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Cretaceous angiosperm flowers: Innovation and evolution in plant reproduction

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Abstract

Information on the fossil record of angiosperms has expanded dramatically over the past twenty-five years, and in particular the discovery of numerous mesofossil floras with fossil flowers has added a completely new element into the study of angiosperm history. A review of the phylogenetic diversification of angiosperms through the Cretaceous is given based mainly on the extensive record of fossil flowers and other reproductive organs. Several major phases in the Cretaceous angiosperm radiation can be distinguished. These are recognised primarily by structural and functional traits of the flowers and by pollen features, as well as distinct changes in the systematic composition of the floras. ANITA grade angiosperms and Chloranthaceae, as well as other magnoliids, early monocots and early eudicots, differentiated almost simultaneously during the Early Cretaceous. There is also strong evidence for extensive diversification of core eudicots during the Late Cretaceous. In addition to patterns of phylogenetic diversification, the fossil record of angiosperm flowers also provides insights into the timing of floral evolution in terms of the functions of the various kinds of floral organs, as well as accompanying patterns of ecological diversification.

Keywords: Angiosperms; Palaeobotany; Cretaceous; Fossil flowers; Floral evolution; Floral function; Mesofossils

Contents

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1. Introduction

While most major groups of land plants have a fossil history extending back to at least the Early Mesozoic, the first unequivocal evidence of angiosperms is from the Early Cretaceous. Nevertheless, despite their relatively late geological appearance, angiosperms are hugely diverse. With perhaps as many as 420,000 extant species (Govaerts, 2001), there are many more species of angiosperm than all other species of land plants combined.

The extraordinary species diversity of angiosperms is also matched by exceptional structural diversity. In habit angiosperms range from minute free floating aquatics to massive forest trees, while their propagules range from the dust seeds of orchids to the giant double coconut. The diversity of angiosperm functional types is overwhelming and underpins their ecological success. Angiosperms dominate the vegetation of most land ecosystems.

Angiosperm flowers also exhibit enormous diversity ranging from the minute male flowers of *Hedyosmum* to the giant blossoms of *Rafflesia*. The diversity of angiosperm flowers reflects extraordinary developmental and evolutionary plasticity (e.g., Endress, 1994). Since the earliest scientific studies it has been clear that these structures provide a great range of features by which different groups of angiosperms may be distinguished and compared. And since Darwin the characteristics of flowers have also been widely used to interpret evolutionary relationships among different angiosperm lineages. Flowers are also of central importance to angiosperm reproductive biology and have been highlighted as key innovations that perhaps facilitated angiosperm diversification through their influence on speciation and extinction rates.

Over the last twenty-five years, information on the flowers of ancient angiosperms has expanded dramatically with the discovery and investigation of fossil floral material from Cretaceous deposits. It is these studies that are mainly reviewed in this work. Together with new insights into angiosperm phylogeny based on analyses of DNA sequences (see references in Soltis and Soltis, 2004), these data now permit critical evaluation of previously hypothesised patterns of angiosperm floral evolution. This, in turn, facilitates a clearer understanding of the developmental and evolutionary processes responsible for angiosperm floral diversity (e.g., Endress, 2001b).

In this paper we review the patterns of floral diversification revealed by our current understanding of the relationships among extant angiosperms and the emerging fossil history of the group. We then discuss the major morphological innovations and recurrent themes that can be detected in the early evolution of angiosperm flowers. In particular, we draw on current hypotheses of angiosperm phylogeny based on molecular data, and the results of our own research on Cretaceous angiosperm flowers.

2. Angiosperm phylogeny and the angiosperm flower

2.1. Relationships of angiosperms and the origin of angiosperm flowers

Understanding the origin of angiosperm flowers requires understanding how angiosperms are related to other seed plants, and therefore homologies among the reproductive structures of different plant groups. Unfortunately, however, there is currently no clear consensus on the pattern of relationships among different groups of seed plants. Phylogenetic analyses of DNA sequence data from the five extant groups yield inconclusive results (Burleigh and Mathews, 2004). Many such analyses resolve Gnetales with Pinaceae as sister group to all other conifers (so-called GNEPINE trees). In most rootings of these trees angiosperms are sister group to all other seed plants, while *Ginkgo* and cycads separate above angiosperms (Burleigh and Mathews, 2004). However, this pattern of relationships is problematic to interpret in evolutionary terms because it is not straightforward to determine the position of the root in this tree (Burleigh and Mathews, 2004) and because it conflicts with stratigraphic evidence.

Despite these continuing uncertainties, the molecular data are sufficient to call into question early cladistic ideas on phylogenetic relationships among seed plants that placed angiosperms and Gnetales, together with extinct Bennettitales and Pentoxylales, in a group referred to as anthophytes based on the aggregation of ovule and pollen-bearing organs into flower-like structures (e.g., Doyle and Donoghue, 1986). In addition, because the phylogenetic relationships of extinct groups are not yet resolved convincingly, there is no firm basis for hypothesising exactly how the characteristic reproductive structures of angiosperms (carpels, stamens, flowers) may have evolved from the very different reproductive organs seen in other groups.

2.2. Flower-like structures in non-angiosperm seed plants

Whatever the potential evolutionary correspondence among the reproductive organs of seed plants, there is no doubt that flower-like structures occur in several non-angiosperm groups. Most strikingly, bisexual reproductive structures that have a flower-like form are known in certain Bennettitales and *Welwitschia* (Gnetales) (Fig. 1).

In Bennettitales, bisexual flower-like structures are known in *Williamsoniella,* as well as in *Cycadeoidea* and similar plants. In *Williamsoniella*, from the Middle Jurassic of Yorkshire, these structures are small

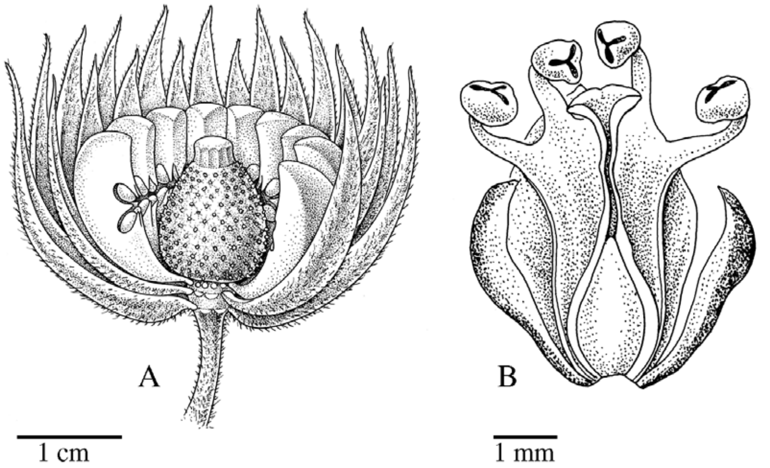


Fig. 1. Flower-like reproductive structures in non-angiosperm seed plants. (A) Reconstruction of *Williamsoniella*, an extinct Middle Jurassic member of the Bennettitales, showing the central ovule bearing part surrounded by wedge-shaped pollen-producing structures and bracts. (B) Section of male flower of *Welwitschia*, an extant member of the Gnetales, showing central “aborted ovule” and surrounding pollen-producing structures. A based on earlier reconstructions and illustrations in Thomas (1915), Harris (1944), and Crane (1985); B based on specimens in the collections of the Swedish Museum of Natural History.

with a central receptacle bearing ovules and interseminal scales (Thomas, 1915; Harris, 1944). This ovule bearing part is surrounded by 12 wedge-shaped pollen-producing structures, each bearing two or three pairs of synangia that contain numerous paired microsporangia. Surrounding both the ovule bearing part and the pollen-producing structures there is a whorl of small bracts (Fig. 1A). In *Cycadeoidea* and similar genera, the flowers are larger, but again consist of bracts surrounding a whorl of pollen-producing structures, which themselves surround a central column bearing ovules and interseminal scales (Wieland, 1906; Crepet, 1974). Based on these features, and traces of insect borings in the flowers, insect pollination was suggested for *Cycadeoidea* (Crepet, 1972).

In extant *Welwitschia*, the pollen-producing structures are borne in a whorl surrounding a single "aborted ovule" (Fig. 1B). At the apex this ovule exudes a sticky substance that appears to function in pollen presentation and attraction of pollinators (Hufford, 1996). The pollen-producing structures and ovule are surrounded by two pairs of bracts placed at right angles to each other.

Bennettitales have a fossil history extending at least as far back as the Triassic (Crane, 1986), and Gnetales are apparently of equal or greater antiquity (Crane, 1996). While the reproductive structures of early Gnetales are not well understood, it is clear that bisexual flower-like structures had already evolved among Bennettitales by the Middle Jurassic. They therefore significantly predate the first appearance of angiosperms in the fossil record. This suggests that key aspects of reproductive biology that are characteristically associated with angiosperm flowers, such as insect pollination and the modification of organs for protection and attraction, appeared earlier, and perhaps independently, in other groups.

2.3. Hypotheses of angiosperm phylogeny

While the origins of the angiosperm flower remain obscure, probable pathways of floral diversification within angiosperms have been greatly clarified by resolution of phylogenetic patterns among extant lineages of flowering plants (for references see Soltis and Soltis, 2004). Phylogenetic analyses based on molecular sequence data almost invariably resolve *Amborella* as the sister group to all other angiosperms, with Nymphaeaceae sensu lato and Austrobaileyales (including Illiciaceae/Schisandraceae, Austrobaileyaceae and Trimeniaceae) as the next two successive branches. This succession of basal lineages was first recognised by Qiu et al. (1999) and termed the "ANITA grade" from the initial letters in ***A****mborella*, *N*ymphaeales, *I*lliciaceae, *T*rimeniaceae, and *A*ustobaileyaceae. These lineages are inferred to have diverged at an early stage from the main line of angiosperm evolution, and prior to divergence of the three major groups of angiosperms: magnoliids sensu stricto, monocots and eudicots (Fig. 2A).

Above the ANITA lineages, monocots and eudicots are placed in a polychotomy with magnoliids sensu

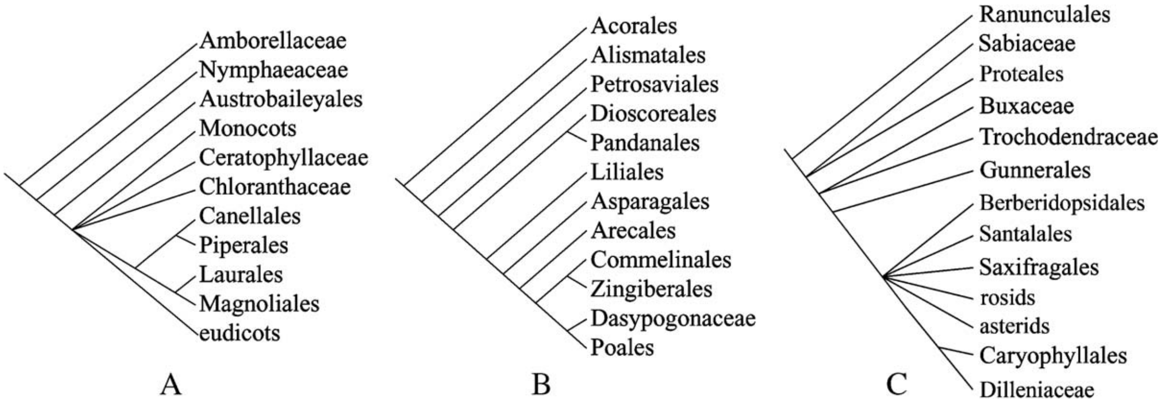


Fig. 2. Summary of phylogenetic relationships of extant major lineages of angiosperms. (A) Overview of tree showing basal lineages and orders of magnoliids sensu stricto. (B) Overview of monocot phylogeny. (C) Overview of eudicot phylogeny. A, C adapted from Soltis and Soltis (2004); B adapted from Chase (2004).

stricto (Canellales, Piperales, Laurales, Magnoliales) and two smaller and apparently phylogenetically isolated groups, Chloranthaceae and Ceratophyllaceae (Fig. 2A). Among magnoliids, Canellales (Winteraceae and Canellaceae) and Piperales are sister taxa. Together they are the sister group to Laurales (including the diverse avocado family) plus Magnoliales.

Monocots comprise about 22% of extant angiosperm species (Herendeen and Crane, 1995) and the genus *Acorus* is sister to all other taxa (Chase, 2004). Above this level, Alismatales, Petrosaviales, Pandanales plus Dioscoreales, Liliales (containing the hyper-diverse angiosperm family Orchidaceae), Asparagales and Arecales (palms) are successive sister groups to the remainder of the monocot clade (Fig. 2B). This group comprises Zingiberales (gingers) plus Commelinales, which are sister to Dasypogonaceae plus Poales (grasses) (Chase, 2004).

Eudicots comprise about 75% of extant angiosperm species (Magallón et al., 1999) with Ranunculales the sister to the remainder of the group. Above this level Sabiaceae and Proteales (Nelumbonaceae, Proteaceae and Platanaceae) form a polychotomy and they are followed by a polychotomy with Buxaceae and Trochodendraceae and the hyper-diverse core eudicots (Fig. 2C). Within core eudicots, Gunnerales are the sister to a polychotomy of Berberidopsidales, Santalales, Saxifragales, Dilleniaceae and Caryophyllales, eurosids plus Vitaceae and asterids (for references see Soltis and Soltis, 2004). Eurosids contain many large and important families such as legumes, roses, Fagaceae (beeches and their relatives) and Myrtaceae (myrtles and their relatives). Asterids contain families such as Asteraceae (sunflowers and their relatives), Lamiaceae (mints and their relatives) and Ericaceae (heathers and their relatives). Eurosids and asterids together account for the bulk of both eudicot and total angiosperm diversity.

3. Age of angiosperms

3.1. Recognising angiosperms in the fossil record

Establishing the first appearance of angiosperms in the fossil record requires a well-constrained stratigraphic framework and the presence of unique defining characters by which the various angiosperm organs can be securely identified. Most angiosperm synapormorphies are related to the reproductive system, but the vegetative parts of most angiosperms also possess a suite of features not seen in other plant groups.

The angiosperm flower is formed by carpels (pistillate organs) and stamens (staminate organs) that are often surrounded by a perianth. Carpels are unique to angiosperms. They enclose and protect the ovules (angiospermy) and provide a specialised region (stigma) where pollen germination takes place. This is different from the naked seeds of gymnosperms where pollen germination takes place inside or close to the ovule. Stamens are also unique and rather uniform in construction in all angiosperms (Endress, 1996). Typically they are bilaterally symmetrical and differentiated into a fertile, synangiate anther formed from four pollen sacs borne in two pairs on a sterile, often thread-like, filament (Endress, 1996).

Pollen of eudicot angiosperms is also easy to distinguish from that of other seed plants by the presence of three or more apertures, typically in a radially symmetrical arrangement around the equator (tricolpate, tricolporate, triporate). Pollen with many pores in an equatorial or global arrangement occurs sporadically in many different groups of angiosperms and is also unique in the context of seed plants as a whole. Most non-eudicot angiosperms have pollen grains with a single aperture. Among extant non-angiospermous seed plants monoaperturate pollen are also found in *Ginkgo* and cycads. In both cases these have a smooth pollen wall and may be difficult to distinguish from smooth-walled, monoaperturate angiosperm pollen grains using only light microscopy.

There are, however, some features of the pollen wall that appear to unite angiosperm pollen, and distinguish it from pollen of other seed plants. One such feature is the lack of a distinct laminated endexine. In non-angiospermous seed plants this layer is well developed, both under the apertures and in non-apertural areas of the grains. However, in angiosperms the endexine is typically thin and granular to faintly laminar, and may even be absent (e.g., Foreman and Sampson, 1987). Many angiosperms also have a reticulate outer pollen wall that is supported by columellae. It is, however, possible that pollen grains with a reticulate–columellate pollen wall were produced by extinct, and currently unrecognised, non-angiospermous seed plants since this feature has been observed in dispersed pollen grains from the Triassic of North America in combination with a uniformly thick endexine typical for non-angiospermous seed plants (Cornet, 1989). Detailed studies of wall structure using SEM and TEM may therefore be required to establish the systematic affinity of dispersed pollen.

Pollen grains with three apertures in an arrangement that is superficially similar to that of tricolpate angiosperm pollen have been found in the dispersed pollen genus *Eucommiidites* that was first thought to be an early angiosperm (Erdtman, 1948). *Eucommiidites* pollen found in situ in the micropyles of seeds of *Erdtmanispermum* from the Early Cretaceous of Bornholm, Denmark, is also superficially similar to angiosperm pollen in the foveolate exine structure (Pedersen et al., 1989). However, the position of the apertures in *Eucommiidites* is not completely radially symmetrical and the apertures are not positioned perpendicular to the equator as in tricolpate angiosperm pollen (Couper, 1956; Pedersen et al., 1989). The endexine is also thick, laminar and evenly distributed, as is typical for non-angiospermous seed plants.

It is usually unproblematic to recognise angiosperms based on dispersed leaves although the possibility of confusing fragmentary remains with the leaves of dipteridaceous ferns needs to be borne in mind. Angiosperm leaves are distinguished from leaves of other plants primarily by a hierarchical system of successively thinner veins, freely-ending veinlets, and anastomoses between two or more orders of veins to form a reticulate pattern of venation (Hickey and Wolfe, 1975). Hickey and Wolfe (1975) also considered stipules as typical of angiosperms although they are not common among monocots.

3.2. Earliest unequivocal angiosperms

No unequivocal angiosperm fossils have been reported from earliest Cretaceous or older strata. Several claims of pre-Cretaceous angiosperm macrofossils and pollen have been published, but all are questionable and in several cases it has been demonstrated convincingly that the fossils were misplaced stratigraphically, or misinterpreted systematically (Hughes, 1976). Most recently, *Archaefructus liaoningensis* from northeastern China was described as a Jurassic angiosperm (Sun et al., 1998). The age of the Yixian Formation from which the fossil was recovered has been much debated, but recent independent radiometric dating from several horizons in the Yixian Formation strongly suggests a mid-Early Cretaceous rather than Late Jurassic age (e.g., Swisher et al., 2002; Zhou et al., 2003). Several pre-Cretaceous macrofossils have also been highlighted as putative early angiosperms. Especially intriguing is the *Sanmiguelia* plant (Brown, 1956; Tidwell et al., 1977; Cornet, 1986) first described as a palm from the Late Triassic of North America based on its large elliptical and plicate leaves. However, the information available is not sufficient for accurate determination of the systematic position of this material (Crane, 1987).

The earliest scattered angiosperm leaf fossils are from around the Barremian–Aptian transition of eastern North America (e.g., Hickey and Doyle, 1977) and eastern China (Li, 2003). The earliest fossil floras with distinctive angiosperm flowers, as well as dispersed carpels, stamens and seeds, are also approximately of this age from localities in Portugal and North America (see Section 4.2). The Yixian Formation of northeastern China, which has yielded the distinctive angiosperm fossil *Sinocarpus* (Leng and Friis, 2003) and the disputed fossil *Archaefructus* (Sun et al., 1998), also dates from around the Barremian–Aptian boundary. The presence of distinctive tricolpate pollen grains in Late Barremian–Early Aptian strata (about 120 Myr) shows that eudicot angiosperms were established in geographically widespread regions early in the history of angiosperms (Hughes and McDougall, 1990; Doyle, 1992; Hughes, 1994).

