of a foliar structure. The variations in number of sterile parts involved makes more varieties possible. It appears that tracing the varieties of such combinations and their history will be the focus of study on evolution of reproductive organs in land plants in the coming decades.

For gymnosperms, the story is similar. Besides angiosperms, various groups of gymnosperms including Caytoniales, Petrielleales, Leptostrobus, Umkomasia, Glossopteridales, Gnetopsis, Bennettitales, Pinaceae, Taxaceae, and Cupressaceae (name a few of many) of various ages and have demonstrated different extent of ovule/seed-protection. Such a protection for ovules and seeds seems to be a common choice for plants of various groups. Better protection means greater chance of genes being passing down to next generation, namely, victory in survival struggle. Thus formerly angiosperms-centered thinking that only angiosperms has the tendency of angiospermy appears over simpler. It is very likely that different plant groups share the same tendency to protect their ovules/seeds. The differences among different groups may lie in the detailed configuration of ovule-protecting structure, precursor of the parts involved in the formation, and time at which the enclosure is completed. Considering all these, the possibility that some of these formerly gymnosperms may reach the status of angio-ovuly cannot be excluded with confidence. Namely, there may be multiple ways to reach angio-ovuly, a status formerly thought restricted to angiosperms. This situation requires extra attention from future botanists to analyze configuration, morphology and anatomy of the gynoecia in angiosperms and female parts in gymnosperms to figure out a network of relationship among them, and give up the idea to find a single bridge between gymnosperms and angiosperms.

8.11.4 Wide Applicable Range

Formerly, the evolution theories are either applied in angiosperms or gymnosperms, not both. Apparently, the Unifying Theory is applicable in a scope beyond seed plants. This wide applicability makes it more meaningful to plant systematics because, for the first time, the gap between angiosperms, gymnosperms, and ferns becomes so narrow (Fig. 8.38). Furthermore, taking ovules in angiosperms as specialized megasporangia retained on mother plants and enclosed in layers of tissues makes the homology and comparison applicable not only in seed plants but also in all land plants.

8.11.5 Settling Controversies

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 (Sun et al. 1998, 2001, 2002; Friis et al. 2003) meaningless and unnecessary. In the meantime, the controversy between the traditional axial and appendicular schools can be settled: each of them is right in the part (placenta or carpel wall) and aspect which it emphasizes, but wrong when all information is taken into consideration.

8.11.6 Goal to Reach

Taylor (1991) once set a goal for research on origin of angiosperms, namely, correlation between carpel in angiosperms and axillary branch in gymnosperms. Now it seems that such correlation can be established among various plant groups, if the discussion presented above is correct. This can bridge the great gap between gymnosperms and angiosperms, reaching a goal for many botanists have been aiming at in the past century. It should be noted that axillary branching is restricted to a subset of seed plants. This means that establishing this correlation cannot resolve the relationship among all seed plants, not mention all land plants. As discussed above, mapping the fate and history of sporangia and branches among all land plants seems to be the only way to understand the relationship among land plants.

