

Diversity in obscurity: fossil flowers and the early history of angiosperms

Else Marie Friis^{1,*}, Kaj Raunsgaard Pedersen² and Peter R. Crane³

¹*Department of Palaeobotany, Swedish Museum of Natural History, Box 50007, 10405 Stockholm, Sweden*

²*Department of Geology, University of Aarhus, Universitetsparken, 8000 Århus C, Denmark*

³*School of Forestry and Environmental Studies, Yale University, 195 Prospect Street, New Haven, CT 06511, USA*

In the second half of the nineteenth century, pioneering discoveries of rich assemblages of fossil plants from the Cretaceous resulted in considerable interest in the first appearance of angiosperms in the geological record. Darwin's famous comment, which labelled the 'rapid development' of angiosperms an 'abominable mystery', dates from this time. Darwin and his contemporaries were puzzled by the relatively late, seemingly sudden and geographically widespread appearance of modern-looking angiosperms in Late Cretaceous floras. Today, the early diversification of angiosperms seems much less 'rapid'. Angiosperms were clearly present in the Early Cretaceous, 20–30 Myr before they attained the level of ecological dominance reflected in some mid-Cretaceous floras, and angiosperm leaves and pollen show a distinct pattern of steadily increasing diversity and complexity through this interval. Early angiosperm fossil flowers show a similar orderly diversification and also provide detailed insights into the changing reproductive biology and phylogenetic diversity of angiosperms from the Early Cretaceous. In addition, newly discovered fossil flowers indicate considerable, previously unrecognized, cryptic diversity among the earliest angiosperms known from the fossil record. Lineages that today have an herbaceous or shrubby habit were well represented. Monocotyledons, which have previously been difficult to recognize among assemblages of early fossil angiosperms, were also diverse and prominent in many Early Cretaceous ecosystems.

Keywords: abominable mystery; Darwin; early angiosperms; Early Cretaceous; fossil flowers; monocots

1. INTRODUCTION

As improved information about the plant fossil record accumulated during the late nineteenth century, the history of flowering plants stood out as increasingly anomalous. Darwin's famous quote, 'The rapid development as far as we can judge of all the higher plants within recent geological times is an abominable mystery', in a letter written to J. D. Hooker 22 July 1879, captures his own reflections on this topic. Not only was the first appearance of angiosperms during the Cretaceous relatively 'recent' in terms of the evolution of other groups of plants, but the apparent rapidity with which modern-looking angiosperm leaves entered the fossil record in several different parts of the world appeared to undermine the possibility of gradual evolution from some pre-existing form.

Central to the mid-nineteenth century interest in early angiosperm evolution was the discovery and study of rich Cretaceous leaf floras from North America, Europe and the Arctic. These leaf floras included the flora of the Dakota group in North America (Newberry 1863; Lesquereux 1874), floras from western Greenland and Spitsbergen (e.g. Heer 1868, 1882; Saporta 1877) and floras from different

parts of Europe (e.g. Saporta 1878). The composition of these floras, which were usually dominated by flowering plants, contrasted strongly with that of earlier floras in the Cretaceous from which angiosperms were apparently absent. To reconcile these observations Darwin speculated that angiosperms perhaps had a long cryptic history in remote areas, which left no trace in the fossil record (Darwin in letter to J. D. Hooker 22 July 1879; see also Friedman 2009). This idea has been reappraised several times since, and it has been suggested that the rapid appearance of angiosperms in the Cretaceous fossil record reflects a pattern resulting from migration rather than *in situ* evolution (e.g. Axelrod 1952).

Over the past 120 years, an improved stratigraphic framework combined with detailed studies of Cretaceous angiosperms has removed some of the tensions at the heart of Darwin's concerns. The discovery of rich Early Cretaceous palynological assemblages showed that angiosperms were present in the Early Cretaceous, but missing from the very large numbers of Jurassic and older samples from all over the world (e.g. Scott *et al.* 1960). It was also recognized that the earliest angiosperm pollen grains were restricted to monocolpate rather than triaperturate forms (Muller 1970; Hughes 1994), which was consistent with phylogenetic interpretations that extant magnoliids were most similar to the common ancestor of all living angiosperms.