Based on the evidence reviewed above, by around the Barremian–Aptian transition the presence of angiosperms is documented by an array of different kinds of fossils (carpels enclosing ovules, pollen grains trapped on stigmatic surfaces, tetrasporangiate stamens, triaperturate eudicot type pollen). Prior to that, evidence of angiosperms consists of diverse and distinctive monoaperturate pollen in Hauterivian strata. These grains closely resemble those of angiosperms in details of their wall structure (Hughes et al., 1991; Hughes, 1994). Some of the Hauterivian pollen types have also been found in situ in angiosperm reproductive organs from the slightly younger Early Cretaceous floras of Portugal adding further support to the inference that these Hauterivian pollen grains were also produced by angiosperms. Currently, however, there are no other fossils than pollen from pre-

Barremian rocks that can be assigned to the angiosperms with certainty.

Triaperturate pollen types from dispersed palynofloras show a dramatic increase in abundance and diversity through the later part of the Aptian and Albian (e.g., Brenner, 1963; Doyle et al., 1977; Penny, 1991), a pattern of evolutionary diversification that is also reflected in the occurrence of abundant and diverse Mid-Cretaceous leaf floras (e.g., Crabtree, 1987), as well as fossil assemblages of reproductive structures dominated by eudicot angiosperms (Crane and Herendeen, 1996).

Although there is currently no direct evidence of pre-Cretaceous angiosperms there are several unusual Triassic pollen types that may have links to the angiosperm lineage (Cornet, 1989; Hochuli et al., 1989; Hochuli and Feist-Burkhardt, 2004). They are all of great interest, but their relationship to angiosperms is currently equivocal. In all cases no additional information is available about the plants that produced these isolated grains.

4. Palaeobotanical evidence of angiosperm flowers and floral organs

4.1. Studies of Cretaceous angiosperms

The pollen record is more extensive than that of other angiosperm organs and has been especially important for studying temporal and spatial patterns in angiosperm radiation (e.g., Brenner, 1963; Doyle and Hickey, 1976; Crane and Lidgard, 1989; Hughes, 1994; Lupia, 1999). Pollen grains have a resistant wall that is conducive to fossilization, they are often dispersed over long distances, and due to their small size they may be present in great quantities even in a few grams of rock.

Most angiosperm pollen grains also have unique characters that are only encountered in angiosperms and this usually makes them easy to recognise in palynological preparations (see Section 3.1). The pollen record can therefore be extremely informative for understanding the temporal and spatial distribution of several major plant groups including angiosperms and eudicots. Unfortunately, this systematic fidelity generally decreases at finer systematic scales. Very frequently, at the family and genus level, iterative patterns of evolution obscure correlations between pollen morphological features and the limits of particular systematic groups.

Angiosperm leaves are of much more restricted occurrence in the fossil record than angiosperm pollen. Nevertheless, extensive macrofossil floras dominated by angiosperm leaves have been recovered at many localities from the Mid-Cretaceous onwards. In many cases systematic determinations based on fossil leaves have been shown to be unreliable, although improved analyses of venation patterns (Hickey and Wolfe, 1975) and cuticular structure (Dilcher, 1974), in both modern and fossil leaves, have greatly improved the possibilities for useful comparative studies (e.g., Upchurch and Dilcher, 1990). The leaves of monocots and other angiosperms are usually relatively easy to distinguish. However, as with pollen grains, systematic determinations of fossil leaves at lower systematic levels are often complicated by extensive patterns of convergent evolution.

Angiosperm reproductive structures uncovered from Cretaceous sediments over the past 25–30 years have dramatically expanded the quality and quantity of useful palaeobotanical data available for studying early angiosperm reproductive biology and the pattern of early angiosperm diversification. The discovery of numerous fossil floras comprising small, structurally preserved flowers, fruits, seeds and other reproductive parts has created new possibilities for comparative studies, and has also catalysed renewed interest in studies of the angiosperm fossil record. Because most of the fossils in these floras fall in the size range between microfossils (such as pollen and spores) and macrofossils (such as leaves and stems) these new floras are generally referred to as mesofossil floras. In addition to the discovery of mesofossil floras, recent investigations of Early Cretaceous macrofossil floras, sometimes with “whole plant” preservation, have also significantly contributed to our understanding of the expansion of angiosperms into Late Mesozoic ecosystems.

4.2. Mesofossil floras

The first major discovery of a mesofossil flora containing well-preserved angiosperm flowers was from the Late Cretaceous (Late Santonian–Early Campanian) of southern Sweden (Friis and Skarby, 1981).

The Swedish flora includes thousands of angiosperm reproductive organs, all of which are very small, typically between 0.5–3 mm in length. Fossil flowers are preserved both as charcoal and lignite, and show considerable diversity in organisation and structure (e.g., Friis and Skarby, 1982; Friis, 1983, 1984, 1985, 1990; Friis et al., 1986, 1988; Friis and Crane, 1989; Eklund et al., 1997; Schönenberger and Friis, 2001; Schönenberger et al., 2001a; Leng et al., 2005). Phylogenetically, they represent a variety of angiosperm lineages, but the mesofossil flora is dominated by eudicots. According to theoretical models prevailing at the time that this and other mesofossil floras were discovered (e.g., Tiffney, 1977; Crane et al., 1986; Friis et al., 1986; Knobloch and Mai, 1986), flowers of primitive angiosperms had often been thought to be large with numerous floral parts. The discovery in Cretaceous strata of fossil floras comprising exclusively minute flowers was therefore unanticipated.

Since these early discoveries, mesofossil floras have been discovered from many other places covering most of the stratigraphic column from the mid-Early Cretaceous to the end of the Cretaceous. From Europe mesofossil floras rich in angiosperm remains have been reported from numerous Late Cretaceous localities in Central Europe (e.g., Knobloch and Mai, 1986, 1991; Eklund and Kvaček, 1998; Kvaček and Eklund, 2003) and from many Early and Late Cretaceous localities in Portugal (e.g., Friis et al., 1992, 1994b, 1997a, 1999, 2000b, 2003b; Schönenberger et al., 2001b).

The oldest assemblages from Europe containing angiosperm floral structures are from Portugal. The precise ages of the early Portuguese floras are not fully established. We have previously indicated that they were approximately of the same age, in the time range from Barremian to Aptian (Friis et al., 1999). Based on our recent studies of these mesofossil floras and new geological/stratigraphic studies (Dinis, 2001; Dinis et al., 2002; Heimhofer, 2004; Heimhofer et al., 2005) we now conclude that some of the floras from the Torres Vedras–Catefica Region are pre-Albian (Late Barremian or Early Aptian) in age (see also discussion in Friis et al., 2004), while floras from the Vale de Agua, Famalicão and Buarcos localities may be younger, perhaps of Late Aptian or Early Albian age, (see also discussion and references in von Balthazar et al., 2005).

From North America an extensive series of mesofossil floras have been recovered from Early and Mid-Cretaceous Potomac Group sediments exposed in Virginia and Maryland (e.g., Friis et al., 1986, 1988; Drinnan et al., 1990, 1991; Crane et al., 1993, 1994; Friis et al., 1994a, 1995, 1997a; Pedersen et al., 1994). The oldest of the Potomac Group mesofossil floras are from the Drewry's Bluff (clay balls) and Dutch Gap localities along the James River in Virginia and are probably of Early Aptian age (Doyle, 1992). These exhibit both low diversity and low abundance in angiosperm fossils compared to younger floras from the Early Cretaceous in the same region. Rich floras are also known from the Late Cretaceous of North Carolina (e.g., Friis, 1988; Mickle, 1996; Eklund, 2000), New Jersey (e.g., Crepet et al., 1992; Herendeen et al., 1993; Nixon and Crepet, 1993; Crepet and Nixon, 1994, 1998a,b; Herendeen et al., 1994; Crepet, 1996; Gandolfo, 1998; Gandolfo et al., 1998, 2002, 2004), Massachusetts (Tiffney, 1977), and Georgia (Herendeen et al., 1995; Magallón-Puebla et al., 1996; Magallón-Puebla et al., 1997; Sims et al., 1998, 1999; Herendeen et al., 1999).

From Asia several mesofossil floras are known from the early Late Cretaceous (Cenomanian–Turonian) of Kazakhstan (Frumin and Friis, 1996, 1999; Frumin et al., 2004) and diverse assemblages have also been reported from the Late Cretaceous (Early Coniacian) of Japan (Takahashi et al., 1999a,b, 2003).

While mesofossil floras with angiosperm floral organs are now known to be widely distributed in the Northern Hemisphere, the only mesofossil floras so far described from the Southern Hemisphere are from the Table Nunatak, Antarctica (e.g., Eklund, 2003; Eklund et al., 2004b).

The angiosperm reproductive organs recovered in all of the Cretaceous mesofossil floras so far studied are typically a few millimetres or less in length, even though these floras often also contain larger fragments of wood, conifer cones and twigs. Most of the plant fossils are preserved in a three-dimensional state (Fig. 3). Often they have a black, highly reflective surface, and internal cellular structures studied in thin sections show homogenisation of the cell walls. These features indicate that many of the plant fossils are charcoalified and preserved as a result of vegetation fire. Charring provides rigidity and resistance to the plant tissue and prevents the fossils from collapsing after burial in the

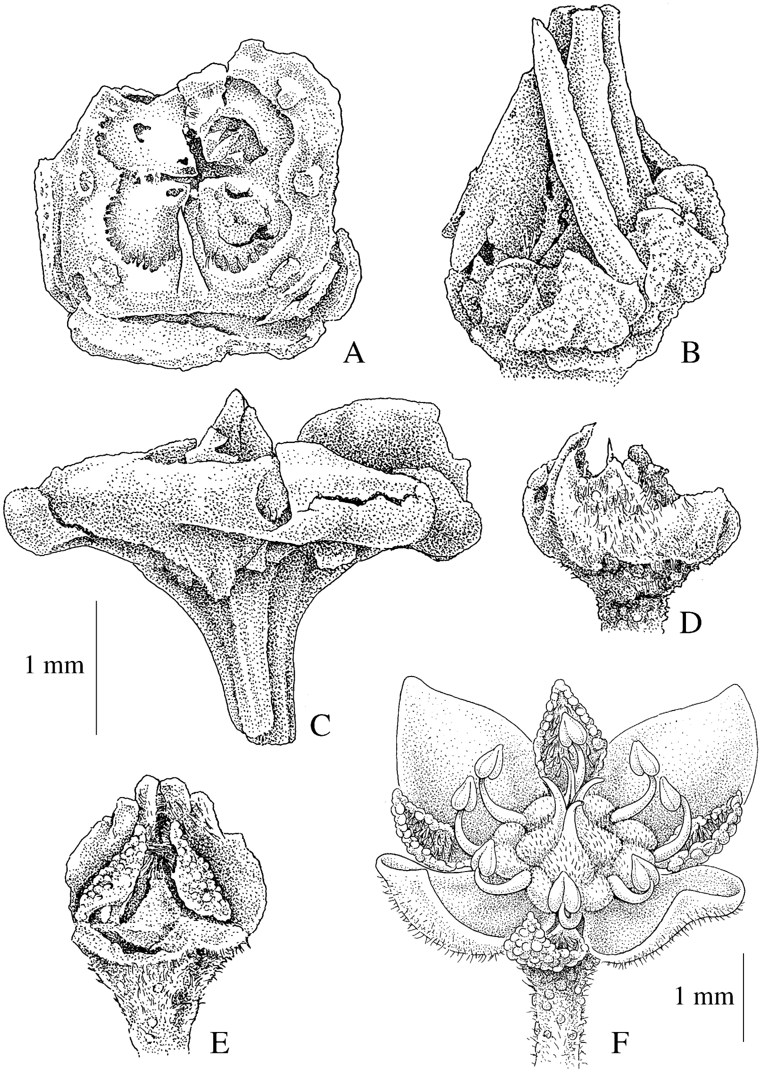


Fig. 3. *Platydiscus peltatus* (Cunoniaceae), charcoalified and three-dimensionally preserved flowers from the Late Cretaceous of southern Sweden (A–E) and reconstruction of the flower (F). (A) Apical view of presumed anthetic flower showing distinct tetramerous organisation and prominent nectary (S107055). (B) Lateral view of presumed anthetic flower showing carpels in the centre, a single, expanded filament and nectary disk (S107137). (C) Lateral view of presumed anthetic flower showing sepals (S107029). (D) Lateral view of pre-anthetic flowers showing indumentum (S107135). (E) Lateral view of pre-anthetic flower showing parts of perianth with longer outer sepals and shorter inner petals; petals characterised by peltate trichomes (S106348). (F) Reconstruction of flower showing tetramerous organisation, four prominent carpels, a prominent lobed nectary disk, eight stamens, small trullate petals, and larger ovate-triangular sepals. Line drawings A–E based on SEM-pictures in Schönenberger et al. (2001a). S-numbers refer to material in the collections of the Swedish Museum of Natural History.

sediments. However, charring also adds to the fragility of the fossils reducing the likelihood of significant transport prior to deposition. Through the charring process plant organs retain their three-dimensional form although experimental studies of modern material show that they may have shrunk to varying degrees (Harris, 1981; Lupia, 1995). Flowers may have all floral parts preserved in their original position, including sepals, petals, stamens and carpels. The three-dimensional form of the flowers allows accurate reconstructions of their original structure and organisation (Fig. 3) as well as detailed comparisons with extant taxa both at a cellular level and through the preparation of floral diagrams.

In addition to charcoalified fossils Cretaceous mesofossil floras often include lignitic material that may be slightly or strongly compressed. These are typically brownish in colour with a non-reflective or only slightly reflective surface. These may also be exceptionally well preserved and where anthers are present the details of pollen wall ultrastructure are often excellent.

4.3. Macrofossil floras

Angiosperm reproductive structures found over the past three decades, in newly discovered or newly studied macrofossil floras, provide another line of evidence for reconstructing early angiosperm floral structure and reproductive biology. These floras typically include compression/impression fossils, such as leaves and stems, preserved in consolidated sediments. In exceptional cases different plant organs may be in organic connection or whole plants may be preserved (Figs. 4 and 5). Two Early Cretaceous and two early Late Cretaceous (Cenomanian) macrofossil floras have been particularly informative.

The Jehol flora from the Yixian Formation of northeastern China has yielded several definite and putative

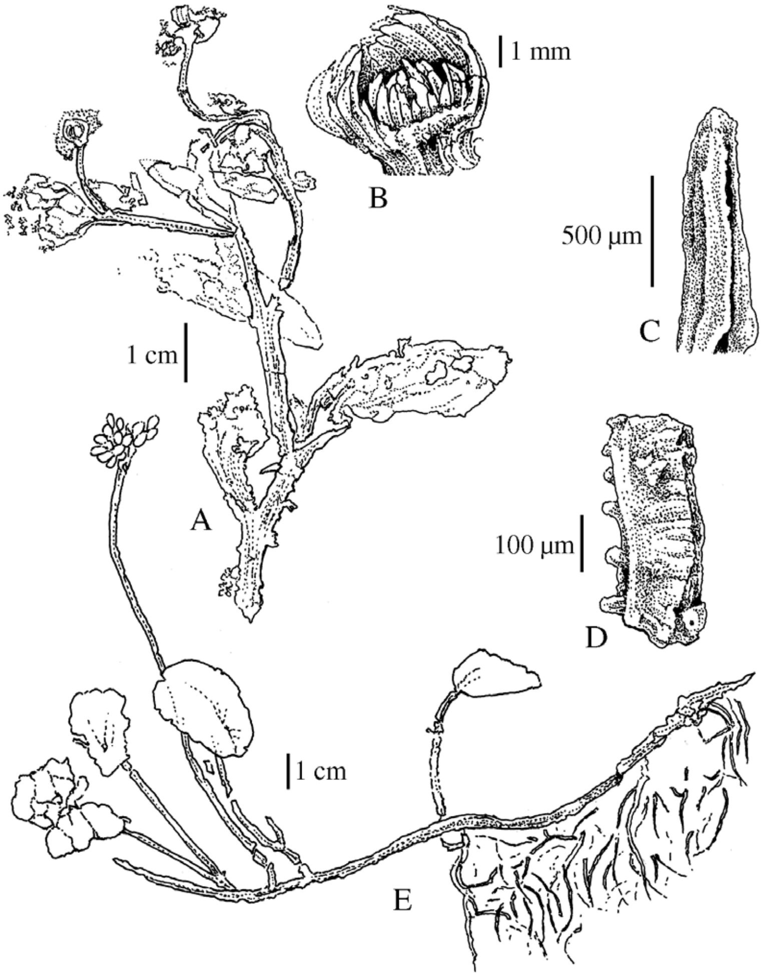


Fig. 4. Early Cretaceous macrofossils from the Crato Formation, Brazil. (A–D) *Endressinia brasiliana*, extinct plant assigned to Magnoliales, with flowers and leaves attached to the same branching system. (A) Overview of fossil. (B) Detail of flower. (C) Isolated follicle-like carpel. (D) Staminode with glands. (E) Herbaceous angiosperm preserved as "whole plant" with leaves and a reproductive structure arising from a horizontal axis with roots. A–D line drawings based on photos in Mohr and Bernardes-de-Oliveira (2004); E line drawing based on photo in Mohr and Friis (2000).

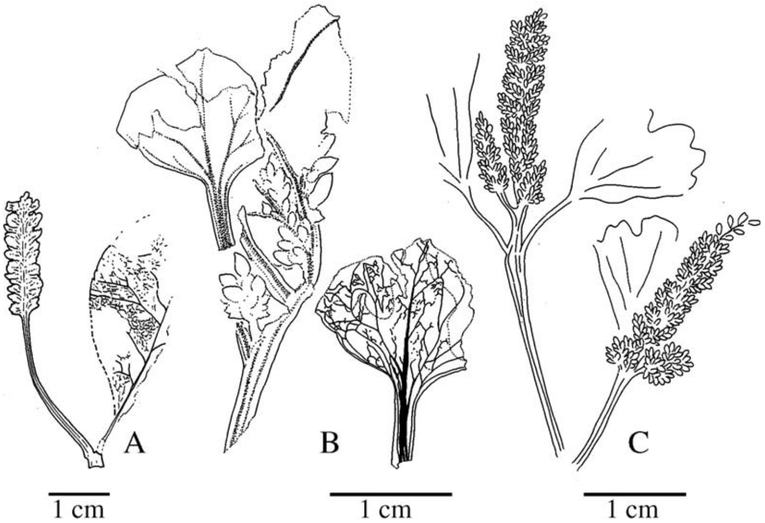


Fig. 5. Early Cretaceous macrofossils with inflorescences of small, densely packed flowers borne on leafy shoots. (A) *Xingxueina heilongjiangensis* from Heilongjiang Province, northeastern China. (B) Fossil from the Koonwarra Fossil Bed, Victoria, Australia, left, overview of specimen showing attached leaves and inflorescence, right, detail of leaf venation. (C) *Caspiocarpus paniculiger* from Kazakhstan. A redrawn from Sun and Dilcher (1996); B redrawn from Taylor and Hickey (1990); C redrawn from Krassilov (1997).

early angiosperms. The age of the fossil plants is controversial, but there is now strong evidence for a mid-Early Cretaceous (Late Barremian–Early Aptian) age (Zhou et al., 2003). The Yixian Formation is famous for its exquisitely preserved fauna and exceptionally well-preserved vertebrates, which include feathered dinosaurs and many birds (Chang et al., 2003; Zhou et al., 2003). The plant fossils are preserved as compressions or impressions in which organic material has often been replaced or infiltrated by pyrite framboids that typically have destroyed all anatomical and micromorphological features (Leng and Yang, 2003). Nevertheless, the Yixian flora is unusually informative because intensive collecting has led to the recovery of fossils with leaves and reproductive organs connected to the same axis. In some remarkable cases roots, stems, leaves, flowers and fruiting structures are preserved as part of the same “whole” fossil plant. Two of the most significant fossils from the Yixian Formation attributed to angiosperms are *Archaefructus* and *Sinocarpus* (Sun et al., 1998, 2001, 2002; Friis et al., 2003a; Leng and Friis, 2003; Leng et al., 2003; Ji et al., 2004). *Archaefructus*, in particular, has been widely discussed in the context of early angiosperm evolution, even though important uncertainties remain about its correct morphological interpretation (for discussion see Section 5.1).