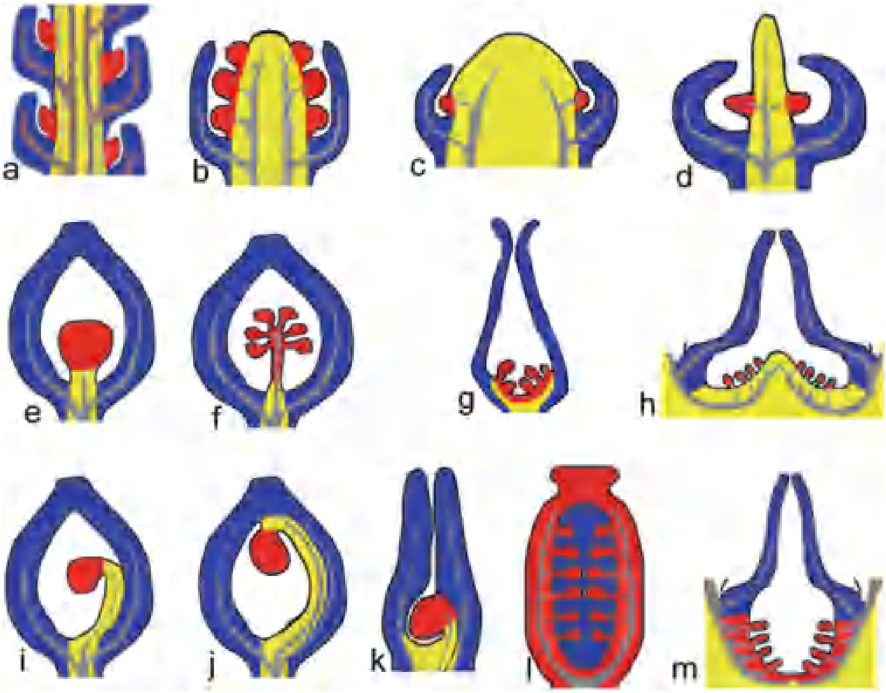

Fig. 8.38 Different structures of various gynoecia in angiosperms. Blue for carpel wall; red for placenta and ovule; yellow for floral axis. Note the variation in spatial relationship among the carpel wall, placenta, ovule, and floral axis. (a) Helically arranged carpels along the floral axis. Note the carpel walls and placentae in their axils, as in Magnoliaceae and Ranunculaceae. (b) Ovules on the lateral of the floral axis enclosed by carpel walls, as in Centrospermae. (c) Ovules arranged in whorls on the lateral of the floral axis enclosed by the carpel walls, as in Gyrostemonaceae. (d) Ovules arranged in whorls on the lateral of the floral axis each enclosed by a carpel wall, as in Illiciaceae. (e) An ovule situated on the bottom of an ovary, as in Basellaceae. (f) A cluster of ovules arranged on the floral axis, enclosed by the carpel walls, as in Centrospermae. (g) Longitudinal section showing ovules inserted on the concave floral axis and enclosed by the carpel walls, as in Salix. (h, m) Ovules arranged on the lateral of the floral axis (protruding or invaginated) enclosed by the carpel walls from the above, as in Cactaceae. (i–k) A single ovule on an elongated funiculus that fuses with one side of the ovarian wall, as in Tapisciaceae and Urticales. (l) Multiple ovules on forked placentae borne on the floral apex enclosed by the carpel wall in the foreground and background, as in Brassicaceae. Reproduced from Wang et al. (2015)

8.12 General Regularities in Seed Plant Evolution

8.12.1 Enclosure and Aggregation

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 recruiting and aggregating additional parts to form a container surrounding the ovules/placentae (the so-called angio-ovuly). In some angiosperms this enclosing is extended 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), Moraceae, and Solanaceae (He and Saedler 2005; Wilf et al. 2017).

8.12.2 Differentiation, Overgrowth and Reduction

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

8.12.3 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 seen in the formation of integument (concentrating nutrition to the ovule) and endosperm (abortion of extra embryo to provide nutrition to viable embryo).

8.12.4 Connation and Adnation

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 forms. The development of leaf, integument, cupule, carpel, perianth, and marginal placentation all require connation or adnation of some formerly separated parts.

8.12.5 Diverted Development

The homogeneity of organization in early land plants means diverted development is necessary to form new plant organs that perform new functions. A similar idea has been advanced by Thompson (1934) and Crane and Kenrick (1997). This is seen in the derivation of leaves from former branches, derivation of vegetative from former fertile parts, occurrence of 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 development through diverted development (Friedman 1994; Raghavan 2005).

8.12.6 Better Conditioning the Growth of Offsprings

Throughout the history, additional protection and extended nutritional bond with mother plants make it possible for the plants to internalize the environment, control the developmental environment, and ensure the nutrition supply for next generation. Such conditioning enhances the probability that the genes of plants of question to be passed on and retain in the gene pool.

8.13 Problems Unsolved

8.13.1 From Unisexual to Bisexual

The cones in gymnosperms are usually unisexual. The reproductive organs in angiosperms are usually bisexual. Therefore how to derive bisexual flowers from the unisexual reproductive cones is a challenge for all evolutionary botanists. However, some bisexual cones in conifers may shed some light on this question. Rudall et al. (2011) reported bisexual cones of *Pinus* and *Tsuga*, a very interesting phenomenon, helpful for explaining the former difference between compound female cones and simple male cones in Coniferales.

Encephalartos is recently found bearing not only bisexual cones but also bisexual “sporophylls” (Rousseau et al. 2015). Such ectopic pollen sacs or ovules in the lateral appendages in seed plants implies that the gender of the sporangia is not fixed and may be transmutated by some gene variations or factors unknown yet. Although such phenomenon appears weird or absurd, it may appear less so when *Dorsalistachya* (Wang et al. 2017) is taken into consideration, in which both microsporangia and megasporangia are hang on the abaxial of the foliar part. The proximal occurrence of both micro- and mega-sporangia in these two taxa makes the occurrence of male and female sporangia in the same unit less challenging.

Differentiation between male and female lateral appendages must be controlled by inherent gene network. Understanding such gene network in the future may help to explain the derivation of bisexual flowers from unisexual cones.