* Author for correspondence (else.marie.friis@nrm.se).

One contribution of 16 to a Discussion Meeting Issue 'Darwin and the evolution of flowers'.

In the mid-1970s, studies of fossil angiosperm pollen and leaves in the Early and mid-Cretaceous Potomac Group of eastern North America demonstrated a coordinated increase in the complexity of both types of organs (Brenner 1963; Doyle & Hickey 1976; Hickey & Doyle 1977). The increase in the architectural complexity of angiosperm leaves was also shown to be broadly consistent with interpretations of leaf evolution based on extant plants (Doyle & Hickey 1976; Hickey & Doyle 1977, see also Hickey & Wolfe 1975).

More recently, the discovery of angiosperm mesofossils containing three-dimensionally preserved angiosperm flowers from the Cretaceous has provided a completely new, and previously unimagined, source of information about the pattern of early angiosperm diversification as well as new insights into the reproductive biology and phylogenetic diversity of angiosperms during the first 70 Myr of their evolutionary history (e.g. Friis & Skarby 1981; Friis 1984; Friis *et al.* 2006a). The more detailed picture that emerges is broadly consistent with the pattern of phylogenetic relationships among extant angiosperms inferred from studies of molecular sequence data (e.g. The Angiosperm Phylogeny Group 2003; Soltis *et al.* 2005). Taken together, several lines of evidence from the fossil record, combined with inferences from extant plants, now provide a strong indication that the first major phylogenetic diversification and ecological radiation of angiosperms took place in the Early Cretaceous over a relatively short interval of some 20–30 Myr (Brenner 1963, 1996; Doyle & Hickey 1976; Hughes 1976, 1994; Crane *et al.* 1995; Friis *et al.* 2006a).

Studies of fossil flowers and other angiosperm reproductive organs from many different stratigraphic levels in the Cretaceous continue to add further details to the emerging picture of early angiosperm evolution (e.g. Friis *et al.* 2006a; Takahashi *et al.* 2008; Viehofen *et al.* 2008; von Balthazar *et al.* 2008; Martinez-Millan *et al.* 2009). However, in this paper, we focus on fossil assemblages from the Early Cretaceous that contain the oldest structurally and phylogenetically informative angiosperm flowers, fruits and seeds. Information from these floras suggests that much angiosperm diversity prior to the mid-Cretaceous was mainly among lineages with an herbaceous or shrubby habit, and that many of these early angiosperms probably grew in wet to fully aquatic environments. Within these assemblages, the presence of Chloranthaceae, Nymphaeales, Alismatales, Ranunculales, Proteales, Buxales and other groups is now well documented, and there is also evidence of many plants that are not closely related to any extant taxa. However, new results reinforce previous indications that monocotyledons were also diverse in these ancient angiosperm communities and contributed substantially to the angiosperm component of Early Cretaceous ecosystems.

2. MORPHOLOGICAL DIVERSITY OF EARLY ANGIOSPERMS: EVIDENCE FROM FOSSIL POLLEN AND FLOWERS

(a) *Morphological diversity of early pollen*

The earliest unequivocal remains of angiosperms are pollen grains from the Early Cretaceous, and some

of the most convincing detailed information is from the Early Cretaceous palynofloras described from southern England by Hughes and colleagues (see overview in Hughes 1994). These records range in age from the Hauterivian through to the Aptian and have been studied with both light and scanning electron microscopy. Grains ascribed to angiosperms from Israel, which are of possible Late Valanginian–Early Hauterivian age (Brenner 1996), are more difficult to evaluate because the available illustrations reveal few structural details.

Hughes (1994) distinguished three phases of angiosperm evolution through the Mid-Hauterivian to Early Barremian (phases 0–2) and three phases (phases 3–5) through the Late Barremian to Aptian.

