

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.

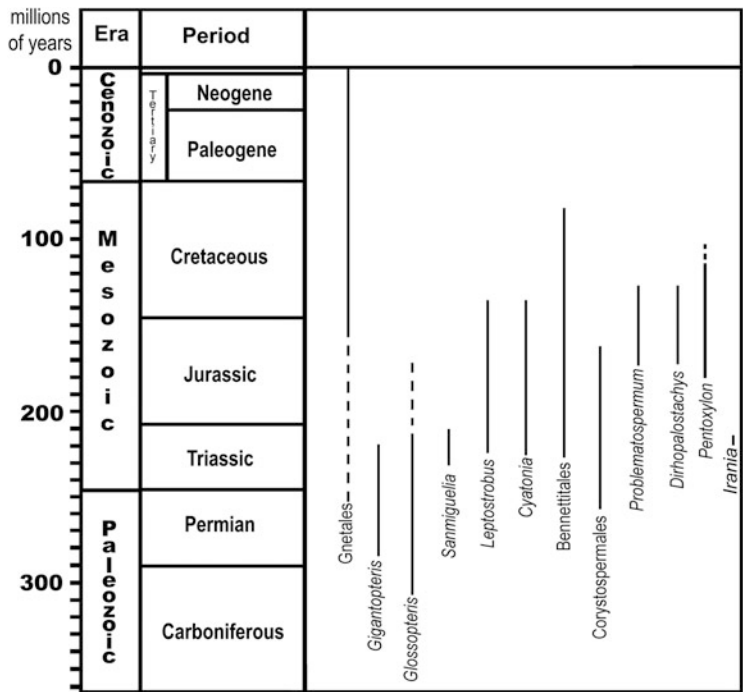


Fig. 2.1 Approximate temporal distribution of the taxa discussed in this chapter. *Dashed lines* indicate uncertainty

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 Bennettiales-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 angiosperms 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 *Pseudoephedra* 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

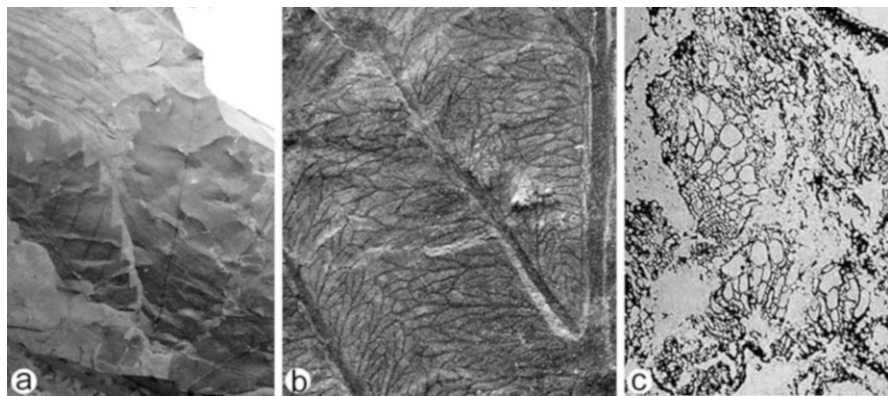


Fig. 2.2 Leaf morphology, venation, and vessel elements of Gigantopterids. (a) Leaf morphology of *Gigantonoclea* (IBCAS). (b) Venation of *Gigantonoclea rosulata* Gu et Zhi (PB4969, NIGPAS). (c) Vessel element of *Vasovineia tianii* Li et Taylor (Courtesy of Dr. Hongqi Li)

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).

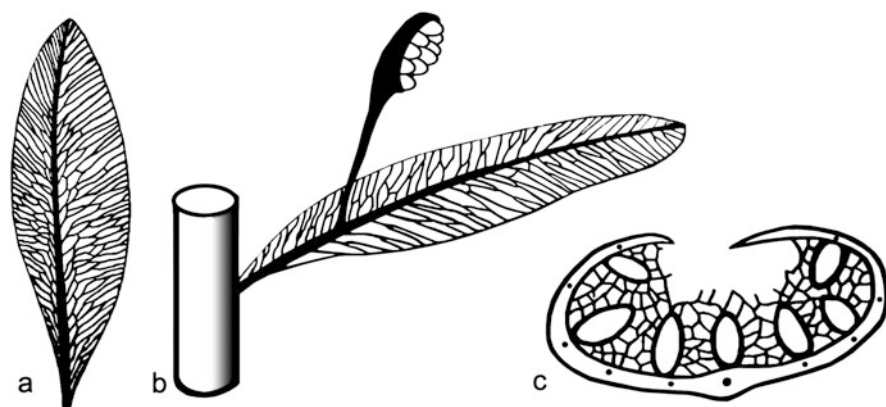


Fig. 2.3 Leaf and reproductive organ of Glossopterids. (a) Leaf. (b) Axis with a megasporophyll. (c) Cross section of cupule showing adaxial arrangement of seeds partially inrolled by the cupule