8.13.2 Boundary Between Gymnosperms and Angiospermae

Caytonia is a fossil plant that initially was placed in angiosperms and its gymnospermous pollination was not revealed until decades later. 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 margins and adaxial of the surrounding sterile scales inserted on the subapical of the secondary shoots in Cordaitales, structures similar to cactaceous gynoecium may come into being. *Pseudoephedra* from the Early Cretaceous Yixian Formation is another perplexing fossil plant (see Chap. 7), which is hard to place in the phylogenetic tree due to its resemblance to both Ephedraceae and some angiosperms. These hard-to-deal fossil plants make drawing a boundary between gymnosperms and angiosperms, especially in the fossil record, a new challenge for botanists. Although the present author has proposed a clear-appearing line between gymnosperms and angiosperms, it is conceivable that the gap between these two groups may be hard to detect in the fossil world as more and more fossils will gradually reduce this gap.

8.13.3 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 would be 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 unknowns and providing guidance for people facing uncertainties.

The Unifying Theory advanced here satisfies first two criteria, at least appearing so to the author. Increasing evidence favoring this theory has been emerging continuously since the publishing of the first edition of this book, making it a very promising candidate for future botanical theory.

8.14 Implications for Seed Plant Phylogeny

The phylogeny of seed plants relies on interpretation of homology of plant (especially reproductive) organs, even in this cladistic age. To test the effect of the new theory in this book, a preliminary cladistic analysis is performed using heuristic search in the Paup software (Swofford 2002). Four equally parsimonious trees of 206 steps are obtained. The data matrix is from Rothwell and Serbet (1994), and only the data about angiosperms are altered according to the theory advanced here: Caryophyllales is taken as the representative of angiosperms, in which the placenta is interpreted as an independent organ rather than an accessory of a folair part.

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 0.5146, homoplasy index (HI) is 0.4854, CI excluding uninformative characters is 0.5122, HI excluding uninformative characters is 0.4878, Retention index (RI) is 0.6951, and Rescaled consistency index (RC) is 0.3577. The strict consensus tree of these four trees is shown in Fig. 8.39. 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. 8.39).

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. 8.36). Although different from the representative tree given by Rothwell and Serbet (1994), it is in agreement with one of the five phylogenetic scenarios obtained by Rothwell and Serbet (1994, Fig. 2a). 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 based on molecular data (Chaw et al. 1997, 2000; Bowe et al. 2000; Frohlich 2003; Qiu et al. 2007). It is noteworthy that the result shown in Fig. 8.39 is a strict consensus tree of all four most parsimonious trees rather than simply one of several most parsimonious trees. It implies that the new information from the theory advanced 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.

8.15 Evolutionary Roadmap of Plants

After the above discussion, taking ovules as specialized sporangia, the evolutionary relationship among land plants, in term of reproductive organs, may be presented as in Fig. 8.40

8.16 Disadvantages of the Classical Theories

Without alternatives to choose, most botanists tend to accept the classic theory of angiosperm evolution unknowing its disadvantage and thus further misled by such a theory. Many problems were introduced by accepting such a theory. Following are some, not all, of the examples in which botanists, including leading ones, were misled to give wrong interpretation of their fossils.