Almost all of the angiosperm grains from the six phases recognized by Hughes (1994) are monoaperturate. Most of the grains have a long straight colpus. More rarely the aperture is expanded and more or less circular. The pollen grains are minute to small and range in size from about 9 µm to about 29 µm in diameter. There is considerable variation in pollen wall structure and ornamentation. This ranges from continuous tectate, with either punctate or spinulate ornamentation, to reticulate semitectate, with muri that are smooth or have various kinds of suprategular ornamentation.

Only two different types of angiosperm pollen are recorded by Hughes (1994) from phase 0: one has a continuous tectum and the other has a reticulate (semitectate) pollen wall. Already by phase 1, there is greater diversity among the reticulate monocolpate grains. Forms that have fine transverse striations on the muri also enter the fossil record at this level and become very common in later Barremian and Aptian palynofloras. Monocolpate and reticulate pollen with spiny ornamentation on the muri first appear in phase 2 and are also common through the later Barremian and Aptian. Crotonoid pollen and pollen with trichotomocolpate apertures occur for the first time in phase 3.

Angiosperm pollen from phases 4 and 5 continues to be small and predominantly monoaperturate. During phase 4, pollen grains with a distinctly graded reticulum are seen in the fossil record for the first time. A significant event in angiosperm evolution is the first appearance of tricolpate pollen grains at around the latest Barremian–Early Aptian. Hughes records a single tricolpate grain in phase 4 and one other tricolpate grain of a different kind in phase 5, which is dated as Early Aptian (Hughes 1994).

Angiosperm pollen is also known in many other parts of the world from the Late Barremian–Early Aptian interval, more or less contemporaneous with phases 4 and 5 of Hughes, and shows the same pattern of diversity as observed for the British sequence. Especially important are sequences of palynofloras from the Potomac Group of eastern North America (e.g. Brenner 1963; Doyle 1969; Doyle & Hickey 1976; Doyle & Robbins 1977), from Egypt (e.g. Penny 1986, 1988b) and from Equatorial Africa (Doyle *et al.* 1977). The evolutionary signal that emerges from these floras is a considerable expansion of angiosperm pollen diversity, both in terms of aperture configuration and also pollen wall sculpture. Scattered records of tricolpate

pollen grains are also known from contemporaneous pollen assemblages from Israel (Brenner 1996), Equatorial Africa (Doyle 1992), Egypt (Penny 1988b) and North America (Doyle 1992).

The first mesofossil floras with angiosperm flowers and pollen *in situ* are also from this time interval. Mesofossil floras consist of three-dimensionally preserved coalified plant remains in the size range between microfossils and macrofossils. The fragments are typically a few millimetres long and may include whole flowers with all floral organs preserved (for a review, see Friis *et al.* 2006a). Flowers sometimes have stamens with pollen *in situ*. Ultrastructural details of the pollen grains *in situ* studied with scanning electron microscopy also indicate that the number of taxa is higher than would be expected from studies of dispersed grains using light microscopy, which has been standard in most palynostratigraphic studies. Scanning electron microscopy of dispersed grains also provides evidence of cryptic diversity through improved discrimination of different pollen types based on fine details of sculpture. Relatively low pollen production in many early angiosperms may also imply that certain pollen types seen in mesofossils are poorly represented in palynofloras that comprise dispersed pollen.

(b) Morphological diversity of early flowers and other reproductive organs

There are now a large number of mesofossil floras described from the Late Cretaceous that contain angiosperm flowers and other reproductive structures. However, the key mesofossil floras from the Early Cretaceous are all from Portugal and eastern North America. Some of the fossils in these floras are preserved as charcoal formed by vegetational fires and have the three-dimensional structure intact. Others are preserved as lignite formed from chemically altered organic material that may be more or less compressed. These fossil assemblages were discovered in the late 1980s in soft clays, silts and sands, which range in age from the Late Barremian–Early Aptian to around the Albian–Cenomanian boundary (for a summary, see Friis *et al.* 2006a).