The other Early Cretaceous macrofossil flora that sometimes shows whole plant preservation is from the Late Aptian or Early Albian Crato Formation, Brazil (Martill et al., 1993; Mohr and Friis, 2000; Mohr and Rydin, 2002; Mohr and Eklund, 2003; Mohr and Bernardes-de-Oliveira, 2004). The flora includes angiosperm fossils that have flowers or fruiting structures attached to leafy stems (Fig. 4). There are also exceptional whole plant fossils that clearly document the presence of aquatic angiosperms. In some cases the organic material has been replaced in an early stage of fossilisation by iron oxide, which has provided well preserved cellular details (Mohr and Bernardes-de-Oliveira, 2004).

From the Czech Republic, the classic Bohemian flora from the Cenomanian Peruc–Korycany Formation has yielded a rich assemblage of leaves and associated reproductive structures (e.g., Velenovský and Viniklár, 1929; Kvaček, 1992). Reproductive structures are typically poorly preserved, but recently sieving of the sediment has uncovered several well-preserved flowers and fragments of reproductive axes. This new material, combined with the traditional macrofossils, offers the potential for a better understanding of structure and organisation of the angiosperms and other plants in this important Mid-Cretaceous flora (Eklund and Kvaček, 1998; Kvaček and Eklund, 2003).

Another classic Mid-Cretaceous flora is that from the Dakota Sandstone (Dakota Formation) of the Western Interior of North America (e.g., Lesquereux, 1892). The Dakota Formation is dated as Late Albian–Early Cenomanian (Dilcher and Crane, 1984; Brenner et al., 2000). The flora is mainly from the Janssen Clay Member (Crane and Dilcher, 1984), which is of Early Cenomanian age (Brenner et al., 2000). The Dakota Formation has yielded several informative angiosperm reproductive organs preserved as three-dimensional impressions and also as compressions (Dilcher, 1979; Retallack and Dilcher, 1981; Basinger and Dilcher, 1984; Crane and Dilcher, 1984; Dilcher and Crane, 1984; Dilcher and Kovach, 1986).

Although not as abundant as mesofossils, flowers from macrofossil floras are important for understanding the overall morphology and organisation of Cretaceous reproductive structures, and in several cases they have also provided invaluable information on the habit of early angiosperms. The compression/impression fossils also include some larger structures, which provide evidence of larger flowers in the later phases of early angiosperm diversification.

4.4. Petrified floras

In addition to the meso- and macrofossil floras that sometimes show whole plant preservation, there are also several important assemblages of fossil plants in which angiosperm reproductive structures are preserved as petrifactions. Petrified fossil plants often have their original three-dimensional form and cellular details well preserved, but generally they are more difficult to study than lignitic or charcoalified material. Sometimes individual plant parts can be isolated completely from the matrix allowing examination of external form (e.g., Nishida and Nishida, 1988), but in other cases the fossils are infiltrated in a massive chert and their form can only be reconstructed from serial peels or sections (Stopes and Fujii, 1910). Petrified floras containing fossil angiosperms are restricted to Late Cretaceous and younger strata and are mainly recorded from Japan, India, Central America and western North America.

Petrified angiosperm fossils from the Late Turonian–Santonian of Hokkaido, Japan, were first described almost hundred years ago in a classic study by Stopes and Fujii (1910). More recently, much new material has been added to the collections and several angiosperm flowers and fruits have now been described (e.g., Nishida and Nishida, 1988; Nishida, 1994; Nishida et al., 1996; Ohana et al., 1999). In North America, petrified angiosperm fossils include mainly fruits and seeds discovered from the Late Santonian–Early Campanian of British Columbia, Canada (Delevoryas and Mickle, 1995), while in Central America petrified fruits are known from the Campanian–Maastrichtian of Mexico (Rodríguez-de la Rosa and Cevallos-Ferriz, 1994; Hernández-Castillo and Cevallos-Ferriz, 1999).

Petrified angiosperm reproductive organs are also very common in the Deccan Intertrappean Beds of India. The plant fossils are found in layers intercalated between the flood basalts of the massive Deccan eruptions. They are thought to represent vegetation surrounding lake systems and coastal estuaries that were silicified as a result of volcanism. Preservation of excellent anatomical details indicates rapid fossilisation. Flowers and other floral organs, as well as vegetative parts of angiosperms, have been described from this sequence for more than 60 years particularly from Mohgaon Kalan (Mohagaonkala) in the Chhindwara district of Madhya Pradesh (e.g., Sahni, 1943; Shukla, 1944; Verma, 1958; Chitaley, 1964; Nambudiri and Tidwell, 1978; Bande et al., 1988; Bonde, 1995; Chitaley and Nambudiri, 1995). The age of this classic flora was previously thought to be Palaeogene. The duration of the Deccan volcanism and the exact timing have been much debated, but there is now growing evidence from radiometric dating that the eruption was very brief (1–5 million years) starting in the latest Cretaceous (Maastrichtian) and spanning into the earliest Palaeogene (Danian) (e.g., Courtillot et al., 1988; Hofmann et al., 2000; Tandon, 2002; Cripps et al., 2005). Studies of palynomorphs (Kar and Srinivasan, 1997; Kumaran et al., 1997), non-marine ostracodes (Whatley et al., 2002), as well as fishes, dinosaurs and mammals (references in Khosla and Sahni, 2003), indicate that the plant bearing Intertrappean beds of Mohgoan Kalan are of Maastrichtian age. The plant fossils from the Deccan Intertrappean Beds thus provide an important insight into latest Cretaceous angiosperm diversity at low palaeolatitudes.

5. Cretaceous angiosperm reproductive structures: a systematic overview

Based on the fossil floral structures currently available, together with information from the record of dispersed fossil pollen, it is clear that angiosperm diversification and systematic differentiation occurred rapidly through the Cretaceous. The stratigraphic resolution and geographic coverage available so far are not sufficiently fine to permit detailed evolutionary conclusions, but several major phases in the Cretaceous angiosperm radiation can be distinguished. These can be recognised primarily by structural and functional traits of the flowers, by pollen features and also by distinct changes in the systematic composition of the floras. In general, in those cases where their systematic relationships can be determined, angiosperms from the Aptian and earlier can be linked to extant lineages that diverged early from the main line of angiosperm evolution based on phylogenetic analyses of DNA data. Later, during the Albian and Early Cenomanian, additional lineages, including a broader range of early diverging eudicots, can be recognised. The major radiation of core eudicots is subsequently reflected in enormous floral diversity in the Late Cretaceous. We discuss the fossil floral structures that are known currently in a phylogenetic context. It is important to recognise, however, that many other fossils from the Early and Mid-Cretaceous are difficult to place systematically and probably belong to extinct lineages of angiosperms.

5.1. Early Cretaceous reproductive structures of putative basalmost angiosperms

The earliest phase of angiosperm differentiation, through the Valanginian to Early Barremian, is represented by a few problematic macrofossils and several kinds of monoaperturate (or occasionally inaperturate) pollen (e.g., Hughes, 1994; Brenner, 1996). None of these very earliest angiosperm fossils can be assigned to a modern angiosperm subgroup at family level or below and they most probably represent extinct lineages. Several pollen types are already present in the Late Hauterivian, but typically each is represented by only few specimens (e.g., Hughes and McDougall, 1987; Hughes et al., 1991; Hughes, 1994). Among extant plants monoaperturate and inaperturate pollen grains are produced by plants of ANITA grade angiosperms, Chloranthaceae, magnoliids sensu stricto and also by monocots, but so far it has not been possible to assign securely any of these early pollen types to a major group of extant angiosperms. In the absence of associated macro- or mesofossils nothing further is known about the plants that produced these pollen grains. Most probably they were produced by extinct taxa at or near the base of the angiosperm phylogenetic tree.

Except for a few questionable records, there are no fossil floral structures from the Valanginian–Hauterivian–Early Barremian. *Bevhalstia pebja*, described as a very early putative angiosperm (Hill, 1996) from the latest Hauterivian (?) of southern England, is not well preserved and is problematic. It consists of small leafy stems with axillary or terminal enlarged structures. Each is composed of a central mass of uncertain nature surrounded by leaf-like structures that have dichotomising non-anastomosing venation. Although Hill (1996) favoured an interpretation of these structures as flowers he also indicated that they might be buds. Better preserved material is needed to provide definitive information on this plant.

A macrofossil flora comprising angiosperm leaves and an inflorescence axis has been described from the upper part of the Chengzihe Formation, Heilongjiang Province, northeastern China, and presented as of Hauterivian or Hauterivian–Early Barremian age (Sun and Dilcher, 1997, 2002). However, based on marine assemblages Sha et al. (2003) considered the Chengzihe Formation to be mainly of Aptian age, with the basal part perhaps of Barremian age. The inflorescence axis, *Xingxueina heilongjiangensis* (Fig. 5A), is small and consists of densely crowded and strongly compressed units (Sun and Dilcher, 1997). The inflorescence appears to be simple, but the preservation does not permit reliable interpretation of the organisation or structure of flowers and inflorescence. Pollen grains with a reticulate–columellate pollen wall are associated with the reproductive axes. They were described as possibly inaperturate, but illustrations of the pollen grains (Pl. 6 Figs. 2 and 6 in Sun and Dilcher, 2002) suggest that they may be monocolpate.

An Aptian fossil from the Koonwarra Fossil Bed in Victoria, Australia, shows an inflorescence axis attached to a leafy shoot (Fig. 5B). It was described as a possible compound inflorescence with a primary

Fig. 6. Reconstruction of *Archaefructus sinensis* from the Early Cretaceous of northeastern China based on specimens housed in the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing showing herbaceous habit and lax reproductive axes (inflorescences and infructescences).

axis bearing densely crowded ovate bracts, each of which subtends two axillary bracteoles and at least one ovary (Taylor and Hickey, 1990). Unfortunately the fossil is strongly compressed and difficult to interpret. As a result, the systematic position of the fossil is uncertain although the authors suggest possible similarities to extant magnoliid angiosperms (Saururaceae, Piperaceae, Aristolochiaceae, Barclayaceae, Chloranthaceae) and some monocots (Dioscoreaceae, Smilacaceae) (Taylor and Hickey, 1990).

There are several other Mid-Cretaceous macrofossils of uncertain affinity with minute flowers crowded in spike-like or compound inflorescences. In *Caspiocarpus paniculiger* (Fig. 5C) from the Middle Albian of Kazakhstan (Krassilov, 1997) the inflorescence is attached to a leaf bearing shoot that perhaps indicates relationship with Ranunculales (see also Section 5.5). *Caloda delevoryana* from the Mid-Cretaceous Dakota Formation of central Kansas (Dilcher and Kovach, 1986) has small, densely crowded, secondary axes borne in a helical arrangement along the main axis. The secondary axis terminates in small receptacles, each bearing 35–50 free carpels. Another inflorescence from the Dakota Formation consists of densely crowded and apparently tetramerous floral units borne in a helical arrangement (Dilcher, 1979). Some of the units appear to be staminate and clusters of reticulate and zonocolpate pollen grains of the *Dichastopollenites* type were observed in several specimens. *Myricanthium amentaceum* and *Myricanthium pragense* from the Cenomanian flora of Bohemia (Velenovský, 1889; Kvaček and Eklund, 2003) are two other Mid-Cretaceous angiosperms with small flowers borne in crowded inflorescences. They probably belong to basal branching angiosperms, but their systematic affinity is currently unresolved (Kvaček and Eklund, 2003).

Archaefructus, described from the Yixian Formation of northeastern China (Sun et al., 1998, 2002; Ji et al., 2004), is among the best known fossil angiosperms from the Barremian–Early Aptian, but its systematic position is uncertain. Three different species have been reported based on macrofossils. A few specimens are preserved as whole plants with roots, stems, leaves, flowers, and fruits attached showing that *Archaefructus* was a small herbaceous plant (Fig. 6). Strongly dissected leaves, and the general appearance of the plant, suggest that it was aquatic (Sun et al., 2002). It may have lived completely submerged and flowered underwater (Friis et al., 2003a). Reproductive axes of *Archaefructus* are mixed: there is a distal pistillate zone, a proximal staminate zone, and no trace of bracts or perianth parts. The carpels often occur in pairs and stamens are typically in groups of 2–3. Carpels are elongate and contain many small seeds. Stamens are apparently tetrasporangiate with a short stalk and short apical expansion of the connective.

Interpretation of the reproductive axis of *Archaefructus* is controversial. According to Sun et al. (2002) it is a single multipartite and naked flower with an apocarpous gynoecium of many spirally arranged stamens and carpels (Sun et al., 1998, 2002). The lack of bracts and perianth parts was interpreted as a primitive feature. Based on this interpretation a new family, Archaefructaceae, was established and it was suggested that *Archaefructus* was a stem group angiosperm (Sun et al., 2002). An alternative interpretation is that *Archaefructus* is within the angiosperm crown group, perhaps close to the Nymphaeales or basal eudicots (Friis et al., 2003a). Under this interpretation the reproductive axis is a simple, ebracteate inflorescence bearing simple, unisexual and naked flowers; the pistillate flowers consisting of a pair of carpels, and the staminate flowers of two or three stamens. The lack of bracts and perianth parts reflects secondary loss, perhaps following adaptation to submerged flowering (Friis et al., 2003a). The discovery of *Archaefructus eoanthus* (Ji et al., 2004) strongly supports the inflorescence interpretation. In this plant a bisexual flower consisting of a single carpel and two or three stamens are present in the region between the pistillate and staminate zone.

5.2. Early Cretaceous reproductive structures of ANITA grade angiosperms and Chloranthaceae

Well-preserved angiosperm floral structures from the mesofossil floras of Portugal include forms that can be related definitively to the extant family Chloranthaceae. In Portugal they are known from the Torres Vedras–Catefica area in floras of presumed Late Barremian or Early Aptian age. They are also known from the floras of Vale de Agua and Buarcos (Late Aptian or Early Albian). The reproductive structures include isolated stamens with in situ *Clavatipollenites*-type pollen, as well as isolated stamens, staminate inflorescences and pistillate flowers with associated *Asteropollis*-type pollen.

The staminate inflorescences are small and simple, borne terminally on a naked axis, and have tetrasporangiate stamens arranged in whorls along the inflorescence axis (Fig. 7A–E). These inflorescences are

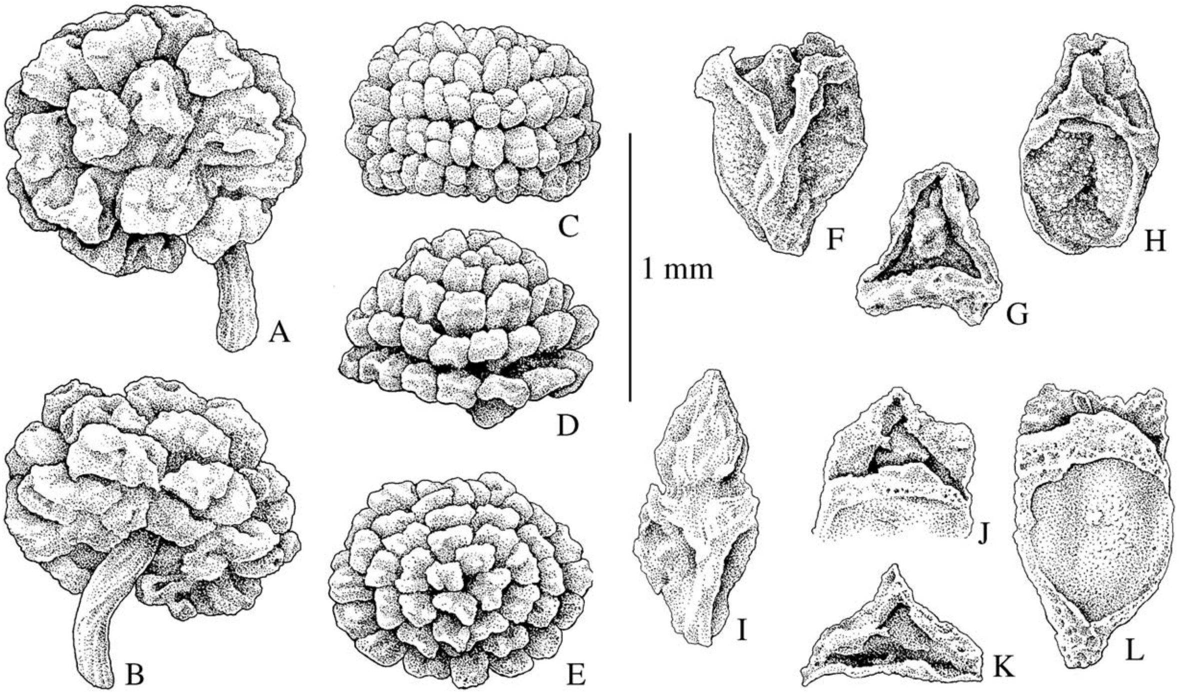


Fig. 7. Fossil *Hedyosmum*-like flowers (Chloranthaceae) from the Early Cretaceous of Portugal. (A–B) Staminate inflorescence from Catefica, apical (A) and basal (B) view (S135451). (C) Staminate inflorescence from Vale de Agua, lateral view (S127047). (D–E) Staminate inflorescence from Torres Vedras, lateral (D) and apical (E) view (S101220). (F–H) Pistillate flower from Torres Vedras, lateral (F, H) and apical (G) view (S101307). (I) Pistillate flower from Vale de Agua with stigma preserved (S105611). (J–L) Pistillate flower from Buarcos in apical (J–K) and lateral (L) view (S101600). A–C and K based on unpublished SEM-pictures in the collections of the Swedish Museum of Natural History; D–E and G–H based on SEM-pictures in Friis et al. (1994b); F based on SEM-picture in Eklund et al. (Eklund et al., 2004a); I based on SEM-picture in Friis et al. (Friis et al., 2000b); J–L based on SEM-pictures in Friis et al. (1997b). S-numbers refer to material in the collections of the Swedish Museum of Natural History.

closely similar to those of extant *Hedyosmum*, which are interpreted as ebracteate inflorescences bearing small naked and unistaminate flowers (Endress, 1987). Associated isolated pistillate flowers are also very similar to pistillate flowers of extant *Hedyosmum*. They are small, and each flower (borne in the axil of a small bract in extant *Hedyosmum*) consists of a single carpel enclosing a single ovule. The carpel is distinctly triangular with sharp corners (Fig. 7F–L). Each side of the carpel wall has a distinct ovate opening corresponding to the “window” seen in ovaries and fruits of extant *Hedyosmum* and each side is extended into a triangular, tepal or tepal-like structure that is also present in extant *Hedyosmum*. The stigma is a bulky, conical structure (Fig. 7I) also closely similar to that of extant *Hedyosmum*, and as in the extant genus the stigma easily breaks away from the rest of the carpel. Early Cretaceous fossil plants related to *Hedyosmum* include several distinct species.