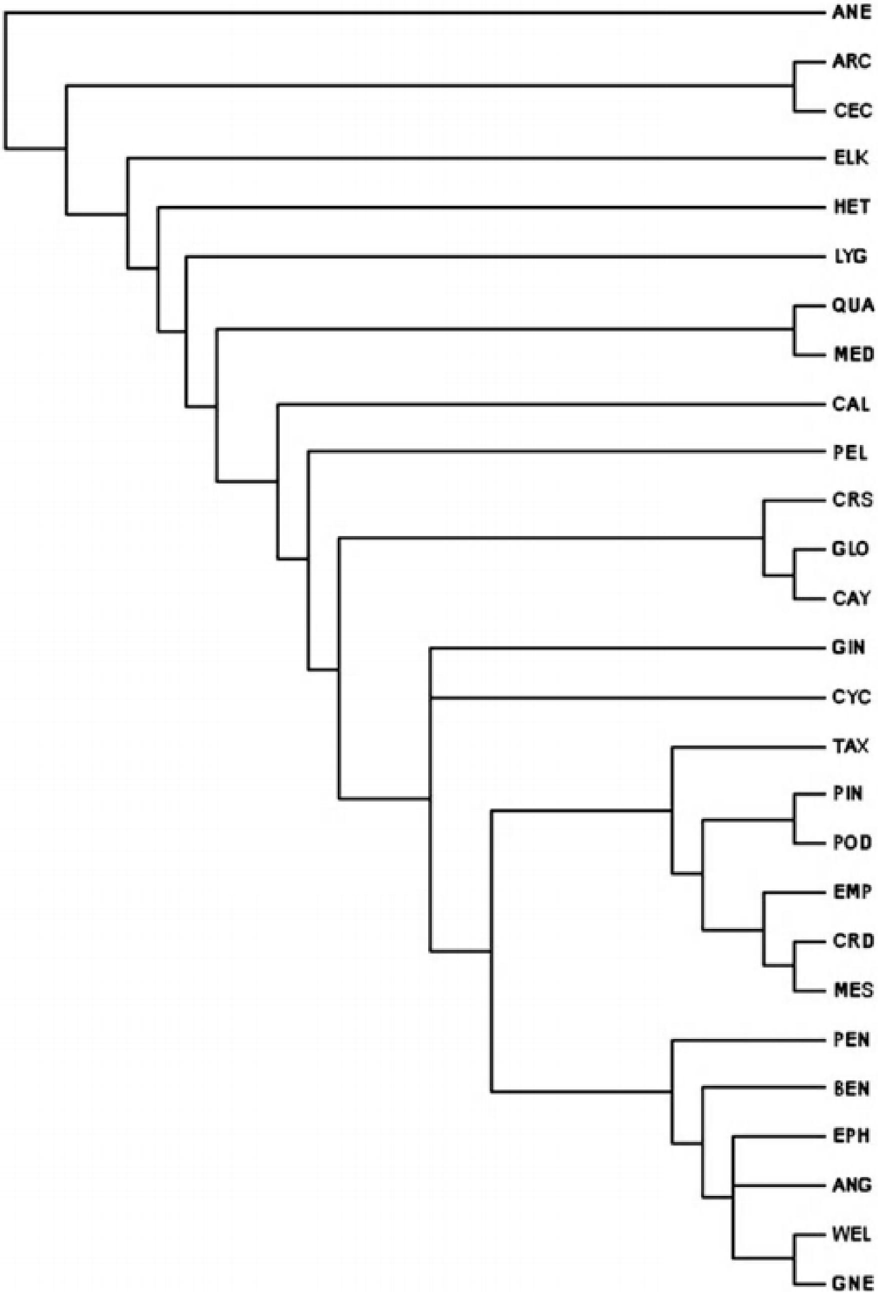

Fig. 8.39 Possible relationship among seed plants, based on morphological matrix modified from Rothwell and Serbet (1994). ANE Aneurophytales, ARC Archaeopteriales, CEC Cecropsidales, ELK Elkinsiales, HET Heterangium, LYG Lyginopteris, CAL Callistophyton, QUA Quaestora, MED Medullosa, GIN Ginkgoales, EMP Emporia, PIN Pinaceae, POD Podocarpaceae,

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According to the mainstream idea about angiosperm evolution, the ancestral angiosperms are supposed to have conduplicate carpels with marginal placentation helically arranged along the floral axis, with bitegmic anatropous ovules, just like in *Magnolia*. Such an image of ancestral angiosperm has been taught in classrooms for decades and is well-entrenched in the mind of many botanists.

1. Marginal placentation Sun et al. (1998, 2002) documented their discoveries of *Archaefructus* on Science. They interpreted the female lateral appendages as conduplicate carpels with marginal placentation. This interpretation was rational and correct if the classic theory is taken as a criterion. However, later more careful examinations by Ji et al. (2004) and Wang and Zheng (2012) found that the seeds in the fruits are actually inserted along the dorsal veins, not ventral veins. Therefore there is no marginal placentation in *Archaefructus*.
2. Helically arranged carpels In their documentations of *Archaefructus* Sun et al. (1998, 2002) interpreted the carpels as helically arranged. This interpretation sounded rational and correct if the classic theory is taken as a criterion. However, as early as 1998 it was obvious that the carpels were no helically arranged, as shown in the Science cover picture. At least some of the carpels appeared oppositely arranged. Later observation of the holotype of *Archaefructus liaoningensis* by Wang and Zheng (2012) found that the carpels are arranged in whorls, or at least oppositely.
3. Two integuments *Monetianthus* is a fossil that has been documented twice on Nature and International Journal of Plant Sciences (Friis et al. 2001, 2009). In their 2009 paper, the ovules of *Monetianthus* were interpreted as with two integuments. They tried to support their interpretation of two integuments with a longitudinal virtual section shown in their Fig. 5f and they stated clearly "two integuments" in their figure caption (Friis et al. 2009). However, careful examining the figure shows no trace of two integuments. Rather the figure shows clearly that there is only one layer of integument in the ovule.
4. Anatropous ovules *Sinocarpus decussatus* is a fossil repeatedly studied by the same authors (Leng and Friis 2003, 2006). The ovules were interpreted as anatropous (Leng and Friis 2006), again a feature frequently seen in so-called basal angiosperms and expected for early angiosperms. My examining of their figures failed to find any trace of anatropous (see Chap. 5). At least the proximal arrangement of micropyle and funiculus expected for anatropous ovule is not documented by any figure in their publications.
5. Free carpels Free carpels were thought ancestral among angiosperms. Therefore people tend to interpret carpels in early angiosperms as free, even though the fact is obviously not so. For example, the carpels in *Kajanthus* were called "free"