The Torres Vedras flora from Portugal is possibly the oldest of these mesofossil floras (Late Barremian–Early Aptian, approximately corresponding to phases 4 and 5 of Hughes). The Torres Vedras assemblage includes three-dimensionally preserved floral structures as well as fruits and seeds, but also contains diverse isolated stamens with pollen *in situ* and many coprolites consisting almost exclusively of pollen. Other important floras from Portugal are slightly younger. Among these are the mesofossil floras from Catefica (Late Barremian–Aptian), Famalicão (Late Aptian) and Buarcos, Vila Verde 2, Vale de Agua and several others (Late Aptian–Early Albian). The most diverse mesofossil flora from the Early Cretaceous of North America is from the Puddledock locality (Early–Middle Albian), but Early Cretaceous mesofossil floras from the Potomac Group sequence range from around the Barremian–Aptian boundary (Drewry's Bluff and Dutch Gap localities) to the end of the Early Cretaceous (West Brothers' locality, latest Albian).

There are also a few other Early Cretaceous floras that contain floral remains of angiosperms from other parts of the world. These include the impression/compression flora from the Yixian Formation (Late Barremian–Early Aptian) from Liaoning Province and adjacent areas in northeastern China (e.g. Sun *et al.* 2001; Leng *et al.* 2003) and from the Late Aptian–Early Albian Crato Formation of northeast Brazil (Mohr *et al.* 2007). Fossils in both these assemblages are important in providing whole plant preservation. Angiosperms are rare in the Yixian Formation, represented by only few taxa and relatively few specimens. Angiosperms are more common in the perhaps slightly younger Crato flora. Further, a petrified floral structure was also recently described from the Late Albian of Australia (Dettmann *et al.* 2009).

(i) Size

All early angiosperm flowers known from the Late Barremian–Middle Albian are of small to medium size. Flowers from the many Early Cretaceous mesofossil floras range from about 0.5 mm up to about 5 mm, while slightly larger flowers are reported from the Crato flora (up to about 6–7 mm; Mohr & Bernardes-de-Oliveira 2004) and from Western Australia (up to about 16 mm; Dettmann *et al.* 2009). Many flowers were borne in dense inflorescences, mostly spikes, but there are also a few solitary flowers, both in the mesofossil floras and in the compression/impression Crato flora. *Archaeofructus* from the Yixian Formation (Sun *et al.* 2002) is relatively large, but if the inflorescence interpretation of Friis *et al.* (2003) and Endress & Doyle (2009) is correct then the individual flowers of *Archaeofructus* are small, simple and also borne in a spike-like inflorescence.

Early angiosperm fruits and seeds are also typically small. In a preliminary analysis of the Famalicão mesofossil flora (Late Aptian), 37 different kinds of angiosperm fruits and 64 different kinds of seeds were identified (Eriksson *et al.* 2000b). This flora is broadly representative of the currently known Early Cretaceous mesofossil floras. Fruits range in volume between 0.12 and 8.34 mm³ and seeds vary between 0.02 and 6.86 mm³ (Eriksson *et al.* 2000b). Fruits and seeds continue to be small compared with their living relatives throughout the Cretaceous (Tiffney 1984; Eriksson *et al.* 2000a).

(ii) Sex expression

All Early Cretaceous mesofossil floras include both unisexual and bisexual flowers. Unisexual flowers seem slightly more common in the Early Cretaceous than in mid-Cretaceous floras. They are certainly much more common than in Late Cretaceous floras where bisexual forms predominate, even among flowers that are most closely related to extant wind-pollinated taxa with unisexual flowers (Friis *et al.* 2006b).

(iii) Position of floral organs

Most of the early angiosperm flowers from the Late Barremian–Early Aptian and through to the Early–Middle Albian are hypogynous, but there are also

several epigynous forms. This is in contrast to flowers from Late Cretaceous floras. Beginning in the Turonian, or perhaps even earlier in the Late Cenomanian, about half of all flowers in typical mesofossil floras are epigynous or semiepigynous. The difference may reflect initial strategies for protection of the ovules in the face of increased biotic pollination, as well as the high relative diversity of particular groups of angiosperms (probably early core eudicots) at this stage in angiosperm evolution.