Also among Chloranthaceae, *Clavatipollenites* pollen known from isolated stamens that co-occur with the *Hedyosmum*-like material, is closely similar to pollen of extant *Ascarina*. This suggests the presence of at least two kinds of ancient chloranthoids very early in angiosperm history. The dispersed pollen record indicates that both *Hedyosmum*-related and *Ascarina*-related plants were widespread, with an almost global distribution, during the Early and Mid-Cretaceous with their first appearance around the Barremian–Aptian (e.g., Walker and Walker, 1984; Friis et al., 1997b; Eklund et al., 2004a). They are a much less conspicuous component of Late Cretaceous pollen floras.

It should be noted that knowledge of fine details of the pollen wall is often required for a secure assignment of fossil pollen to Chloranthaceae and that some dispersed pollen assigned to *Clavatipollenites* may not represent the same complex of plants (Hughes, 1994). This is also indicated by the *Clavatipollenites*-like pollen grains found on the stigmatic surface of the *Couperites mauldinensis* fruits from the Late Cretaceous (Early Cenomanian) Mauldin Mountain locality of Maryland (Pedersen et al., 1991). Pedersen et al. (1991) emphasised similarities to Chloranthaceae but concluded that *Couperites* could not be included in the modern family as currently circumscribed. The seeds of *Couperites* are anatropous in contrast to the orthotropous seeds of all extant Chloranthaceae and the pollen has a distinct colpus margin delimitating the aperture. This contrasts with the gradual transition from aperture to non-aperture exine that is characteristic for pollen of extant *Ascarina* and other Chloranthaceae. Based on a phylogenetic study of Chloranthaceae using morphological characters Eklund et al. (2004a) noted that *Couperites* could either be a sister to Chloranthaceae or among crown group Chloranthaceae. However, more information is needed before the exact systematic position of *Couperites* can be established.

In the Late Cretaceous the presence of other Chloranthaceae is documented by several species of *Chloranthistemon* from Europe and North America (Crane et al., 1989; Herendeen et al., 1993; Eklund et al., 1997). In floral form and inflorescence structure these fossils are closely similar to flowers and inflorescences of extant *Chloranthus*. This group of Chloranthaceae was evidently well differentiated and widespread by the mid-Late Cretaceous.

Several fossil reproductive structures from the Early Cretaceous of Portugal have features suggesting relationship to ANITA grade angiosperms. Among these is a small staminate flower from Catefica consisting of about 10–15 stamens surrounded by an outer set of small triangular tepals and an inner set of broader tepals (Friis et al., 2000b). Stamens have long, broadly flattened filaments and small triangular, tetrasporangiate anthers with the thecae separated by an extensive, slightly extended, connective. Pollen grains are monoaperturate with a trichotomocolpate aperture. The fossil flower is similar to flowers of *Amborella* and some extant Schisandraceae. Pollen morphology, however, is different from that of extant taxa and the fossil probably represents an extinct lineage within or near the ANITA grade (Friis et al., 2000b).

Another early floral structure that can be related to ANITA grade angiosperms is a small perigynous flower from the Vale de Agua flora (Late Aptian or Early Albian) (Friis et al., 2001a). It is actinomorphic with a central columnar structure surrounded by a whorl of 12, apparently multiovulate, carpels (Fig. 8). Outside the carpels are 24 diamond shaped scars in two whorls, which are interpreted as the attachment scars of stamens, and about six transversely elongate scars, which are interpreted as the attachment scars of spirally arranged tepals. The features of the flower indicate

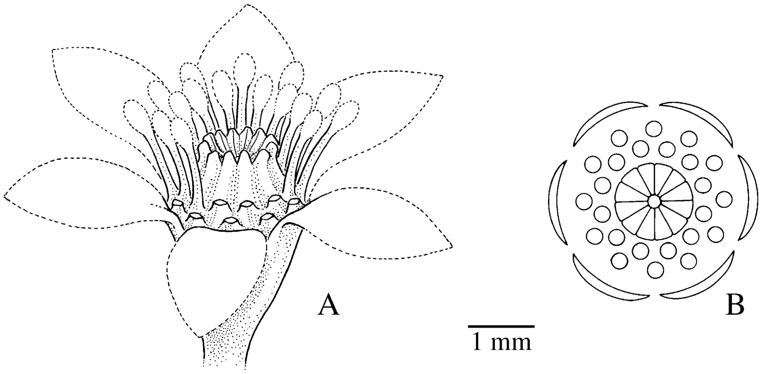


Fig. 8. Early Cretaceous flower from Vale de Agua, Portugal, related to ANITA-grade angiosperms (Nymphaeales) (S122015). (A) Reconstruction of flower. (B) Floral diagram showing organisation of flower. A from Friis et al. (2001a,b) with permission). S-numbers refer to material in the collections of the Swedish Museum of Natural History.

relationship to Nymphaeaceae or Illiciaceae. Based on the apparent multiovulate nature of the carpels the fossil is probably most close to extant Nymphaeaceae. *Microvictoria* from the Turonian of New Jersey (Gandolfo et al., 2004) is another putative Nymphaeaceae flower from later in the Cretaceous. The flower is small and multiparted with features indicating a possible relationship with extant *Victoria* (Nymphaeaceae).

There are various kinds of fossil seeds from the Early Cretaceous that probably represent ANITA grade angiosperms. These have a distinctive outer epidermis composed of palisade cells that have undulate anticlinal cell walls, which give the seed surface a jigsaw puzzle appearance (Fig. 9). This combination of features is characteristic of the seeds of extant Illiciaceae and Nymphaeaceae. Some of these seeds also have a distinctive micropylar cap strongly resembling the embryotheca of extant Nymphaeaceae. Seeds of this kind are already diverse in the earliest mesofossil floras of Portugal and have been recovered also from the oldest horizons of the Potomac Group sequence (Drewry's Bluff clay balls, Early Aptian). Seeds that can be assigned unequivocally to Illiciaceae are known from the early part of the Late Cretaceous (Cenomanian–Turonian) of Kazakhstan (Frumin and Friis, 1999).

5.3. Fossil reproductive structures of magnoliids sensu stricto

A review of the fossil history of magnoliids (sensu lato) was published earlier (Friis et al., 1997b). Here we provide a short summary of previous records together with an account of some of the more recent discoveries.

The earliest fossils that can be assigned confidently to the magnoliids sensu stricto are dispersed pollen tetrads from the Early Cretaceous (Late Barremian or Early Aptian) of Gabon assigned to the extinct genus *Walkeripollis* (Doyle et al., 1990) and thought to represent stem group Winteraceae (Canellales) (Doyle, 2000). Other dispersed pollen grains from the early phases of the angiosperm radiation such as *Tucanopollis* and *Transitoripollis* may represent Piperales. Pollen grains comparable in shape and pollen wall structure to *Tucanopollis*/*Transitoripollis* have been found on the stigma of *Appomattoxia* fruits from the Early Cretaceous (early-Mid-Albian) Puddledock flora of Virginia, North America, and from the Early Cretaceous (Late Barremian or Early Aptian) flora of Torres Vedras, Portugal (Fig. 10). From the Torres Vedras flora this kind of pollen has also been found in situ in isolated stamens and in coprolites (Fig. 10). *Appomattoxia* shares several features with modern Piperales and also shows some resemblance to the basal eudicot family Circaeasteraceae (Friis et al., 1995). However, based on current information, *Appomattoxia* is most closely related to members of the Piperales.

Magnoliales are more extensively represented in the Mid-Cretaceous than Canellales and Piperales. Fossil plants definitely assignable to the Magnoliales are rare in Early Cretaceous floras (Friis et al., 1997b), but the group was established at least by the Aptian/

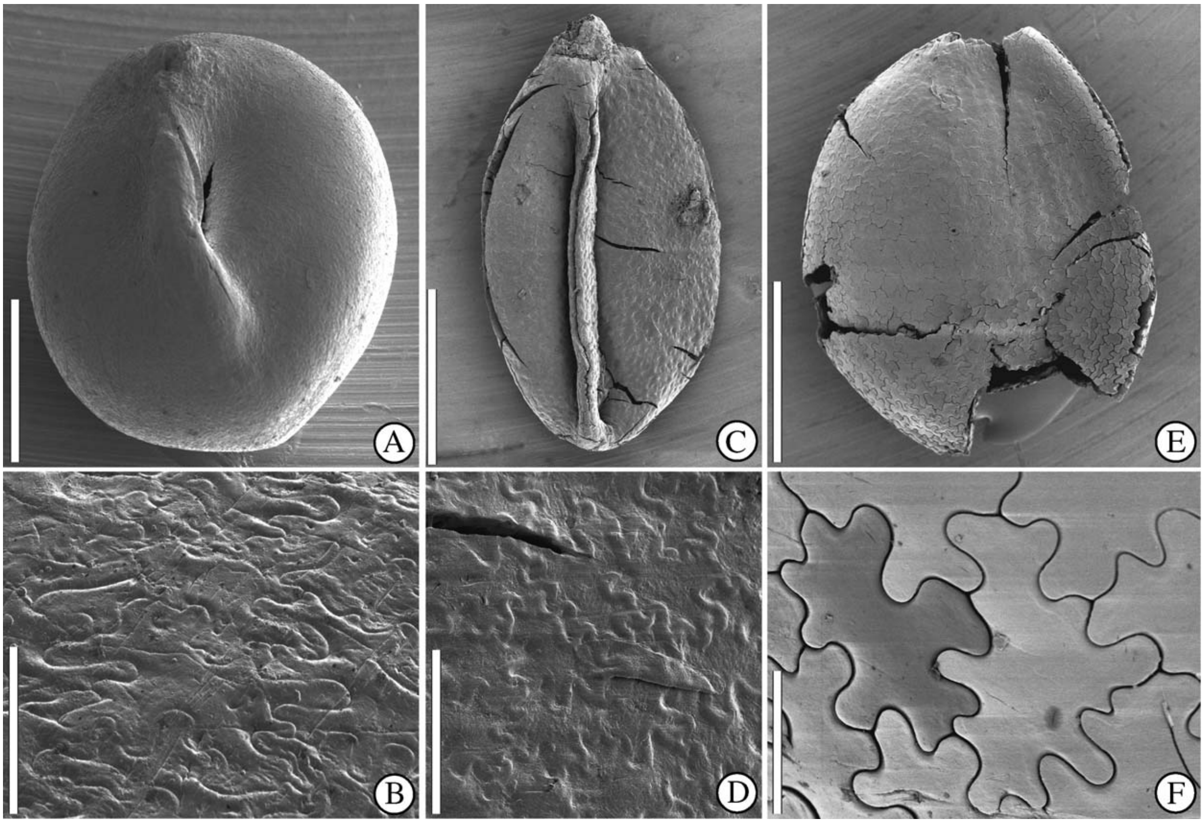


Fig. 9. Early Cretaceous seeds related to ANITA-grade angiosperms (Nymphaeales); all figures SEM. (A–B) Seed from the Drewry's Bluff locality, Virginia, USA (PP). (A) Overview of seed, scale bar = 300 μm. (B) Detail of seed surface showing undulate anticlinal walls of palisade cells; scale bar = 30 μm. (C–D) Seed from Torres Vedras, Portugal (S136740). (C) Overview of seed, scale bar = 300 μm. (D) Detail of seed surface showing undulate anticlinal walls of palisade cells; scale bar = 60 μm. (E–F) Seed from Torres Vedras (S136741). (E) Overview of seed, scale bar = 300 μm. (F) Detail of seed surface showing undulate anticlinal walls of palisade cells; scale bar = 30 μm. S-numbers refer to material in the collections of the Swedish Museum of Natural History. PP numbers refer to material in the collections of the Field Museum, Chicago.

Albian where it is represented by *Endressinia brasiliana* described from the Crato Formation of Brazil (Mohr and Bernardes-de-Oliveira, 2004). The fossil is a branching axis with entire margined leaves in an alternate arrangement and attached solitary flowers (Fig. 4A–D). The flowers are hypogynous, multiparted, and apocarpous. Carpels are follicle-like and surrounded by numerous, narrow flattened structures of uncertain nature. The innermost of these have distinct glandular knobs (Fig. 4D) closely resembling the staminodes of some extant Magnoliales. The flattened structures are surrounded by several broad tepal-like structures. *Endressinia* shows many features seen in extant Magnoliales and is particularly similar to extant Eupomatiaceae and Himantandraceae.

Araripia florifera, also from the Crato Formation of Brazil, is another early angiosperm that has been compared to extant Magnoliales and Calycanthaceae (Laurales). The fossil has floral structures and leaves borne on the same branching axis (Mohr and Eklund, 2003). The preservation is rather poor, but it is clear that *Araripia* is also a multiparted flower with helically arranged parts and an undifferentiated perianth.

Laurales were established at least by the Aptian/Albian and were diverse and widespread by the early Late Cretaceous. One of the most conspicuous fossil members of the group is the peculiar lauraceous plant *Mauldinia*. The genus was established based on three-dimensionally preserved flowers and small fragments of inflorescences from the Early Cenomanian flora of

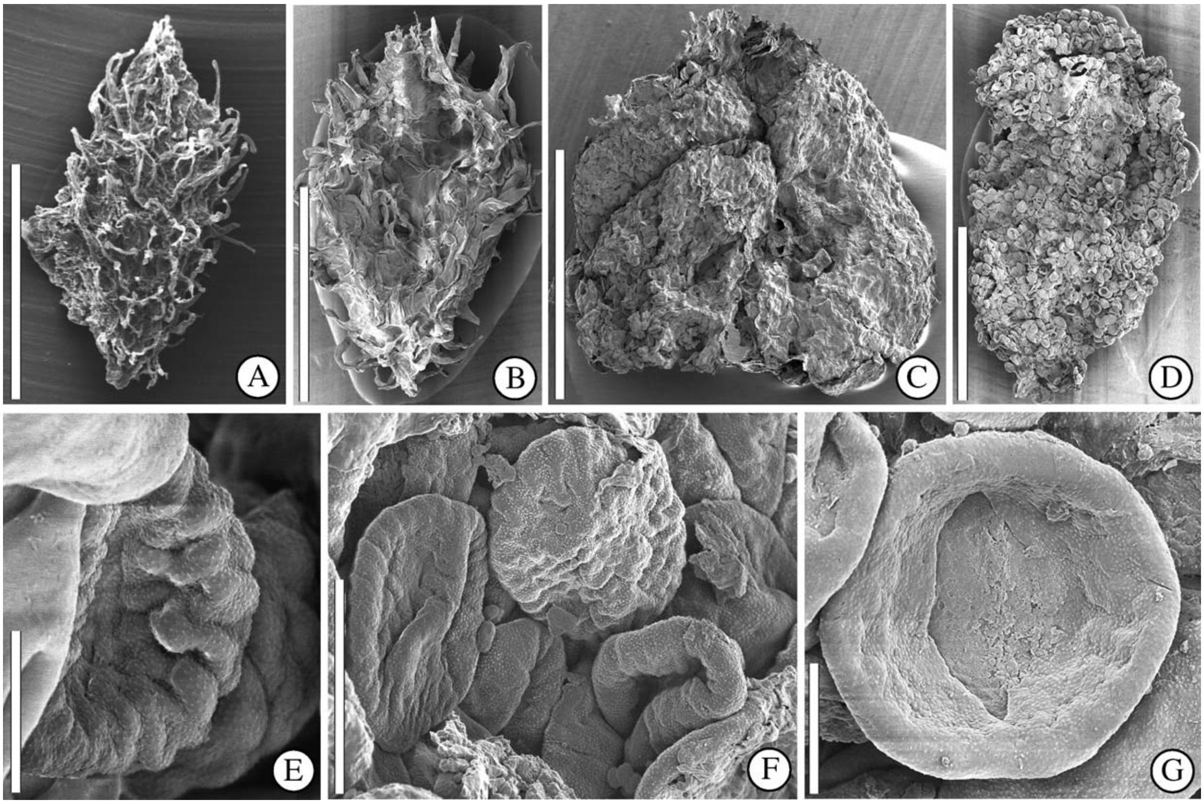


Fig. 10. *Appomattoxia*-like fossils (Piperales?) from the Early Cretaceous of Torres Vedras, Portugal; all figures SEM. (A) Spiny fruit, scale bar = 500 μm (S105022). (B) Spiny fruit, scale bar = 300 μm (S136787). (C) Tetrasporangiate stamen, scale bar = 300 μm (S136688). (D) Coprolite consisting exclusively of pollen, scale bar = 150 μm (S136766). (E–G) Monoaperturate, tectate and finely spiny pollen grains. (E) Pollen from surface of fruit shown in figure B, scale bar = 6 μm. (F) Pollen found in situ in stamen shown in figure C, scale bar = 15 μm. (G) Pollen found in coprolite shown in figure D, scale bar = 6 μm. S-numbers refer to material in the collections of the Swedish Museum of Natural History.

Mauldin Mountain, Maryland (Drinnan et al., 1990). Subsequently *Mauldinia* has been described also from early Late Cretaceous floras in Europe (Eklund and Kvaček, 1998) and Asia (Frumin et al., 2004). The inflorescences are long and slender. Partial inflorescences are bilobed, flattened, cladode-like structures with irregularly margins (Fig. 11). Their structure is not fully understood, but Eklund and Kvaček (1998) suggested that they might correspond to homocladic thyrses where flowers and scales are arranged on a strongly condensed flattened branching system. Flowers of *Mauldinia* (Fig. 11) are bisexual, with a trimerous perianth and androecium and a monomerous gynoecium. The flowers are structurally identical to flowers of extant Lauraceae, but the inflorescences are unique and appear strongly modified compared to inflorescences of all extant lauraceous plants.