Fig. 8.39 (continued) TAX Taxaceae, CRD *Cordaixylon*, MES *Mesoxylon*, CYC Cycadales, CRS Corystosperms, PEL Peltasperms, GLO *Glossopteris*, CAY Caytoniales, BEN Bennettitales, PEN Pentoxylales, EPH *Ephedra*, WEL *Welwitschia*, GNE *Gnetum*, ANG Angiosperms (Caryophyllales)

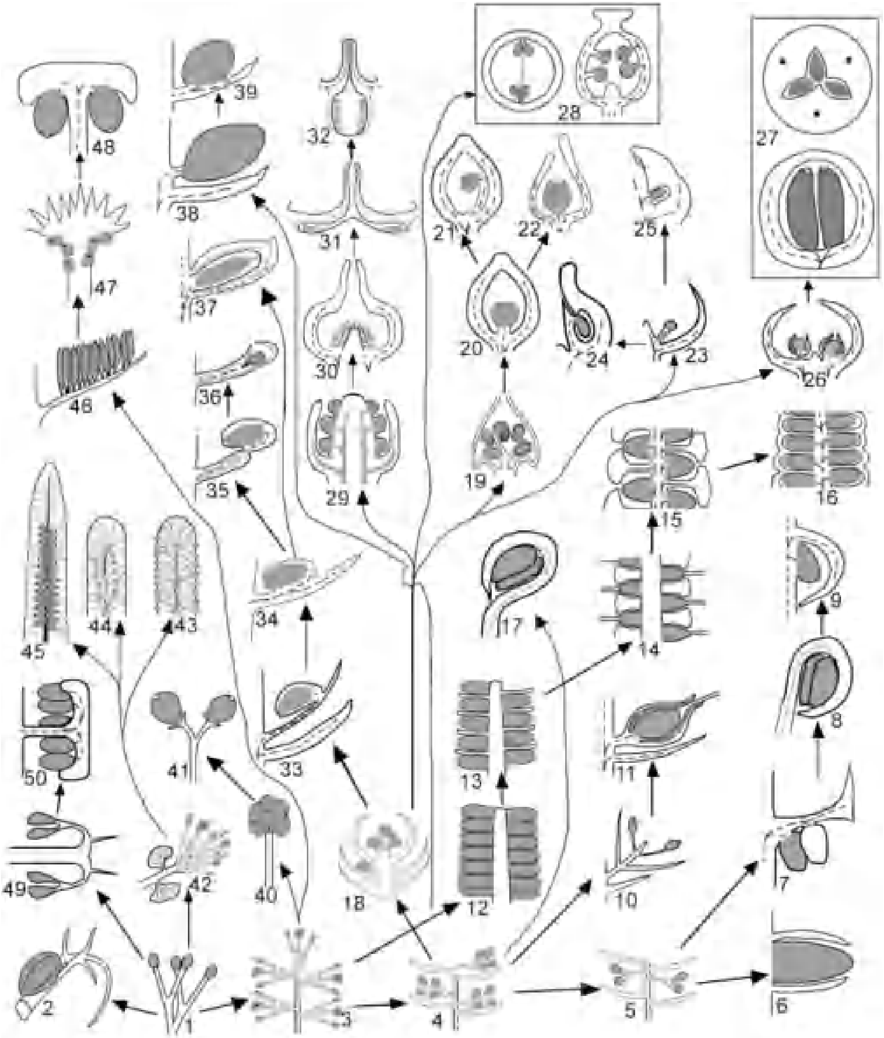

Fig. 8.40 Arrangement of sporangia (including ovules) in various taxa of land plants. The above arrows represent evolutionary pathway, but not necessarily phylogenetic relationship among the exemplifying taxa. 1. Rhynia. 2. Leclercqia. 3. Assumed intermediate status 1. 4. Assumed intermediate status 2. 5. Assumed intermediate status 3. 6. Dibracophyton. 7.Dorsalistachya, male sporangiophore of Coniferales. 8. Petriellaea. 9. Yuhania. 10. Assumed ancestor of Gnetales. 11. Gnetales. 12. Carnoconites. 13. Vojnovskyaceae. 14. Bennettitales. 15. Foxeoidea. 16. Zhangwuia. 17. Caytonia. 18. Cordaites. 19. Amarathaceae. 20. Piperaceae. 21. Urticales. 22. Basellaceae. 23. Assumed intermediate status. 24. Amborellaceae. 25. Phytolaccaceae. 26. Platycladus. 27. Juniperus macrocarpa. 28. Brassicaceae. 29. Caryophyllaceae. 30. Portulaccaceae. 31, 32. Cactaceae. 33. Pseudovoltzia. 34. Stachytaxus. 35. Podocarpus. 36. Parapodocarpus. 37. Nubilora. 38, 39. Selaginellaceae. 40. Yimaia. 41. Ginkgo. 42. Shougangia. 43, 44. Ferns. 45. Phasmatocycas. 46. Archaeopteris. 47. Cycas. 48. Zamia. 49. Eviostachya. 50. Sphenophyllaceae , male sporangiophore of Coniferales

although they are fused each other from the bottom to the apex. Probably the authors were attracted to do so because the extant taxon to which they wanted to relate their fossil has “free” (rather than fused) carpels.