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. Unitegmatic 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

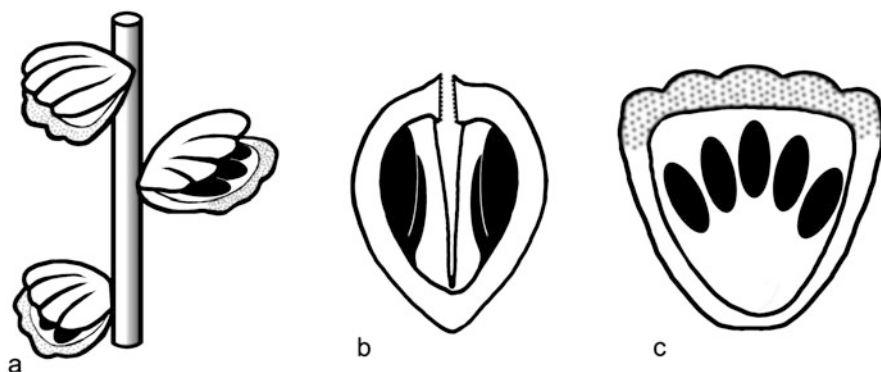


Fig. 2.5 Reproductive organ of Czekanowskiales. (a) *Leptostrobus*, showing capsules attached to an axis. (b) Longitudinal section of capsule showing two identical facing valves forming a capsule. (c) Interior view of a valve of the capsule showing seeds and papillate flange (dotted)

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

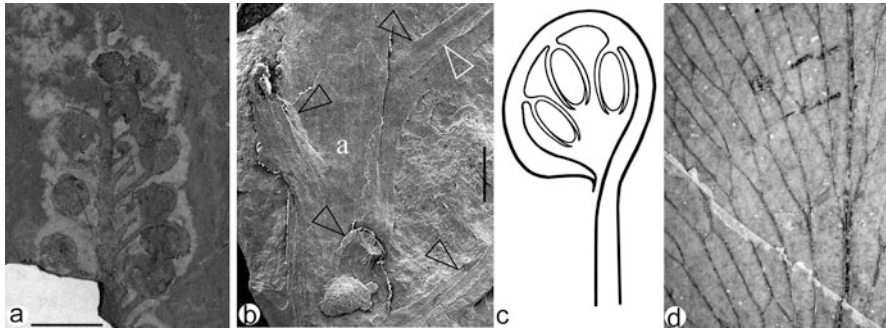


Fig. 2.6 *Paracaytonia* and *Sagenopteris*. (a) General view of the reproductive organ. Note the multiple cupules physically connected to the same axis (GBM1, SFLBG). Bar = 1 cm. (b) Detailed view of the cupules helically arranged around the axis. Note the cupule stalks (black arrows) and the stub of another broken one suggesting a helical arrangement along the axis (a). Bar = 1 mm. (c) Idealized longitudinal section of a caytonian 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 Centrolepidiaceae, 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, Ertmanithecales, 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 Erdtmanithecates (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).