The Early Cenomanian fossil *Prisca reynoldsii* described from the Dakota Formation of Kansas, USA (Retallack and Dilcher, 1981) also has long, slender reproductive axes similar to those of *Mauldinia*. Each axis was originally interpreted as a naked pistillate flower consisting of numerous carpels borne in a spiral arrangement along a very long receptacle and *Prisca* was placed in a new family, Priscaceae (Retallack and Dilcher, 1981). Structures interpreted as carpels are, however, clearly lobed and compound and Drinnan et al. (1990) suggested that the reproductive axes of *Prisca* are not large, multipartite flowers, but inflorescences with many small subunits and small flowers similar to those of *Mauldinia*. The type specimen of *Prisca* and other specimens from the type locality are too poorly preserved for detailed comparison with *Mauldinia* (Drinnan et al., 1990), but close

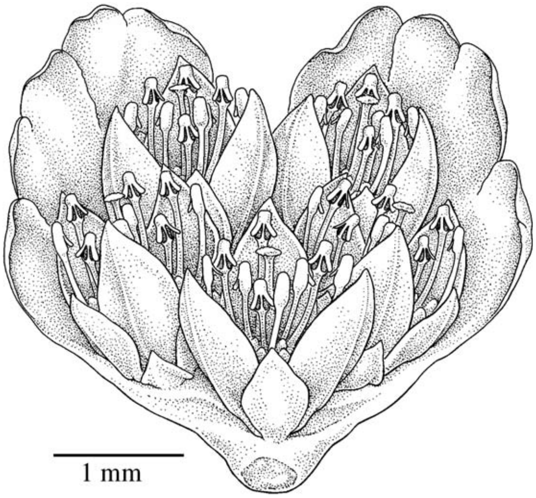


Fig. 11. Reconstruction of bilobed partial inflorescence of *Mauldinia mirabilis* (Lauraceae) from the Late Cretaceous of Maryland, USA, showing five trimerous flowers borne on the ventral side of inflorescence unit. Reconstruction based on SEM-illustrations in Drinnan et al. (1990) and material in the collections of the Field Museum, Chicago.

affinity between *Mauldinia* and *Prisca* is also suggested by strong similarities between the leaves of *Magnoliaephyllum* sp. associated with *Prisca*, and leaves of "*Eucalyptus*" *geinitzii* associated with *Mauldinia boehemica* from Bohemia (Eklund and Kvaček, 1998).

Pragocladus lauroides is another Cenomanian fossil from Bohemia with distinctive lauraceous flowers borne in an elongated inflorescence (Kvaček and Eklund, 2003). Also from later in the Late Cretaceous there are a diversity of flowers that document considerable further diversification of the Lauraceae such as *Perseanthus* from the Turonian of New Jersey (Herendeen et al., 1994), *Neusenia* and four unnamed flowers from the Santonian/Campanian Neuse river flora of North Carolina (Eklund, 2000), as well as *Lauranthus* from the Early Coniacian Kamikitaba flora of Japan (Takahashi et al., 2001).

Virginianthus is another unequivocal magnoliid fossil from the Early Cretaceous based on a single flower discovered from the Early Cretaceous (early-Mid-Albian) Puddledock flora (Friis et al., 1994a). The flower is small, multipartite and bisexual with a distinct, deep floral cup and an apocarpous gynoecium. The perianth and androecium are borne in dense series on the floral rim. The fossil shares many features with flowers of some extant Magnoliales and Laurales, but most particularly with extant Calycanthaceae (Laurales). The most significant difference between *Virginianthus* and extant Calycanthaceae is the presence of simple monocolpate, rather than dicolpate, pollen and it is likely that the flowers represent an extinct group that could be on the stem lineage of the extant family.

In Late Cretaceous floras fossil reproductive structures assignable to magnoliids sensu stricto are known from many areas. They are mostly related to Magnoliales and Laurales and include fossils that can be clearly related to the Magnoliaceae, such as species of *Liriodendroidea* described based on mesofossils from Central Asia, Europe and North America (Knobloch and Mai, 1986; Frumin and Friis, 1996, 1999), which extend stratigraphically from the Cenomanian–Turonian to the Maastrichtian, and petrified fruits of *Litocarpon* from the Santonian–Campanian of Canada (Delevoryas and Mickle, 1995).

The Early Cenomanian flower *Archaeanthus* from the Dakota Formation is a large, multipartite structure with many carpels borne in a spiral arrangement along an extended receptacle. There are also associated leaves, stipular bud scales and tepals. Scars on *Archaeanthus* axes show how these organs were probably attached. *Archaeanthus* shares many features with modern Magnoliaceae and may be an early representative of the family (Dilcher and Crane, 1984).

Lesqueria elocata is another fruiting structure with a multipartite, apocarpous gynoecium from the Early Cenomanian Dakota Formation of central Kansas and from the Cenomanian Woodbine Formation of northern Texas, USA (Lesquereux, 1892; Crane and Dilcher, 1984). It was first assigned to the Bennettitales as *Williamsonia elocata* (Lesquereux, 1892), but Crane and Dilcher (Crane and Dilcher, 1984) documented the presence of distinctive carpels with bifid tips. The fossil shows similarity with multipartite flowers of Magnoliaceae, Annonaceae and Austrobaileyaceae, but cannot be assigned to a specific angiosperm family.

Two multipartite flowers, *Detrusandra* and *Cronquistiflora*, from the Late Cretaceous (Turonian) of New Jersey (Crepet and Nixon, 1998b) also resemble flowers of Magnoliales and Laurales, but the character combination in these fossil is unlike that of any extant taxon and both genera probably represent extinct lineages.

Several petrified multipartite angiosperm reproductive structures have been reported from the Late Cretaceous (Late Turonian–Santonian) of Hokkaido, Japan, that may also be representatives of magnoliids sensu stricto (Fig. 12). *Protomonimia* is a multicarpellate fruiting structure, about 20–25 mm in diameter, consisting of about 55 sessile carpels arranged on a slightly concave receptacle (Nishida and Nishida, 1988). Each carpel has many ovules/seeds. Isolated seeds similar to those found in the carpels of *Protomonimia* are known from the Early Coniacian Kamikitaba flora of Japan (Takahashi et al., 1999b). *Protomonimia* has been compared to extant Monimiaceae, but the multiovulate carpels may indicate closer relationships with Magnoliales than to Laurales. *Hidakanthus*, also described from Hokkaido (Nishida et al., 1996), is very similar in general organisation to *Protomonimia*, but has many more carpels (about 170) and is somewhat larger, about 40 mm in diameter. Other petrified fossils from the Late Turonian–Santonian of Hokkaido of possible magnolialean affinity are the two species of *Keraocarpon* comprising multicarpellate, apocarpous fruits with many carpels (Ohana et al., 1999). Carpel number in *Keraocarpon yasujii* is perhaps as high as 470, while *Keraocarpon masotoshii* is more comparable with *Protomonimia* with about 70 carpels (Ohana et al., 1999).

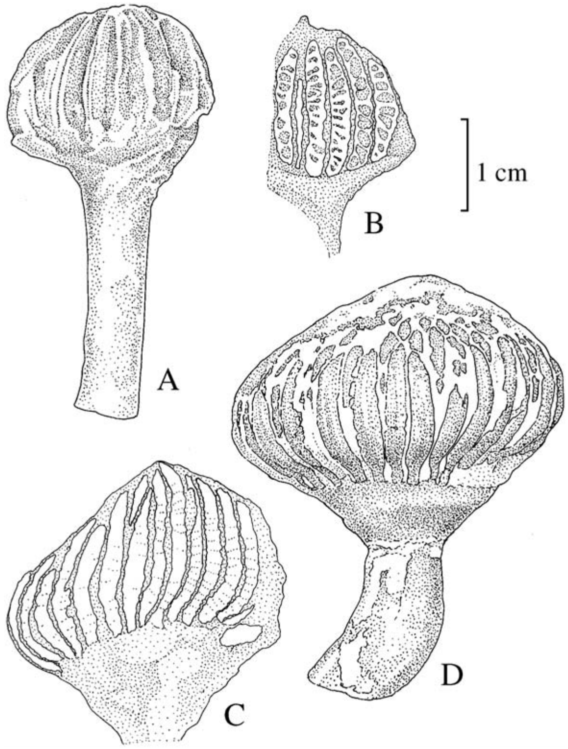


Fig. 12. Multicarpellate and apocarpous petrified fruits (magnoliids sensu stricto) from the Late Cretaceous of Hokkaido, Japan. (A–B) *Protomonimia kasai-nakajhongii* in lateral view (A) and longitudinal section (B). (C–D) *Hidakanthus shiinae* in lateral view (C) and longitudinal section (D). A–B redrawing from illustrations in Nishida and Nishida (1988); C–D redrawn from illustrations in Nishida et al. (1996).

5.4. Fossil reproductive structures of monocots

Despite their inferred long geological history (Bremer, 2000) very few monocot fossils have been recorded from Mid-Cretaceous or older strata (Doyle, 1973; Daghlian, 1981; Herendeen and Crane, 1995; Gandolfo et al., 2000), therefore the role of monocots in early angiosperm evolution, and also in Mid-Cretaceous vegetation, is currently unclear. Several kinds of dispersed pollen grains from the Early Cretaceous, such as *Liliacidites* and other forms with distinct graded reticulum, have long been regarded as evidence of early monocots (Doyle, 1973; Walker and Walker, 1984, 1986). However, Gandolfo et al. (2000) discarded all Early Cretaceous records of the group and stated that the earliest securely identified monocot fossils are from the Turonian.

One difficulty in tracing the fossil history of monocots is that the paucity of vegetative remains probably reflects discrimination against the preservation of herbaceous plants (Herendeen and Crane, 1995; Friis et al., 1999). The apparent scarcity of monocot pollen may also, in part, reflect under-representation in the fossil record. However, it is also possible that many pollen grains of monocots have not yet been recognised due to a lack of distinctive features, as well as incomplete knowledge of pollen morphology in extant plants. The most diverse Cretaceous assemblage of monocot reproductive structures described so far is from the petrified Maastrichtian Deccan Intertrappean flora of India, which includes a variety of stems, flowers and fruits of unequivocal monocot affinity (see below). The presence of diverse monocot fossils in this flora may reflect rapid burial of plants growing close to the depositional basin followed by infiltration with silica-rich water as a result of Deccan volcanism.

In contrast to the view of Gandolfo et al. (2000) we agree with Doyle (1973) and Walker and Walker (1984, 1986) that monocots were already present in the Early Cretaceous. This conclusion is also supported by recent discoveries of Early Cretaceous fossils with distinct affinity to monocots. The earliest unequivocal monocot is *Mayoa portugallica*, which is related to extant Arales, an early diverging group of Alismatales. The fossil is from the Torres Vedras locality, Portugal (Late Barremian–Early Aptian) (Friis et al., 2004).

Mayoa is based on a small, poorly preserved cutinised structure, probably a fragment of an inflorescence axis, with masses of associated polyplicate and inaperturate pollen grains. However, the pollen grains have very distinctive characters. The tectum of the pollen grains is ribbed, with the ribs arranged in a distinctive cross-wise pattern (Fig. 13A–B). The infratectal layer is extremely thin, granular or weakly columellar. Tectum and infratectal layer rest directly on a thin, granular endexine. In morphology and ultrastructure the fossil pollen is closely similar to that of extant *Holochlamys* in the tribe Spathiphylleae of the family Araceae (Friis et al., 2004).

The *Pennistemon*/*Pennipollis* plant is another early fossil angiosperm perhaps related to Alismatales (Friis et al., 2000a). *Pennipollis*-type pollen first enters the fossil record around the Barremian–Aptian boundary and is common in Aptian and Albian palynofloras (e.g., Penny, 1988; Hughes, 1994). They are characterised by their coarsely reticulate and acolumellate pollen wall (Fig. 13C–D), although some of the earliest types have few scattered columellae (Penny, 1988). The muri are only loosely attached to the foot layer by a thin granular infratectal layer, and the reticulum is often detached from the main body of the grains. *Pennipollis*-type pollen has been found in situ in stamens assigned to the extinct genus *Pennistemon*, as well as on the surface of small unicarpellate and uniovulate pistillate structures (Pennicarpus, Friis et al., 2000a) and in coprolites. Most of the stamens and pistillate structures are isolated, but a single fragment

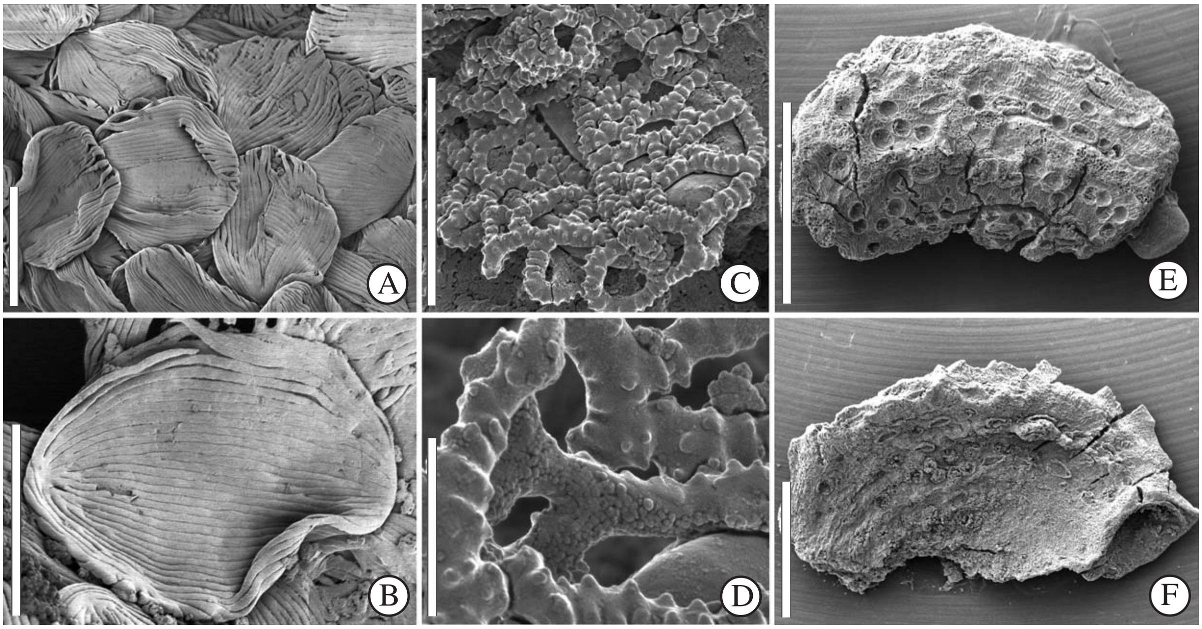


Fig. 13. Fossil monocot or putative monocot pollen (Early Cretaceous) and seeds (Late Cretaceous) of Portugal; all figures SEM. (A–B) Polyplicate pollen of *Mayoa portugallica* (Araceae) from Torres Vedras (S136663). (A) Group of pollen grains, scale bar = 30 μm. (B) Single pollen grain, scale bar = 12 μm. (C–D) Acolummelate pollen grains of *Pennipollis* (Alismatales?) found in coprolite from Vale de Agua, (S105603). (C) Distal view of pollen grain, scale bar = 12 μm. (D) Detail of pollen wall showing detached reticulum with thin granular infratectal layer on the inner side of the muri, scale bar = 3 μm. (E–F) Fossil seeds (Araceae) from Mira, scale bar = 1 mm (E: S122030; F: S122028). S-numbers refer to material in the collections of the Swedish Museum of Natural History.

of an inflorescence axis with spirally arranged stamens indicates that the flowers were naked and simple, each staminate flower consisting merely of a single stamen. Pollen wall structure in *Pennipollis* is closely similar to that in some Alismatales, but the systematic position of the *Pennistemon*/*Pennipollis* plant is not fully resolved. The extremely thin, granular infratectal layer is comparable to that of the fossil *Mayoa* and is a feature that we have observed only in monocot pollen. Other in situ pollen grains from the Early Cretaceous of Portugal and North America that are of possible alismatalean affinity are currently being investigated (Friis, Pedersen and Crane, unpublished data).

Other Early Cretaceous pollen types that may also be early records of monocots include various grains assigned to *Liliacidites*, *Similipollis*, and *Retimonocolpites* (e,g., Doyle, 1973; Walker and Walker, 1984, 1986; Juhász and Góczán, 1985) and a number of unnamed pollen types from Portugal (Friis et al., 1999). All these grains have a strongly graded reticulum in which the size of the lumina decreases either towards the ends of the grains or towards the polar regions (Doyle, 1973; Juhász and Góczán, 1985; Walker and Walker, 1986; Friis et al., 1999); a feature that was suggested to be indicative of monocots (Doyle, 1973). Although a graded reticulum is known also for other angiosperms, the combination of the monoaperturate condition with a graded reticulum is to our knowledge restricted to monocots. *Similipollis*-type pollen was found on the stigmatic surfaces of fruits from the Early Cretaceous of North America and Portugal described as *Anacostia* (Friis et al., 1997a). The fruits and seed have features indicating closer relationship with magnoliid angiosperms, but the systematic affinity of *Anacostia* is currently unresolved.

Several flowers with distinctive probable monocot features have also been identified from the Early Cretaceous of Portugal. One, from the Torres Vedras locality (Late Barremian or Early Aptian), is a small bisexual, trimerous and hypogynous flower. The three fused carpels are surrounded by nine stamens, which in turn are surrounded by an undifferentiated perianth consisting of three tepals (Fig. 14E–G). Pollen grains found in the stamens are monoaperturate and finely reticulate with muri supported by short, densely spaced columellae. Another flower type, including two or perhaps more species, is known from several Early Cretaceous localities in Portugal (Catefica, Famalicão, Vale de Agua). These flowers are bisexual and epigynous with five to eight tepals and stamens, and with monoaperturate (monocolpate and trichotomocolpate) or dicolpate pollen with characteristic finely striate sculpture. The flowers from Catefica are predominantly with six tepals and six stamens, but specimens with seven sepals and seven stamens are also present (Fig. 14A–D).

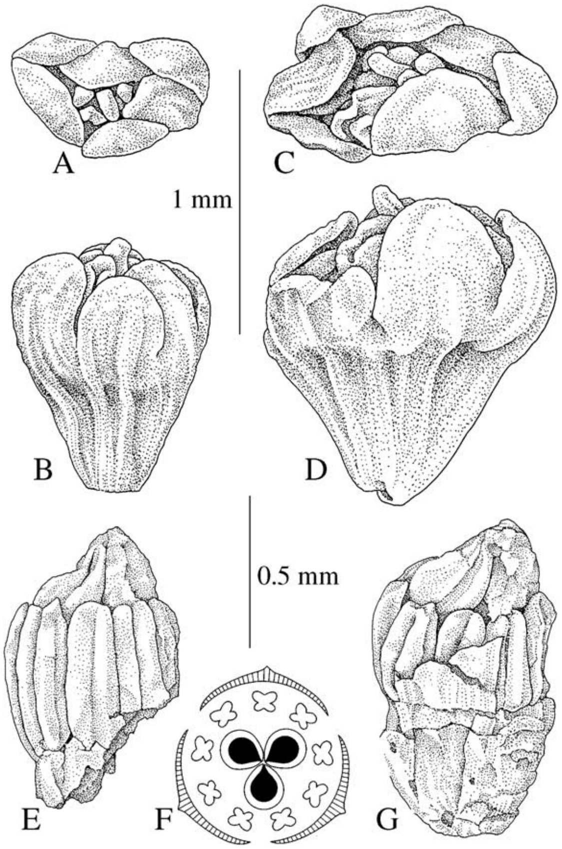


Fig. 14. Putative monocot flowers from the Early Cretaceous of Portugal. (A–D) Epigynous flowers from Catefica. (A–B) Flower with six tepals and six stamens in apical (A) and lateral (B) view (S107775). (C–D) Flower with seven tepals and seven stamens in apical (C) and lateral (D) view (S100757). (E–G) Trimerous and hypogynous flower from Torres Vedras (S101306) with perianth preserved (G) and perianth removed (E). (F) Floral diagram of trimerous flower in Fig. 14E and G. A–C, E based on unpublished SEM-pictures in the collections of the Swedish Museum of Natural History; D based on SEM-picture published in Friis et al. (1999); G based on SEM-picture in Friis et al. (1994b). S-numbers refer to material in the collections of the Swedish Museum of Natural History.