In all above cases, the misinterpretations are rational and “should-be” according to the classic theory of angiosperm evolution or the need of the conclusion preferred by the authors. Over-trusting such theory appears to be the only culprit behind these wrong interpretations because the observations by these authors did not support their claims. Apparently, getting rid of such misleading classical theory is necessary for a healthy development of botany as a science.

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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, progress 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 yet. Based on various evidence, some scholars believe that angiosperms originated in the Carboniferous or Permian (Wieland 1926; Eames 1961; Long 1977a, b), some in Triassic and Jurassic (Darrah 1960; Cornet 1986, 1989a, b, 1993; Hochuli and Feist-Burkhardt 2004, 2013; Lu and Tang 2005), still others 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).

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), 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 (Rydin et al. 2004, 2006a, b; Wang and Zheng 2010). Apparently, fossil plants are the final data source on age.

X. Wang, *The Dawn Angiosperms*, Springer Geology,
DOI 10.1007/978-3-319-58325-9_9

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 pursuit for an acceptable definition of fossil angiosperms.

The angiosperms documented in this book satisfy the criterion for angiosperms 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 extant angiosperms and many, if not all, can be related to living angiosperms.
3. Late stage: the Post-Cretaceous

   Angiosperms dominate in this period. They play increasingly 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 leads to many specialized features in both.

9.1.2 Location and Habitat of Early Angiosperms

There is no consensus on the location of angiosperm origin, either. 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 fully-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). D. I. Axelrod proposed a tropical origin (Brenner 1976). People who believed in an earlier origin of angiosperms frequently thought that angiosperms originated in remote, bleak highland, the harsh environment (including strong ultraviolet rays) there being 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 (Sun et al. 1998, 2001, 2002; Ji et al. 2004). 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, 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 various angiosperms in the 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 (1993), Wang et al. (2003), and Hilton et al. (2009a, b), are worth future attention.

The mainstream idea about angiosperm evolution thinks that angiosperms are monophyletic and has a single origin. However, Wu et al. (2002), based on their comprehensive analysis, think that angiosperms are polyphyletic and have undergone multiple radiations starting from multiple origins. Considering the occurrence of distinct types of gynoecia in early angiosperms, the author tends to favor the hypothesis advanced by Wu et al.

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 advanced based on various kinds of evidence. Engler and Prantl (1889) claimed that Amentiferae were the most primitive angiosperms. These plants have flowers that are not colorful and usually anemophilous. This idea was refuted by Hutchinson (1926) and Eames (1926). Hutchinson (1926), Eames (1961), and Takhtajan (1969) 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). 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 semiherbaceous 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). This appears to be further supported by the discovery of herbaceous angiosperm (Juraherba bodae) from the Jurassic (Han et al. 2016). However, this hypothesis apparently still needs more data to test, considering the occurrence of woody Schmeissneria in the Early Jurassic.

Considering there may be several separated lineages leading to the angiosperms, searching for a single ancestor for angiosperms appears naïve. Apparently, more fossil evidence is required to elucidate the situation.

9.2 Monophyly or Polyphyly

Angiosperms are thought polyphyletic by many (Wieland 1926; Hutchinson 1926; Hughes 1994; Krassilov 1977). According to Krassilov (1977), 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, for example, sistering all remaining angiosperms (Qiu et al. 1999; Soltis et al. 2004, 2008; Doyle 2006, 2008; Graham and Iles 2009). This is supported by molecular data and some morphological analysis (Doyle 2006, 2008).

The author proposed a new theory predicting angiosperm relatives dated back to the Palaeozoic in Chap. 8. The long gap between the Permian and Early Cretaceous allows for diversification from a single ancestor to many varieties of angiosperms. But it is equally possible that several lineages were approaching angio-ovuly independently. Future fossil evidence will test which is correct.

9.3 Animals and Plants

Insects have a long history of cooperation 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 Craboniferous (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). The occurrence of hairy styles in both of Schmeissneria, Euanthus and Callianthus as well as punctate styles in Chaoyangia, Xingxueanthus and Baicarpus gives mixing information on the role of animal in angiosperm pollination. How much animals have contributed to the success of angiosperms is an open question, as there seem to be 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 dragonfly played in the pollination and dispersal of Schmeissneria, it is conceivable that Schmeissneria lived in an aquatic or semi-aquatic environment.