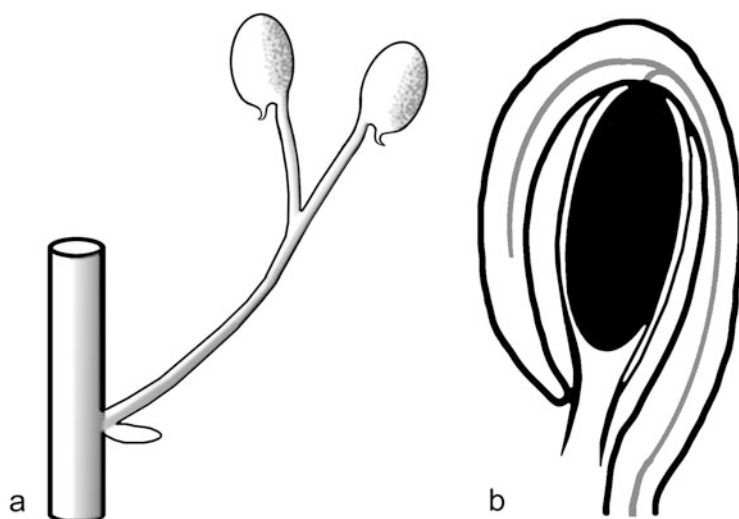


Fig. 2.7 *Umkomasia* and its details. (a) Reconstructed branch bearing a pair of cupules. (b) Longitudinal section showing cupule surrounding a seed with a protruding micropyle. Gray color stands for vascular bundles

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

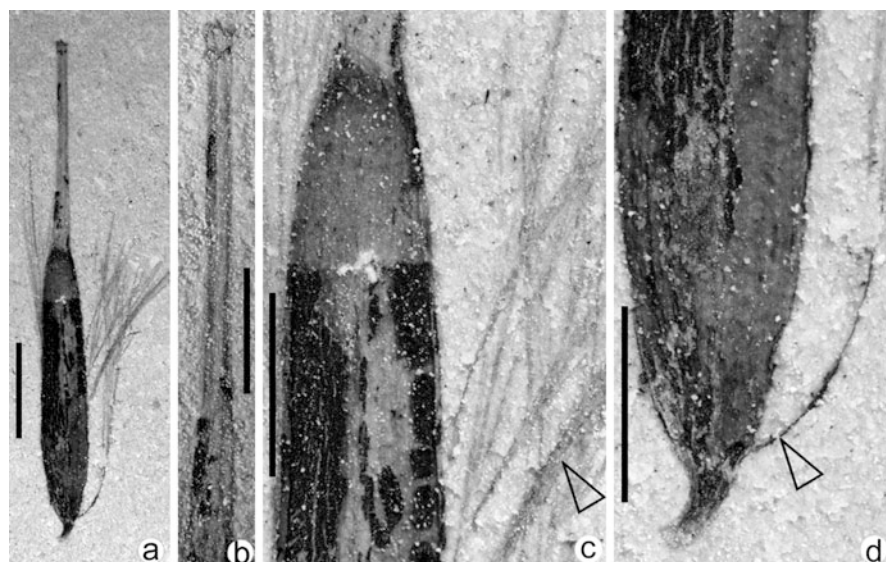


Fig. 2.8 Seeds of *Problematospermum ovale* (PB21392, NIGPAS). (a) Complete seed. Bar = 2 mm. (b) Seed with an apical projection. Bar = 1 mm. (c) Seed with filamentous appendages (arrow). Bar = 1 mm. (d) Seed body with filamentous appendages attached (arrow). Bar = 1 mm

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 *Rufflorinia*. 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,

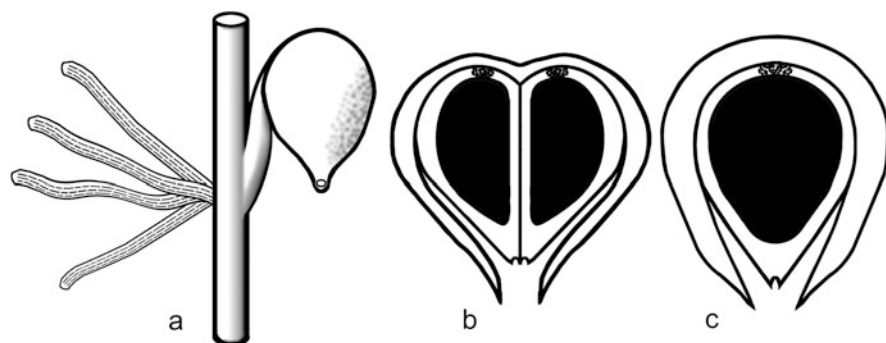


Fig. 2.9 Reconstructed *Ktalenia*. (a) Fertile axis bearing cluster of a bract at *left* and cupule at *right*. (b) Cross section of a cupule containing two ovules. (c) Cross section of a cupule containing one ovule

see Chap. 6), it is hard to take *Ktalenia* as an angiosperm ancestor because the pre-Aptian age of megafossil angiosperms including *Yuhania*, *Chaoyangia*, *Archaeofructus*, *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, unitegmatic 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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