By the middle of the Late Cretaceous there is clear evidence that monocots were both diverse and widespread (Herendeen and Crane, 1995). Even so, many monocot orders are entirely unrepresented during the Late Cretaceous, or are represented by only few scattered records. For example, *Cretovarium* from the Late Cretaceous petrified flora of Hokkaido (Stopes and Fujii, 1910), which is characterised by a trilocular and hypogynous gynoecium and intercarpellary nectaries, is the only Cretaceous floral structure that may be referable to Liliales. Alismatales are known based on several probable araceous fossils including monsteroid seeds from the Campanian–Maastrichtian of the Mira locality, Portugal (Fig. 13E–F), an orontioid inflorescence from the Late Cretaceous of Canada (Bogner, personal communication 2004) and various aroid leaf fossils (for references see Friis et al., 2004).

Mabelia and *Nuhliantha* are two genera established for small staminate flowers from the Late Cretaceous (Turonian) of New Jersey assigned to the Triuridaceae (Gandolfo et al., 2002). The fossil flowers consist of six basally fused tepals and three stamens with sessile or almost sessile anthers and extrorse dehiscence. Pollen grains are monoaperturate and smooth. Although the flowers share many features with extant monocots their affinity to Triuridaceae is not clear. As noted by Rudall (2003), there are differences between some features of these fossils and extant Triuridaceae. Most notably, pollen in Triuridaceae is inaperturate or with an indistinct aperture and has a gemmate wall sculpture. The fossils also share features with some Myristicaceae (Magnoliales), especially the form of the distinctive staminate column. The possible relationships of these fossils require further investigation.

Arecaceae (palms) are particularly common in Late Cretaceous floras from low and middle palaeolatitudes. The group first appeared in the Coniacian and underwent major diversification through the rest of the Late Cretaceous. Dispersed pollen grains of palms, including genera such as *Spinozonocolpites* (related to extant *Nypa*) and *Mauritiidites* (related to extant Mauritieae) constitute up to 50% of some palynological assemblages in the so-called Palmae Province, which extended across northern South America, most of Africa and India during the Coniacian–Maastrichtian (Herngreen et al., 1996). Fruits of palms are also known from the Maastrichtian Deccan Intertrappean flora of India and include several species of *Nypa* (Chitaley, 1960; Chitaley and Nambudiri, 1995) and *Palmocarpon* (Prakash, 1954). Two closely related fossil taxa from the Deccan Intertrappean flora, *Shuklanthus* and *Viracarpon* (Verma, 1958; Nambudiri and Tidwell, 1978) may also be palms, but have also been compared to other monocot groups, particularly Pandanaceae (Nambudiri and Tidwell, 1978). They comprise small flowers or fruits that are densely arranged in six vertical rows along an elongated inflorescence axis. The flowers are pistillate and apparently perigynous with a perianth consisting of six tepals and a gynoecium of six free carpels. Each carpel contains a single ovule. *Tricoccites trigonum* is another Deccan Intertrappean fossil that has been compared to Arecaceae and Pandanaceae (Chitaley, 1956). The trimerous flowers of *Deccananthus savitrii* (Chitaley and Kate, 1974) from the same flora was also noted to have similarities with modern palms.

Zingiberales are known from several Late Cretaceous localities and were apparently widely distributed by the end of the Cretaceous. Seeds of *Spirematospermum*, an extinct genus of Musaceae, are reported from Europe and North America (Goth, 1986; Knobloch and Mai, 1986; Friis, 1988), while fruits and seeds assigned to the extant genus *Musa* (Musaceae) are reported from the Deccan Intertrappean flora of India (Jain, 1963).

5.5. Fossil reproductive structures of basal eudicots

The earliest evidence of eudicots in the fossil record is provided by dispersed tricolpate pollen grains recovered from the Late Barremian–Early Aptian (e.g., Doyle, 1992). In these palynofloras eudicot pollen typically is of low abundance, but shows considerable structural variety and the fossil record indicates a dramatic increase in diversity and abundance through the later part of the Aptian and the Albian. A rapid diversification of eudicots, with the emergence of all lineages of basal eudicots before the end of the Albian has also been inferred using molecular dating methods (Anderson et al., 2005). The earliest tricolpate grains (assigned to genera such as *Tricolpites*, *Retitricolpites* and *Striatopollenites*), are typically small, simple forms with a semi-tectate reticulate or striate tectum, and columellar or granular infratectal layer. Based on pollen wall structure and aperture configuration a potential relationship of some of the striate grains to extant members of early diverging eudicot lineages, such as Buxaceae, has been suggested (Doyle, 1992).

Several floral structures of eudicot angiosperms have been discovered in Early Cretaceous mesofossil floras from Portugal and North America. Most of them remain to be described in detail. They are typically small, unisexual or bisexual, and few-parted with a perianth of undifferentiated tepals. One of these early eudicot flowers, from the Vale de Agua flora (Late Aptian or Early Albian), Portugal, is the small staminate flower *Teixeiria lusitanica* (von Balthazar et al., 2005). The flower is preserved in pre-anthetic stage. It is actinomorphic with several bracts and tepals apparently in a spiral arrangement. The androecium has about 20 stamens of two sizes that are apparently in two whorls. In situ pollen grains are small and tricolpate with a perforate tectum. The relationships of this flower appear to be to extant Ranunculales, but the fossil cannot be accommodated easily in any existing family.

Spanomera is another early eudicot with small unisexual flowers. It includes two species from Maryland, one from the Late Albian flora of West Brothers clay pit and one from the Early Cenomanian flora of Mauldin Mountain (Drinnan et al., 1991). Staminate and pistillate flowers are borne in diclinous inflorescences. The organisation of both inflorescence units and floral organs is opposite and decussate (Fig. 15). Staminate flowers consist of four to five tepals, each opposite a stamen. The stamens have a short filament; anthers are tetrasporangiate with a short apical extension of the connective. Pollen grains are tricolpate with semi-tectate pollen wall and a striate–rugulate to reticulate–rugulate sculpture. Pistillate flowers are bicarpellate with basally fused carpels and with long decurrent stigma along most of the ventral suture. *Spanomera* shows a close relationship to extant Buxaceae, but the pollen is distinct from that of modern members of the family. The fossil most likely represents an extinct taxon close to the base of the Buxaceae.

Sinocarpus decussatus, an early compression/impression fossil from the Yixian Formation of northeastern China, may also be related to basal eudicots (Leng and Friis, 2003). In addition to the published inflorescence axis (see, Leng and Friis, 2003) another inflorescence has now been discovered associated with minute angiosperm leaves (Leng and Friis in progress). The inflorescence is compound and preserved at fruiting stage. Each fruit is composed of three or four carpels that are united at the base and that apparently have a decurrent stigma that extends along the free part of the ventral suture. There is no information on other floral organs and the organisation of the original flower is unknown. The character combination of *Sinocarpus* indicates a relationship to basal eudicots such as Ranunculaceae, Buxaceae and Myrothamnaceae, but based on the information currently available more precise evalua-

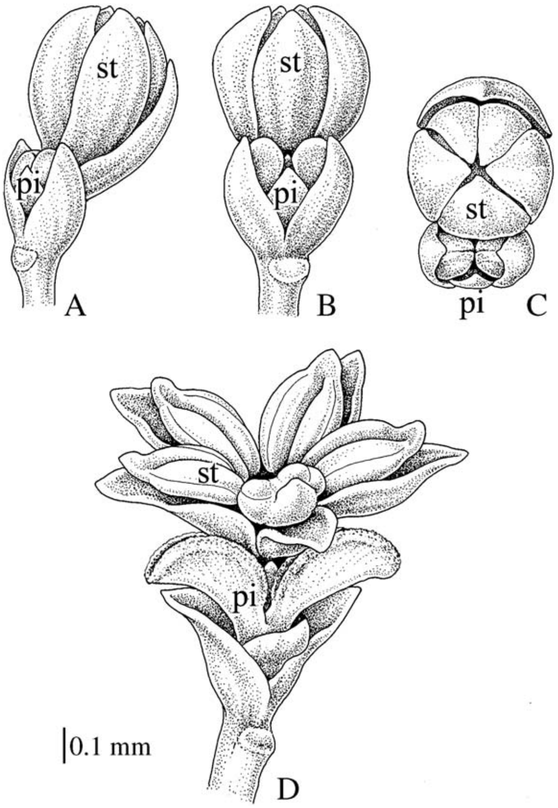


Fig. 15. Reconstruction of the Late Cretaceous *Spanomera mauldinensis* (Buxales) from Maryland, USA. (A–C) Part of inflorescence with staminate (st) and pistillate (pi) flowers in bud stage, lateral (A–B) and apical (C) view. (D) Lateral view of inflorescence in flowering stage showing pentamerous staminate flower (st) and bicarpellate pistillate flower (pi). Reconstruction new, based on SEM-pictures in Drinnan et al. (1991) and material in the collections of the Field Museum, Chicago.

tion of the systematic position of the fossil is not possible.

Another potential early eudicot is *C. paniculiger* from the Middle Albian of Kazakhstan (Fig. 5C). The inflorescence of the plant is strongly compressed but has densely crowded flowers and is described as a compound structure (Krassilov, 1997). It is attached to a shoot that bears leaves similar to *Vitiphyllum*, which have been compared to leaves of extant Ranunculales (Doyle, 2001).

Small platanoid inflorescence-heads and dispersed flowers are common in the Early Cretaceous floras of eastern North America, where they are first recorded from the Early to Middle Albian (e.g., Friis et al., 1988; Crane et al., 1993; Pedersen et al., 1994). They are referred to a number of extinct genera such as *Aquia* (Crane et al., 1993), *Hamatia* (Pedersen et al., 1994) and *Platananthus* (e.g., Friis et al., 1988). The inflorescence heads are monoclinous and consist of minute flowers that are densely crowded on a more or less spherical central axis. Both pistillate and staminate flowers are more or less actinomorphic, generally pentamerous and often with distinct tepals (Fig. 16A–C). The stamens have a short filament and tetrasporangiate anthers with valvate dehiscence. There is usually a prominent apical extension of the connective, which may be variously developed. Flowers of Cretaceous platanoids are distinct from those of extant *Platanus* in their pentamerous (or occasionally tetramerous) organisation and valvate anther dehiscence. It has been suggested that they were insect pollinated rather than wind pollinated like their living relatives (Friis et al., 1988).

In Late Cretaceous floras basal eudicots continue to diversify and are represented most conspicuously by diverse floral structures (Friis et al., 1988; Magallón-Puebla et al., 1997; Maslova and Kodrul, 2003) and leaves of Platanaceae. Based on the fossil pollen record it is clear that the Proteaceae also diversified through the Late Cretaceous (Dettmann and Jarzen, 1998), but currently no floral structures of this family have been recovered from sediments of this age.

From the Late Cretaceous (Late Santonian–Early Campanian) Åsen flora of southern Sweden there are several intriguing follicular fossils that are thought to represent an extinct complex of basal eudicot angiosperms perhaps close to Proteales. They include species assigned to the fossil genera *Maiandrocarpus*, *Mitocarpus*, and *Zeugarocarpus* that have follicles in distinct pairs supported by a cup-like bract and borne spirally on an infructescence axis (Leng et al., 2005). There are no traces of a perianth and the flowers have been interpreted as naked. The orientation of the follicles strongly indicate that the paired carpels were

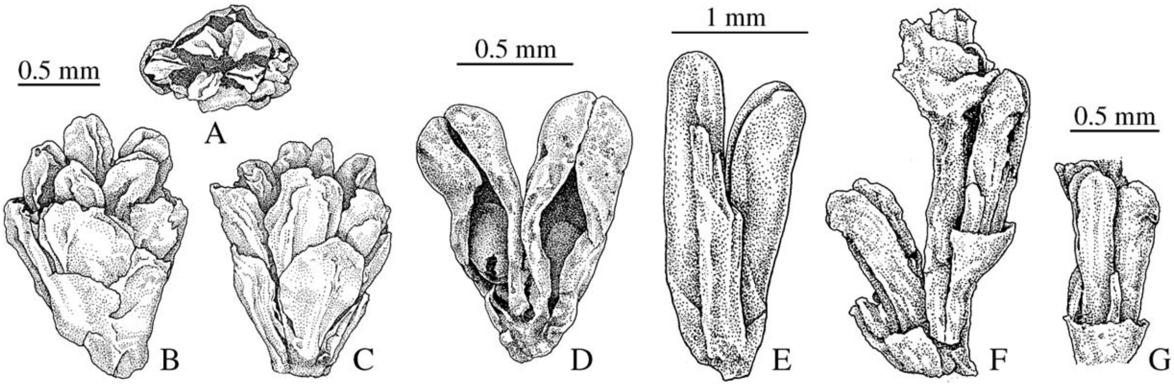


Fig. 16. Basal eudicots from the Cretaceous. (A–C) *Platanocarpus brookensis* from the Early Cretaceous of the Bank near Brooke locality, Virginia, USA, showing distinct tepals and five carpels of pistillate flower. (A) Apical view (PP43038). B. Lateral view (PP42998). C. Lateral view (PP43044). (D–G) Paired follicular fruits from the Late Cretaceous of southern Sweden. (D) *Maiandrocarpus moirasmenus*, ventral view of paired follicles with ventral suture split open exposing the seeds (S106080). (E) *Zeugarocarpus adroagathus*, ventral view of paired follicles with remnants of inflorescence axis (S106350). (F–G) *Mitocarpus elegans*, inflorescence fragment with bracts bearing paired follicles (F) and paired follicles in dorsal view (G) (S107034). A–C based on SEM-pictures in Crane et al. (1993); D–G based on SEM-pictures in Leng et al. (2005). S-numbers refer to material in the collections of the Swedish Museum of Natural History. PP numbers refer to material in the collections of the Field Museum, Chicago.

derived from two monocarpellate flowers arranged in pairs rather than from a single bicarpellate flower (Fig. 16D–G). Paired monocarpellate flowers with plicate carpels are known in extant plants only for Proteaceae. Other species from the Åsen flora assigned to the genera *Agapitocarpus*, *Chontrocarpus*, and *Xylocarpus* (Leng et al., 2005) are known only as dispersed, isolated follicles, but they share many features with the paired follicles, and are thought to belong to the same complex of taxa. The material also includes a single taxon assigned to the genus *Malliocarpus*, which has spirally arranged cup-like bracts supporting a single follicle only (Leng et al., 2005). Comparison with extant angiosperms suggest that these fossils probably belong to an extinct lineage within or close to basal eudicots. The fossils share many characters with extant Proteaceae, but they also show some resemblance to extant *Didymeles* (Didymelaceae, Buxales), a basal eudicot now restricted to Madagascar. The fossil are, however, distinct from extant Proteaceae and Didymeles in several important aspects including number and structure of seeds and nature of perianth, and they cannot be assigned to a modern family based on current information (Leng et al., 2005).

5.6. Fossil reproductive structures of core eudicots

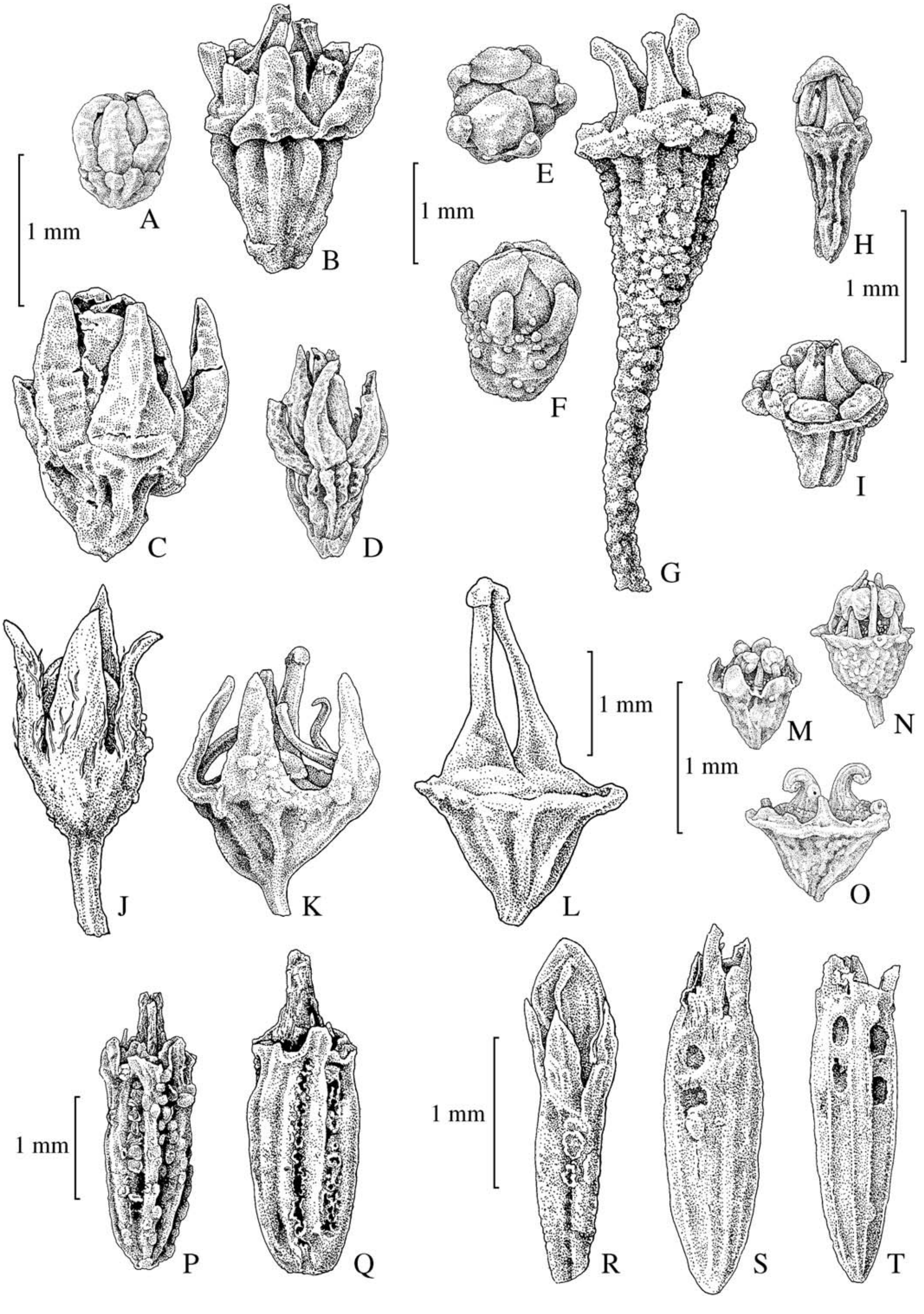
In general, flowers of core eudicots are characterised by their whorled organisation, fixed number of floral parts, and the presence of a distinct calyx and corolla. Pollen grains also show much greater variation in aperture configuration than those of basal eudicots. For instance, tricolporate and triporate pollen are common among core eudicots. Age estimates based on molecular clock calculations suggest that core eudicots originated in the Early Cretaceous (e.g., Bremer et al., 2004). Several different species of tricolporate pollen in the Albian (Doyle and Hickey, 1976) may represent early core eudicots. However, most of these early tricolporate grains are dispersed and the nature of the parent plants is unknown. Since tricolporate pollen also occurs among basal eudicots (e.g., most Menispermaceae, Thanikaimoni, 1984) and have been found in situ in Early Cretaceous platanoid flowers (Pedersen et al., 1994) grains of this type cannot be used as definite indicators of the presence of core eudicots. The earliest floral structures assignable to the group are from the early Late Cretaceous. It is, however, clear that core eudicots differentiated extremely rapidly during the Late Cretaceous and already by the Turonian–Coniacian they dominate many plant fossil assemblages.