The spiny fruits of Early Cretaceous Chaoyangia and fleshy fruits in Early Cretaceous Callianthus and Jurassic Juraherba 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 angio-ovuly has appeared much earlier than the ecological dominance of angiosperms. Namely, the key traits of angiosperms arose well before the diversification of the lineage (Feild and Arens 2005). It appears that angiospermy alone cannot account for the success of the angiosperms. It may have been combination of many features including biotic and abiotic factors that have contributed to the success of angiosperms since the Middle Cretaceous. 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, lower carbon costs for shoot, reticulate leaf venation, more efficient light usage, herbaceous 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), plant-bacteria association (Johri and Ambegaokar 1984), short reproductive cycle (Williams 2009), occurrence of endosperm (Friedman 1992), landscape connectivity (Riba et al. 2009), environment influence (Wake 2010), and horizontal gene transfer (Krassilov 1973, 1977), which has been found among more and more organisms (Diao et al. 2006; Richardson and Palmer 2007; Williamson and Vickers 2007; Rumpho et al. 2008; Pace et al. 2008; Sanchez-Puerta et al. 2008). Lack of these features and factors or their combination may explain the subordinate role angiosperms in their early stages.

9.5 The Idiosyncrasy of Angiospermae or a Grade of Evolution?

Among the living plants, angio-ovuly appears to be a feature unique to angiosperms since it is frequently thought that no other living plants demonstrate its existence. According to the “angio-ovuly ¼ angiosperms” concept, those plants documented in the 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 may need a re-orientation, and the existing system of angiosperms will need a revision. However, if these plants were not accepted as angiosperms, then angio-ovuly would be taken as a grade of evolution rather than the idiosyncrasy of Angiospermae. This is possible because, theoretically, some other seed plants may have reached the status of angio-ovuly 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 distinguish the angio-ovuly in such “gymnosperms” and in “true” angiosperms.

9.6 Digging Deeper

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 plants, and neither can reflect the history of plants completely faithfully. Tangible fossils can preserve the morphology and anatomy, but they are susceptible to preservation filtration and may lose labile information. 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 by time (Wake 2010). Thus the information embodied in living plants cannot reflect the original status of their ancestral plants. Therefore it is no wonder that different or even conflicting conclusions may be drawn based on molecular 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 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.

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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.

X. Wang, The Dawn Angiosperms, Springer Geology,
DOI 10.1007/978-3-319-58325-9_10

21. Storied structure (in tracheids and axial parenchyma, phloem) (0) absent, (1) present.
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 (>1/2width 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 (¼type 2 of Endress and Igersheim 2000), (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 (¼drupe), (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 ($<$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
0100100100000010000100--(01)(01)??00?31100?00000010?21001?2????????
0?????000?0(01)0001000000 1??????????????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???????
12110110???0001120000001?----------?0?2101020?0101010?000?10100
Pinus
010001120??01000100000--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-------
2102011010000000010000001?-------------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????
1002000?11100014121010 1?001300000000(01)
000000210020020400000000000
Platanus
101001011111?1000000010(01)01000000001001?0010131110001201(12)
20001202000(01)1110001412100011002311000000010010?112002(01)
00100000100100
Trochodendron
101001011111?100000000?001?0000100030(01)0011001101(01)0010(01)112?
0?1(02)020101111000141211001100 2(23)11000200200000(01)02002102?
40000000001
Amborella
101001011111?100000000?000?0000(12)00120000100010000000(12)
2100000000010000000??0101100101000000002100000010?
1110010000000000?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)0013100011000201010002111100110200002000001(01)12(01)00011002311010200201000(01)01002100?02000000000

Austrobaileya

101001011111?1010000010000?000010022000010000000010000000000000000000000001012100011100011-001000201000021200010300100?00000

Brasenia

101001011111?10100?101?0????????1?0??00111100?21000000111100110201000(12)0-01000120000010001110(01)0000112000??0?021?1???01000100?

Calycanthus

100001011111?10011000112100000120022 0000(01)0000000010001000000000000002000001212100001102301101?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?01002000001012100000002110?0?100(12)0100101100000100000(01)?0000?

Chloranthus

111001011111?101000001000100?000002202000000110?01010??3??????(01)1010(01)0000001?121010110100000(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)00000000000000?

Degeneria

101001011111?10000000110110111100010?000000000100100000011000000000121000000000000021123100 1?000201001021000110320100000000

Eupomatia

101001011111?1000000011011000010001010000000000011010001?2??1?00100001010000121000000210?310111?002010000210000102001 00?00000

Illicium

101001011111?1001000010000000000000001000000(01)00011100000000000000010100000131210001100111100101000200112(12)0021(01)1100000000000

Liriodendron

101001011111?1000000011(01)(01)00111(01)000(01)00?000000001111000010(01)(01)0000000001(02)(01)00000001000000002201(01)00000101000021002(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?1011000010100000001000100?00000100?1110200000000110100(02)000001312100011000010001010101000(01)21000001100000000000

Ceratophyllum

101001000001?1?1?0?1000?????003002-?00-2?012???000020122?0000000010(12)0?1(01)0111?2000?10100?10000001011???0?021??000000001100

Acorus

101001011111?1012001???0????0?2(13)001011112?0000?001010011100011020100000010001200000100121010?2(01)02?010?0100100000002000001010

Gyrocarpus

101001011111?100000001021(01)10??120001?000110(01)002101?202120?0?10021111220110111??0?1??01132110?000000000022001010430000010101

Saururus

101001011111?1010000?11001??0001001011001100030101?100?3????110201011000001022000011002301000110(12)0110?10100(02)(01)00?01000001000

Saruma

101001011111?10100001112?1??002(01)0013100011000201010002111100110200002000001(01)12(01)00011002311010200201000(01)01002100?02000000000

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)00201001000001412(01)01011002311100000(12)0?00(01)(01)(12)2012101000000100000

Sabia

101001011111?1(01)110?00101?00????010??00000000(02)???00200112100120101(01)0(02)000?014221000110001?11002011?(12)11???2?011???0000?20?100

Gnetum

0111010111111000100001(01)2000001?31020?00010000?01111?2???????12110110???00011200010010----------?0?1101022?0101010?000?10100

Welwitschia
0101110201011000000001010000001?-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??????02010?
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 (Wang 1987; Deng et al. 2003; Huang et al. 2006, 2008a, b, c; Huang and Nel 2007a, b, 2008a, b; Petrulevicius et al. 2007; Nel et al. 2007, 2008; Lin and Huang 2008; Lin et al. 2007; Selden et al. 2008; Wang and Zhang 2009a, b; Wang et al. 2009a, b, c; Fang et al. 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. 2004; 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 1987; 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, 2009c; Huang and Lin 2007; Lin et al. 2007; Liu et al. 2007).

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 (Deng et al. 2003; Wang et al. 2004; Ji et al. 2004; Liu et al. 2006a, b, 2007, 2008).

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, Yanliaoia 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 (Zhang and Zheng 1987; Wang et al. 1997, 2007; Deng et al. 2003; Li et al. 2004; Wang and Wang 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 decussates, 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).

10.5 Morphological Matrix for Seed Plant Cladistics

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

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ANC
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ARC
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CEC
11??103?0000?1000000001000020001001 0?????0??00010?000??0??0??????
ELK
11??120?00???0000000010001000100102100?0010000000000????1000??0?
HET
11??120?0000?100000101001 10?010?10220000001000000000?00????10?0??0?
LYG
11?112010000?10100010200110001001022000000100000000000??001000??0?
CAL
11?1130100???101000102001101000210220101120110111 10?00?1?10?0??0?
QUA
11?12?????????100200103?0??0??00???220000020?10??????0????1000??0?
MED
11?1120?0000?10120110300110000001022000000201100100000??011000??0?
GIN
1101103100000111110102405100000?002201000201011101010001110001010
EMP
11?111200000?11100010152510010010022000?22010001110?0?????0?0??1?
PIN
1101132100000111010103525122100200220102321201111101001121000201 1
POD
1101133100000111010103525122120200220102021201111101001121000201 1
TAX
1101132100000111010103205110030000220101001201100101111121000201 1
CRD
11?11331000001110001016131000000000220101120110?1110?00???10?0??0?
MES
11?213310000?111000101615100000000022010112011 00?110?0????10?0??0?
CYC
110?131100000111100103304100000200220100020110110101000111000 10?0
CRS
11?112110000?1?11001020011020202002201120 20?1111110?1????????????
PEL
11???30100?0??????0???0011010002002 2?????2???1110?0?0????????????
GLO
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11?113111000?1?1?00100001102020?0022010?1211?011111?0???????0????
CAY
11?113111010?1????0???00110202020 0220?01??1?0011110?1????????????
BEN
11?113110001?111?0000340?10003011122110200?211110201 1?????0?0??1?
PEN
11?113110000?101101000?021000?000?220102????1111020?0????????????
EPH
1112232100001111110110605000001011221112021211110211101121000001 1
WEL
111223311101111 1?1011360?010001011221111001211110211111120111011 1
GNE
111223111011111110?1060?01000010?1221110021201 1?02?1111120110111
ANG
1111131111101111?00011603020?4001022001?2012?1110211?2?120010001?

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Index

X. Wang, *The Dawn Angiosperms*, Springer Geology,
DOI 10.1007/978-3-319-58325-9