The earliest fossils of unequivocal core eudicots are pentamerous flowers from the Cenomanian Rose Creek flora of Kansas. These unnamed flowers have been compared tentatively to those of extant Celastraceae (Basinger and Dilcher, 1984). The material comprises many compression/impression flowers, mainly preserved at fruiting stage, with a distinctive pentamerous and whorled organisation. The perianth is differentiated into a calyx and corolla, and stamens have a clearly differentiated filament and anther. The gynoecium is syncarpous and superior. A nectary disk appears to be inserted between the androecium and gynoecium. Flowers that have petals preserved are about 1–2 cm in diameter (Basinger and Dilcher, 1984) and are thus among the larger flowers so far recorded from Cretaceous floras.

In mesofossil floras from the Turonian and onwards eudicot flowers rapidly become more diverse, both structurally and in terms of their systematic affinity. There is clear evidence for a rapid and simultaneous diversification of both the rosid and asterid lineages (Magallón et al., 1999; Crepet et al., 2004).

Also in macrofossil floras core eudicots become the dominant angiosperm element during the Late Cretaceous. In the Maastrichtian Deccan Intertrappean flora core eudicots are common and include flowers and fruits described as extinct taxa such as *Chitaleypushpam mohgaoense* (Paradkar, 1973), *Raoanthus intertrappea* (Chitaley and Patel, 1975), *Sahnianthus shuklai* (Shukla, 1944) and *Sahnianthus dinectrianum* (Shukla, 1958). In the Late Cretaceous (Late Turonian–Santonian) petrified flora of Hokkaido, Japan, *Elsemaria* is a calcified fruit that has also been assigned to the core eudicots (Nishida, 1994). The fruit is a capsule with many locules. Each locule has more than 40 anatropous ovules. The fossil is preserved in the fruiting stage with no information on perianth and androecium and its systematic position is not fully resolved.

The most common types of flowers among the mesofossil from the Late Cretaceous are small pentamerous, actinomorphic and bisexual forms that are often epigynous and have a pronounced nectary disk (Fig. 17). The gynoecium is typically syncarpous and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often formed from two or three carpels. The fruits are often capsules containing many small, anatropous seeds. The first flowers of this general organisation to be described from the Cretaceous were *Scandianthus costatus* (Fig. 17A–B, D) and *Scandianthus major* (Fig. 17C) from the Late Santonian–Early Campanian flora of Åsen, southern Sweden (Friis and Skarby, 1982). They are probably related to extant families of the asterid clade (compared to Vahliaceae and other members of the Saxifragales sensu lato that are now resolved as asterids). Other flowers that conform to this general floral type, and that probably also belong to the asterids, are flowers of *Silvianthemum* (Fig 17E–G) compared to extant *Quintinia* and Escalloniaceae (Friis, 1990), an unnamed flower with strongly lobed nectary (Fig. 17 H–I) from southern Sweden, as well as two genera from the Turonian flora of New Jersey: *Divisestylus* (Fig. 17J–L) with affinity to Iteaceae (Hermsen et al., 2003) and *Tylerianthus* (Fig. 17M–O) with affinity to Hydrangeaceae (Gandolfo, 1998). Others, such as *Platydiscus peltatus* (Cunoniaceae) (Fig. 3) (Schönenberger et al., 2001a) from southern Sweden and species of *Esqueiria* (related to Combretaceae) from the Campanian–Maastrichtian floras of Mira and Esgueira, Portugal (Fig. 17R–T)(Friis et al., 1992) and the Early Coniacian Kamikitaba flora of Japan (Fig. 17P–Q) (Takahashi et al., 1999a) also indicate the presence of rosids. In addition to these named fossils there are also numerous undescribed flowers from the Late Cretaceous floras including many from North America (Herendeen et al., 1999) and Japan (Takahashi et al., 1999b).

A further common type of flower from the Late Cretaceous is pentamerous, hypogynous, with well-differentiated calyx and corolla, and a gynoecium of two, three or five carpels. Some of these flowers have a nectary, but this is lacking in others. Most of these flowers apparently belong to groups that diverged early from the asterid line. For example, *Hironoia fusiformis* from the Late Cretaceous (Early Coniacian) Kamikitaba flora of Japan (Takahashi et al., 2003) is the oldest well-documented member of the Cornaceae. Other early representatives of Cornaceae include diverse mastixiod fruits from the Campanian–Maastrichtian of Europe (Knobloch and Mai, 1986).

Flowers related to extant Ericales are especially common in the Late Cretaceous. Ericales are also represented by abundant and widespread records of fruits and seeds. Among the Late Cretaceous ericalean reproductive structures that have been described in detail are flowers of *Parasaurauia* from the Allon flora of Georgia assigned to the Actinidiaceae (Keller et al., 1996), *Actinocalyx* and *Paradinandra* from southern Sweden (Friis, 1985; Schönenberger and Friis, 2001), *Paleoenkianthus* and several unnamed flowers from the Turonian of New Jersey (Nixon and Crepet, 1993; Crepet, 1996) as well as numerous taxa based on fruits and seeds from Central Europe including fossils that have been assigned to modern genera such as *Eurya*, *Leucothoe*, and *Saurauia* (Knobloch and Mai, 1986).

Among the pentamerous and hypogynous group of fossil flowers are also several forms of rosid affinity. These include two flowers from the Turonian of New Jersey, *Dressiantha bicarpellata* originally assigned to the Capparales (now incorporated in Brassicales) (Gandolfo et al., 1998) and *Paleoclusia chevalieri* assigned to the Clusiaceae (Crepet and Nixon, 1998a), now placed in Malphigiales.

Fig. 17. Core eudicots from the Late Cretaceous of Europe, North America, and Asia with small actinomorphic and epigynous flowers. (A–B, D) Three specimens of *Scandianthus costatus* from southern Sweden showing small flower bud (A: S105316), post-anthetic flower (B: S105313) and anthetic flower (D: S127398). (C) *Scandianthus major* from southern Sweden (S105314). (E–G) Two specimens of *Silvianthemum suecicum* from southern Sweden showing flower bud (S100376) in apical (E) and lateral (F) view and post-anthetic flower (G: S100377) in fruiting stage. (H–I) Two specimens of unnamed eudicot flower from southern Sweden showing flower bud (H: S106382) and fragment of possible anthetic flower (I: S127329) with distinctive five-lobed nectary disk. (J–L) Flowers of *Divisestylus brevistamineus* (J) and *Divisestylus longistamineus* (K–L) from New Jersey. (M–O) Three specimens of *Tylerianthus crossmanensis* from New Jersey showing flowers close to anthesis (M–N) and at post-anthetic stage (O). (P–Q) two flowers of *Esgueiria futabensis* from Japan probably preserved at anthesis. (R–S) Three specimens of *Esgueiria adenocarpa* from Esgueira, Portugal, showing flower bud (R: S100639) and flowers at anthesis (S–T; S:S100676; T:100678). A based on SEM-picture in Friis et al. (Friis et al., 2001b); B–C and T based on unpublished SEM-pictures in the collection of the Swedish Museum of Natural History; D, H–I based on SEM-pictures in Friis (1984); E–G based on SEM-pictures in Friis (1990); J–L based on SEM-pictures in Hermsen et al. (2003); M–O based on SEM-pictures in Gandolfo et al. (1998); P–Q based on SEM-pictures in Takahashi et al. (1999a); R–T based on SEM-pictures in Friis et al. (1992). S-numbers refer to material in the collections of the Swedish Museum of Natural History.

Fagales are another important group of rosids that diversified in the Late Cretaceous and that dominate certain Late Cretaceous floras. Based on the pollen record, as well as data from mesofossil floras, Fagales were both phylogenetically diverse and ecologically important in the Late Cretaceous. Most Late Cretaceous fossil Fagales cannot be assigned to a particular extant family and extinctions among the diverse Cretaceous lineages were apparently extensive. The earliest record of the group is probably provided by various kinds of Normapolles type pollen from the Late Cenomanian (Batten, 1981; Kedves, 1989) and this is followed by rapid diversification through the Late Cretaceous.

The Normapolles complex comprises a group of characteristic pollen that typically has three complex apertures with three internal pores and often three short external colpi. More than 100 species in more than 80 genera have been described (e.g., Góczán et al., 1967; Batten and Christopher, 1981) and Normapolles pollen is a conspicuous element in many Late Cretaceous palynofloras from the Northern Hemisphere making up more than 80% of all angiosperm pollen in some European palynofloras from the Late Cretaceous (Pacltová, 1981).

Normapolles pollen has been found in situ in several distinct fossil flowers. They include species of *Antiquocarya*, *Caryanthus* and *Manningia* first described from the Late Santonian–Early Campanian of southern Sweden (Friis, 1983) and later reported from several Late Cretaceous floras of Central Europe together with a number of other possible Normapolles flowers (Knobloch and Mai, 1986; Friis and Crane, 1989). *Normanthus* and *Endressianthus* described from the Campanian–Maastrichtian of Portugal (Schönenberger et al., 2001b; Friis et al., 2003b), and *Bedellia* described from the Santonian Allon flora of Georgia (Sims et al., 1999) also have in situ Normapolles pollen. All these flowers either lack a perianth, or have simple perianth consisting of a single whorl of tepals. All those described so far also have inferior ovaries that develop into nuts or drupes with one or two seeds. A recently discovered Normapolles taxon with hypogynous flowers expands the organisational diversity of the group in having hypogynous flowers (Friis, Pedersen and Schönenberger in progress). Except for *Endressianthus* (Fig. 18) all Normapolles flowers currently described are bisexual, which is probably a plesiomorphic feature within Fagales as a whole.

All Normapolles flowers currently known show close similarities to various extant Fagales, but are all considered to represent extinct lineages within the order close to Betulaceae, Rhoipteleaceae, Myrtaceae, and Juglandaceae (Friis et al., 2003b).

As would be expected from phylogenetic relationships among Fagales, plants sharing features with extant Fagaceae and Nothofagaceae were also well established and diverse in the Late Cretaceous. They are represented in the Northern Hemisphere by fossil flowers of *Antiquacupula* and *Protofagacea* known from isolated flowers as well as inflorescences preserved at different developmental stages (Fig. 19) (Herendeen et al., 1995; Sims et al., 1998). In the Southern Hemisphere the presence of Nothofagaceae

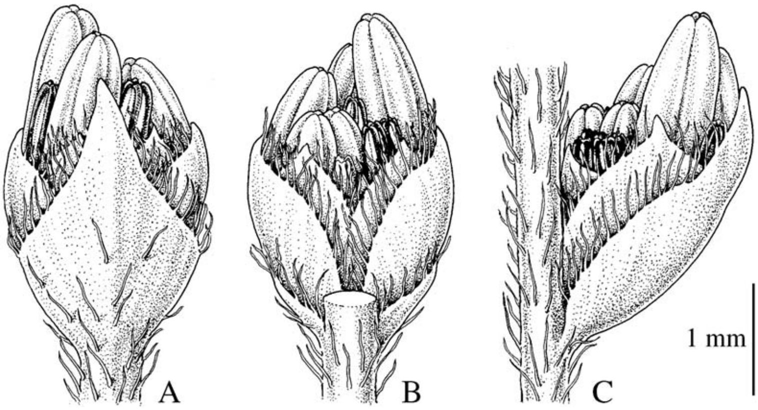


Fig. 18. Reconstruction of partial staminate inflorescence of *Endressianthus miraensis,* a Normapolles flower from the Late Cretaceous of Portugal, in abaxial (A), adaxial (B) and lateral (C) view. Redrawn from Friis et al. (2003b).

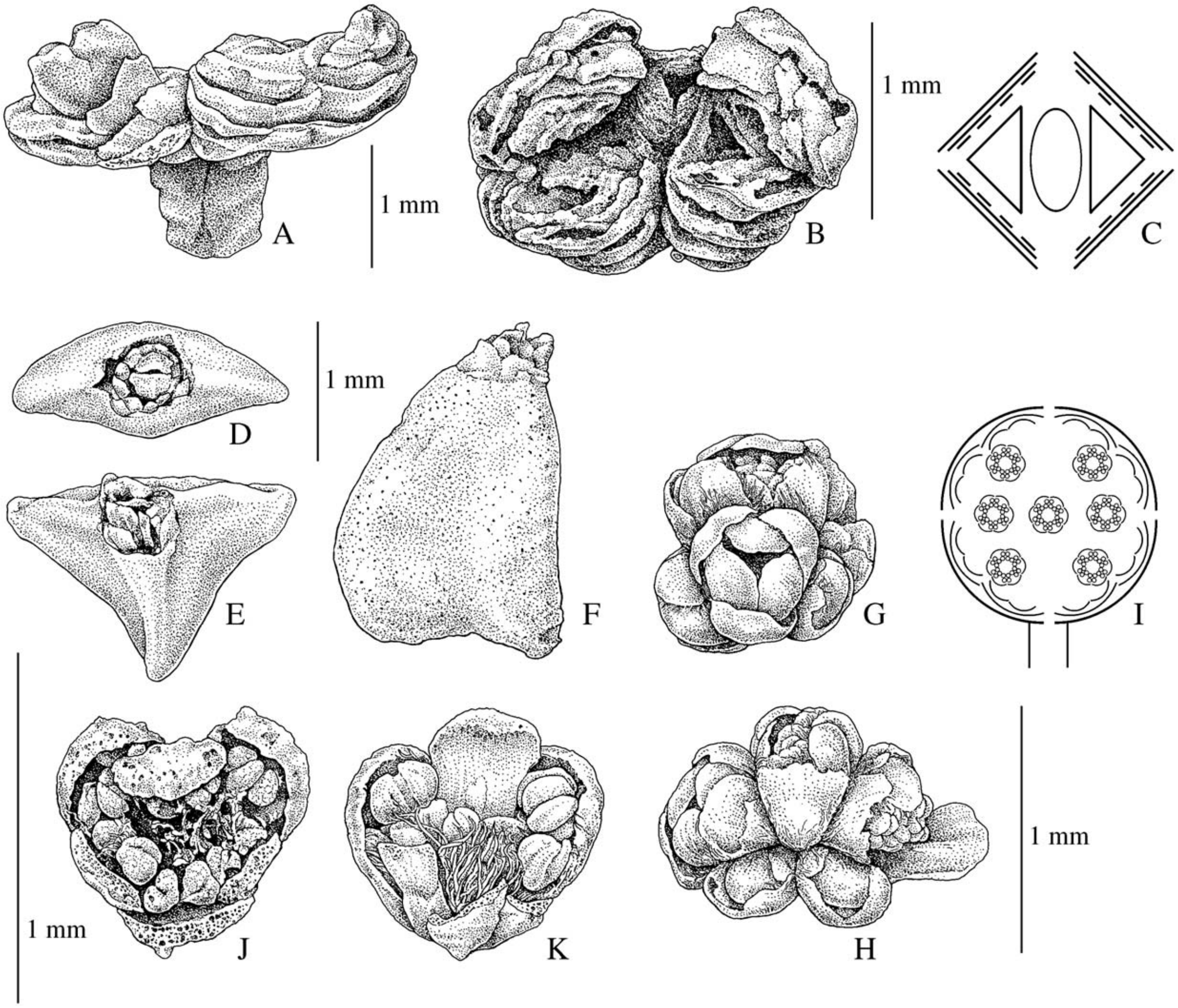


Fig. 19. Charcoalified flowers and inflorescences of Fagaceae from the Late Cretaceous of Georgia, USA, allowing detailed reconstruction of organisation and structure including construction of floral diagrams. (A–B) Mature cupules of fagaceous plant in lateral (A) and apical view (B). (C) Floral diagram of cupules. (D–F) Fruits of *Protofagacea allonensis* in apical (D–E) and lateral (F) view. (G–H) Staminate partial inflorescence in apical (G) and lateral (H) view. (I) Floral diagram of partial inflorescence and staminate flowers. (J–K) Isolated staminate flower in apical (J) and lateral (K) view. All figures based on SEM pictures and floral diagrams in Herendeen et al. (1995).

in the Late Cretaceous is well established by the presence of several dispersed pollen taxa assigned to *Nothofagites* (e.g., Dettmann, 1994).

6. Conclusion

6.1. Phylogenetic diversification

It is very clear from the fossil record that the first major differentiation of angiosperms took place over a relatively short time during the Early Cretaceous. This is clearly recognised in the record of fossil angiosperm pollen, but is also supported by patterns in the changing diversity and abundance of angiosperm reproductive structures through this interval. A rapid Early Cretaceous diversification of angiosperms is also inferred from recent dating of phylogenetic trees based on molecular data (e.g., Bremer, 2000; Bremer et al., 2004; Anderson et al., 2005). The precise details of this rapid diversification, and extant groups involved, remain uncertain, but the major patterns are becoming steadily clearer.

There is no convincing evidence of angiosperms from pre-Cretaceous strata. But palaeobotanical data indicate that ANITA grade angiosperms and Chloranthaceae, as well as magnoliids sensu stricto, early eudicots, and early monocots, were present by the Late Barremian–Aptian. At this time, angiosperms did not yet dominate Cretaceous vegetation, but their initial phylogenetic diversification was already well under way. Many lineages of angiosperms were present during the Barremian–Aptian that are now extinct. Further differentiation of the three major lineages of angiosperm (magnoliids sensu stricto, monocots, eudicots) took place during the Late Cretaceous and is well documented by the palaeobotanical record. In particular there is strong evidence for extensive diversification among core eudicots during the Late Cretaceous. This included rapid diversification of rosids, as well as diversification of lineages such as Ericales that differentiated early within the asterid clade.

With regard to the overall accumulation of angiosperm species diversity it is interesting that many of the earliest lineages, such as ANITA grade angiosperms, Chloranthaceae, and basal grade eudicots, show extremely low extant species diversity, despite their long geological history. This may reflect both inherently low speciation rates as well as significant extinction. In contrast, much of the species-richness of extant angiosperms is contributed by hyper-diverse families that first appeared and diversified relatively late in the geological history of angiosperms (Magallón et al., 1999; Friis et al., 2005). For instance, among extant angiosperms asterids are especially species-rich, but so far evidence of many of the most diverse asterid families such as the Asteraceae with more than 20,000 species does not appear until the Cainozoic. Similarly, legumes are one of the most species-rich of all angiosperm families, but there is no secure fossil evidence of the group until the very latest Cretaceous or earliest Cainozoic (Herendeen et al., 1992).

6.2. Functional diversification

In addition to patterns of phylogenetic diversification, the fossil record of angiosperm flowers also provides insights into the timing of floral evolution in terms of functions of the various kinds of floral organs. In part this reflects phylogenetic differentiation, but it also reflects common trends linked to ecology and reproductive biology that evidently occurred in parallel in different angiosperm lineages (Fig. 20).

Primary functions of flowers are the production of pollen and ovules in the stamens and pistils, which is accompanied by mechanisms to promote fertilisation; secondary functions are protection of the developing flower against desiccation and the development of mechanisms that promote cross-pollination (Endress, 1994).

Ovule production per flower was probably low in most Early Cretaceous angiosperms. In most flowers of this age the gynoecium typically consists of a single carpel or is apocarpous consisting of few free carpels. Typically the stigmatic region of the carpels is insignificant and not highly elaborated. Many of the fossil flowers with these characteristics were probably insect-pollinated. Each pollination event would only have created possibility for limited fertilization of ovules, and therefore limited production of seed. Only the *Hedyosmum*-like plants, which are thought to have been wind-pollinated as in the extant genus, have a distinct and expanded stigma that is almost as big as the remaining pistil (Fig. 7I).

Similarly, the carpels of Early Cretaceous angiosperms usually contain one to few ovules. This is in contrast to expectations based on earlier ideas of classical morphology, but in line with results from recent molecular and modern morphological studies of extant angiosperms (Endress, 2001a). Elaboration of the number of ovules per carpel appears secondary in angiosperm evolution as a whole and this has important implications for ideas about the origin and subsequent evolution of carpel form and function. Nevertheless, *Archaefructus* and *Sinocarpus* from the Yixian Formation of China, which have several ovules per carpel, show that an increase in ovule number per carpel occurred at an early stage in some angiosperm lineages.

The synorganisation of carpels observed in *Sinocarpus* from the Early Cretaceous Yixian Formation of China and in the trimerous, putative monocot flower from the Early Cretaceous of Portugal documents that by the Late Barremian–Early Aptian syncarpy (fusion of carpels) had evolved perhaps together with the establishment of a common pollen tube transmission tract. This potentially permits mul-

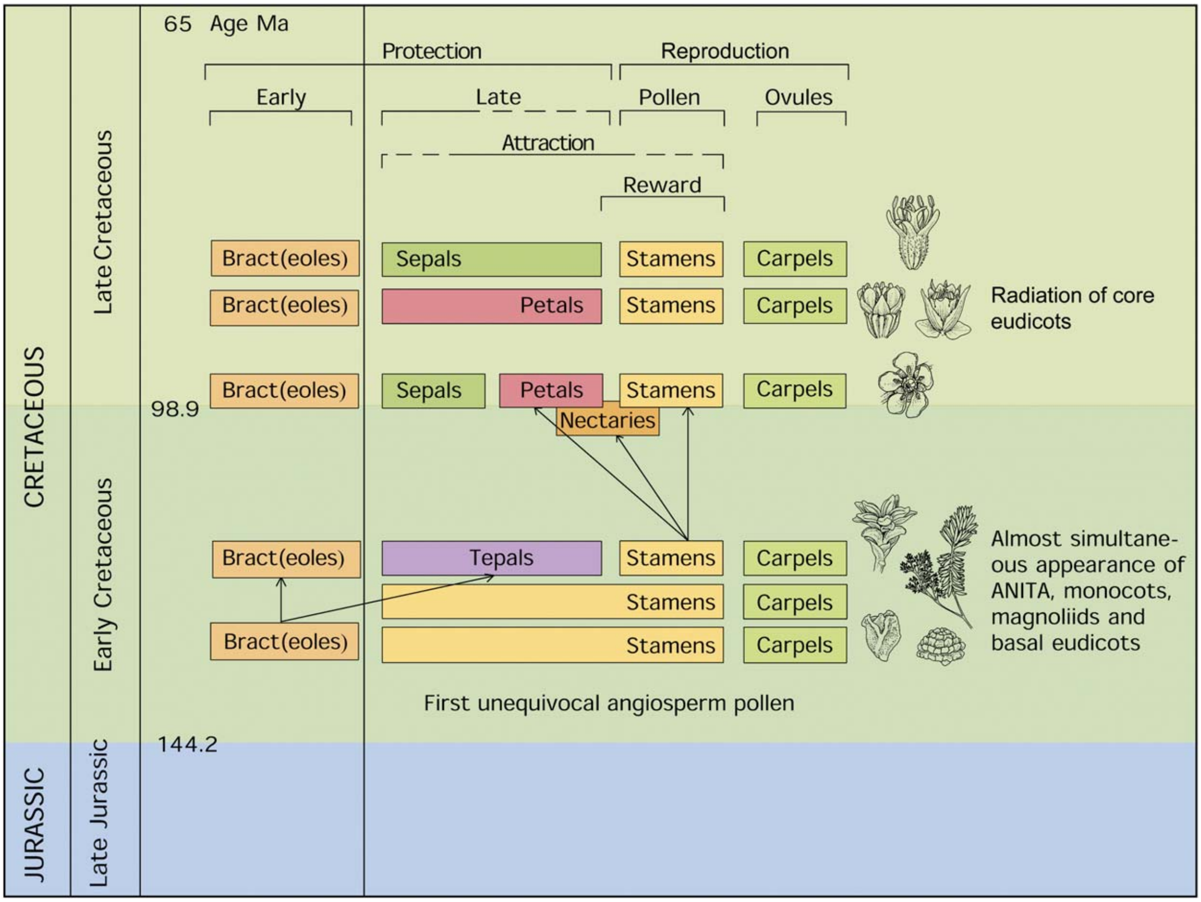
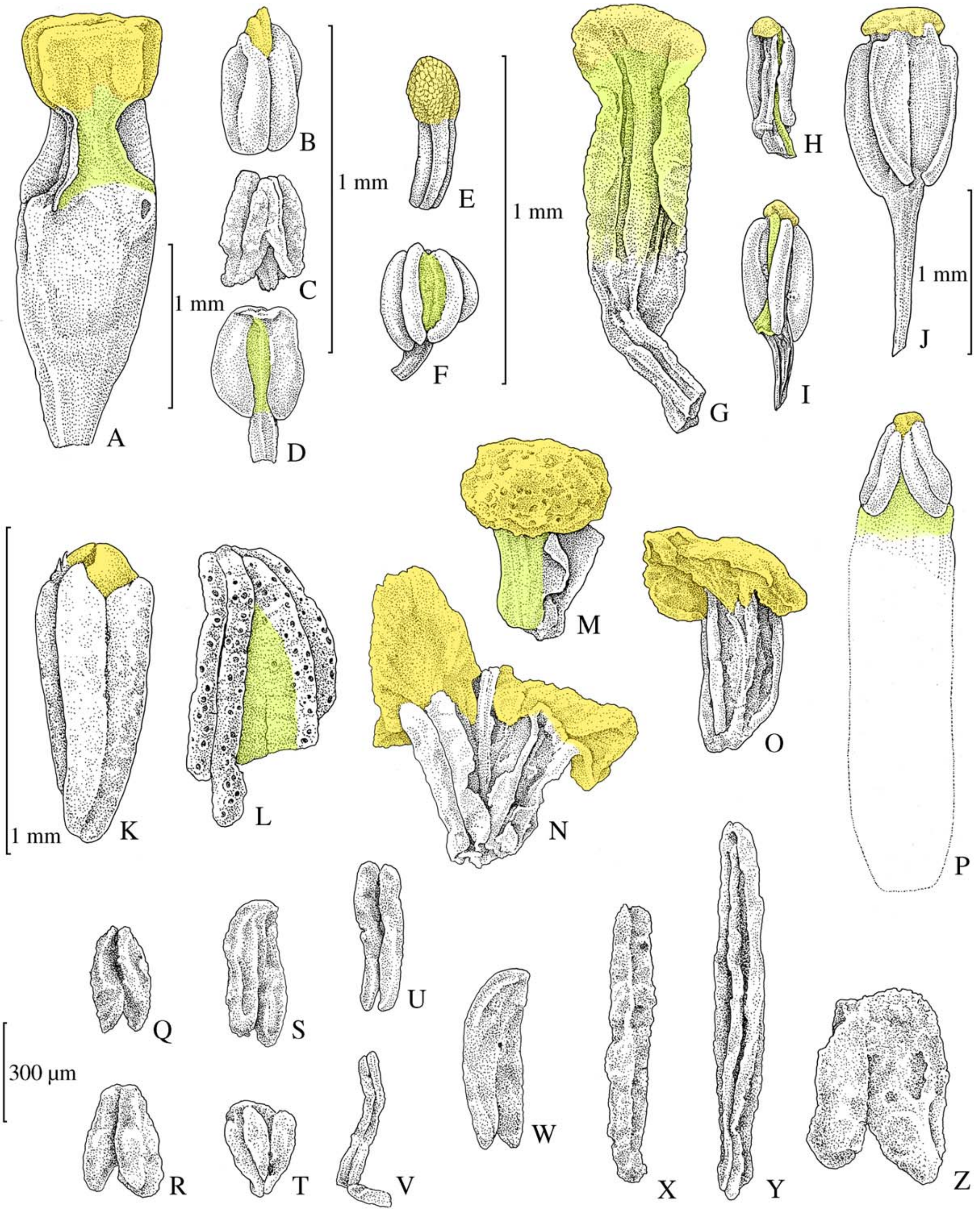


Fig. 20. Angiosperm floral organs and their major functions (based on Endress, 1994) set in a stratigraphic perspective and illustrating the shift in protection and attraction by the early Late Cretaceous with the first occurrence of flowers with a corolla in the Late Cretaceous.

tiple fertilizations to result from a single pollination event and may have been one of the most important innovations that appeared initially both among early eudicots and early monocots. Syncarpy is the dominant mode of gynoecium organisation in Late Cretaceous angiosperms.

Pollen production per stamen appears to have been low in most Early Cretaceous angiosperms. Pollen sacs are typically small and in many stamens sterile tissue (connective) makes up the bulk of the anthers (Fig. 21). Often these stamens have valvate dehiscence, a feature that in extant angiosperms is restricted to insect-pollinated plants (Friis et al., 1991). Stamens with *Clavatipollenites* and *Asteropollis* pollen in situ, and stamens of other possible wind-pollinated plants, differ from other Early Cretaceous stamens in having larger pollen sacs and a connective that is typically more poorly developed.

It is interesting to note that all the stamens recovered so far from the Torres Vedras locality (Late Barremian or Early Aptian) have little sterile tissue (Fig. 21Q–Z), which may indicate wind-pollination. However, the coarsely reticulate pollen wall of many of the in situ pollen grains, and the frequent occurrence of the pollen also in coprolites suggests insect pollination for some of these early angiosperms. Versatility in pollination, as hypothesized previously for early angiosperms (Dilcher, 1979), could be one explanation for these apparently conflicting indications of pollination from the fossil record. It is also interesting that those pollen types that are inferred to come from wind-pollinated plants (*Asteropollis* and *Clavatipollenites*) based on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floral morphology and comparison to extant plants frequently occur in coprolites indicating that their flowers were also visited by insects.

In the Late Cretaceous there is much greater variation in stamen morphology than is seen in the Early Cretaceous, but most anthers are still of simple organisation (Friis et al., 1991; Crepet and Nixon, 1996). Typically they are dithecate and tetrasporangiate with dehiscence by simple longitudinal slits or by valves. Except perhaps in *Paleoenkianthus* from the Turonian of New Jersey (Nixon and Crepet, 1993) there is no indication in the Late Cretaceous of more sophisticated pollen presentation associated with specialised insect pollination. In some of the Normapolles flowers such as *Normanthus* the filament apparently elongated at anthesis: a specialisation that probably resulted in anthers that protruded in a lax arrangement (Schönenberger et al., 2001b).

In the Early Cretaceous there are two main types of fossil flowers in terms of perianth development: naked flowers that lack a perianth, as in the staminate *Hedyosmum*-like flowers and *Archaefructus*; and flowers with a perianth in which the tepals are undifferentiated as in *Endressinia*, *Virginianthus* (both magnoliids sensu stricto), the pistillate *Hedyosmum*-like flowers (Chloranthaceae) and several basal eudicots, such as *Spanomera* and various platanoid flowers. The perianth of *Teixeira* is also undifferentiated but shows a transition from more sepal-like to more petal-like tepals (von Balthazar et al., 2005). Where a perianth is lacking protection was most likely by floral bracts as in comparable extant plants, for example as in the staminate flowers of extant *Hedyosmum*. The apparent absence of both bracts and perianth parts in *Archaefructus* may reflect secondary loss associated with extreme specialisation of flower development and function in an aquatic habitat as suggested by Friis et al. (2003a).

In some Early Cretaceous flowers, such as *Virginianthus*, *Endressinia* and *Teixeiria*, tepals may have been showy but the prominent androecium in these taxa may also have been important in the attraction of pollinators. A further consideration is that since Cretaceous flowers were typically very small, dense packing into larger inflorescences may also have served in the promotion of pollination efficiency, both for insect pollinated and wind-pollinated flowers. This is observed in *Xingxueina*, *Hedyosmum*-like flowers, *Caspiocarpus*, the Koonwarra fossil, *Pennistemon*, *Mauldinia*, *Prisca*, *Caloda*, *Myricanthium*, *Pragocladus*, and many others. It is also inferred for *Archaefructus* that may have been pollinated under water.

By the early Late Cretaceous flowers with a perianth that is clearly differentiated into sepals (calyx) and petals (corolla) are first recorded and these represent core eudicots. In these flowers the calyx has the most important protective role, whereas the corolla is often modified for the attraction of pollinators. Secondary loss of one or both perianth whorls has occurred in many lineages of core eudicots. Among Late Cretaceous flowers this is seen most obviously in flowers of the Normapolles complex (Fagales), where it may be associated with a trend towards wind-pollination. In these cases the protective function often again reverts to the bracts. In *Endressianthus*, for instance, where the perianth is reduced to small thorn-like structures, protection appears to have been by the enlarged bracts that subtended the flowers.

In many Early Cretaceous flowers the stamens too appear to have functioned in both protection and attraction, as well as in the production and release of pollen. In particular, the stamens of many fossil magnoliids and early eudicots have a distinctive connective that is expanded between and above the pollen sacs (Fig. 21). This expanded connective may have helped protect the developing pollen sacs and pollen during flower development. In many cases the connective is also swollen and sometimes glandular, indicating that it may have been involved in the attraction of pollinators as is the case for similar structures in extant angiosperms (e.g., Endress, 1996). The reward to pollinators visiting Early Cretaceous flowers was most likely pollen. Flowers with nectaries developed

Fig. 21. Selection of Early Cretaceous stamens from Portugal and North America. Several of these probably functioned in early protection of the developing flower and probably also in attraction of pollinators by the extensive connective between (green) and above (yellow) the pollen sacs. (A–D) Stamens from the Vale de Agua (A–C) and Buarcos (D) floras of Portugal. (E–J) Stamen from the Puddledock flora of Virginia, USA. (K–P) Stamens from the Catefica flora of Portugal. (Q–Z) Stamens from the Torres Vedras flora, Portugal. A based on SEM picture in Friis et al. (1994b); B based on SEM-picture in Friis et al. (2000a); C, G–J, N–O and Q–Z based on unpublished SEM-picture in the collections of the Swedish Museum of Natural History; D based on SEM-picture in Friis et al. (1999); E–F based on SEM-pictures in Crane et al. (1994); K–L, M and P based on SEM-pictures in Friis et al. Friis et al., 2000b.

early in the Late Cretaceous and are very common among Late Cretaceous core eudicots.

In core eudicots attraction of pollinators is mostly by the petals and these are generally believed to have evolved by the sterilisation of stamens in the course of evolution (Kramer et al., 1998). This developmental innovation must have occurred sometime in the Mid-Cretaceous. The first appearance of flowers with clearly differentiated petals is in the earliest Cenomanian. All Late Cretaceous flowers with perianth parts preserved are small and typically actinomorphic with simple petals. *Actinocalyx* is significant as the oldest flower with a sympetalous corolla (Friis, 1985). So far there is no direct evidence for more elaborate and showy flowers although fruits and seeds assigned to the Musaceae (*Musa* and *Spirematospermum*) provide indirect evidence for the presence of larger zygomorphic flowers among Late Cretaceous monocots.

6.3. Ecological diversification

Our studies of angiosperm reproductive organs show that while angiosperms were probably diverse at the species level by around the middle of the Early Cretaceous diversity in the three main groups of angiosperms was still low compared to their modern representatives. In the Early Cretaceous there is also a preponderance of taxa that are now extinct. Only a few extant lineages at the family level can be recognised with confidence. In the middle of the Early Cretaceous, angiosperms may also not have been of overriding ecological importance and may have occurred only in scattered patches in certain kinds of environments. Several lines of evidence suggest that early angiosperms were predominantly herbaceous or small shrubby forms rather than large trees.

Insect pollination appears to have been common in Early Cretaceous angiosperms. This is indicated by the morphology of the stamens and by the common occurrence of certain types of angiosperm pollen in coprolites. Inferred from the small size of the pollen sacs, pollen production may have been low. Dispersal potential for pollen may also have been inhibited by the relatively low stature of early angiosperms. These interpretations are consistent with the marked discrepancy in diversity of angiosperms in mesofossil floras and dispersed palynological assemblages from the same layers. For instance the Buarcos flora of Portugal (Late Aptian or Early Albian) has yielded a rich angiosperm mesofossil flora with perhaps more than 100 taxa (Friis et al., 1999)(and personal observations), while the dispersed palynoflora from the same locality has only two different kind of angiosperms (*Clavatipollenites* and *Asteropollis*) (Pais and Reyre, 1981) both of which are probably from wind-pollinated or mostly wind-pollinated plants.

From the Albian onwards angiosperms are more easily assigned to extant families. They also occur more abundantly in fossil floras and are geographically much more widely distributed. This probably reflects both extensive phylogenetic and ecological expansion during the Mid-Cretaceous following the somewhat earlier establishment of the main lines of angiosperms. In the Late Cretaceous angiosperms dominate many habitats at a worldwide scale (Crane and Lidgard, 1989), although even relatively late in the Late Cretaceous diversity is not always reflected in ecological dominance (Wing et al., 1993). In the latest Cretaceous many of the survivors from older Mesozoic vegetation were apparently finally extinguished. Only during the Early Cainozoic do angiosperms seem to have attained a level of ecological prominence comparable to that of today.

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