(iv) *Perianth*

A surprisingly high proportion of ancient angiosperm flowers appear to lack a perianth or to have a simple undifferentiated perianth. None of the flowers from the Early Cretaceous have a perianth that is clearly differentiated into calyx and corolla. The number of floral parts is usually also low. Exceptions to this generalization are *Virginianthus* and *Carpestella* from the Early–Middle Albian Puddledock flora, *Endressinia* from the Late Aptian–Early Albian of Brazil and *Lovellea* from the Albian of Australia, all of which have multipartite flowers with numerous floral organs (Friis *et al.* 1994; Mohr & Bernardes-de-Oliveira 2004; von Balthazar *et al.* 2008; Dettmann *et al.* 2009). In *Virginianthus*, and also in *Teixeiraea lusitanica* (von Balthazar *et al.* 2005), the tepals grade from sepaloid on the outside to petaloid on the inside.

In many Early Cretaceous fossil flowers, the phyllotaxis of the floral organs, including the perianth, is difficult to establish. In some cases this may be because of distortion during fossilization, but in other cases floral phyllotaxis may be irregular. This is in contrast to Late Cretaceous flowers that predominantly have distinct heterochlamydous perianth of sepals (calyx) and petals (corolla) that are clearly arranged in whorls.

(v) *Stamens*

Evidence from mesofossils shows that there is considerable diversity in the organization of the androecium among the earliest angiosperm flowers. Early Cretaceous floras also include a surprisingly large number of dispersed stamens with pollen *in situ*.

In the Torres Vedras mesofossil flora (Late Barremian–Early Aptian) stamens typically have simple anthers with only modest development of the connective between the pollen sacs. The filament is not well developed and the stamen base is short. Anthers vary in shape and size from short and sagittate to narrow and elongate. Sometimes there is an apical expansion of the connective, but typically it is small.

On average, anthers in Early Cretaceous floras are relatively large compared with those from Late Cretaceous floras. Many of the Late Aptian–Albian stamens are also bulky with extensive development of the connective, both between the pollen sacs and at the stamen apex. This apical extension may be strongly developed and in some cases it may be as long as the pollen sacs. The lower part of the stamen may be short, or longer and developed into a filament, but it is often flattened and always grades into the anther without a distinct joint. Even though anthers are

relatively large, the pollen sacs are often very small compared with the total size of the stamen. Flattened stamens typically have pollen sacs borne on one surface. Anther dehiscence in the earliest known angiosperm stamens (Late Barremian–Early Aptian) was probably by longitudinal slits, but none of the available specimens show the mode of dehiscence very clearly. However, in floras from the Late Aptian–Early Albian, the variety of anthers is greater and many have valvate dehiscence (e.g. Friis *et al.* 2006a). Most anthers with valvate dehiscence have laterally hinged valves over each theca. These open like shutters to expose the two pollen sacs of each theca.

In general, the form of the androecium in Turonian–Maastrichtian flowers is markedly different from that of flowers from the Early Cretaceous. In the Late Cretaceous, dispersed stamens are much less common and bulky stamen types are rare. Stamen phyllotaxis is mainly whorled and the number of androecial whorls is typically one or two, rarely more. Anthers are mostly dithecate with a distinct band- or thread-shaped filament that is separated from the anther by a distinct joint.

(vi) *Gynoecium*

Most Early Cretaceous angiosperm flowers apparently had monocarpellate flowers, judging from the many unilocular, often one-seeded fruits in the early floras. However, multicarpellate flowers were also present early in angiosperm history. In the Torres Vedras flora, both apocarpous fruits with many free carpels and syncarpous gynoecia formed from two or three carpels are present. From the contemporaneous Yixian flora, *Archaeofructus* has a gynoecium of one or two free carpels (inflorescence interpretation) and *Sinocarpus* is syncarpous.

None of the early flowers have a distinct style with an elevated stigma. Instead, the stigmatic surface is often extended or indistinct. This is in strong contrast to flowers from the Late Cretaceous, which normally have distinct styles that elevate the stigma. From the Turonian through to the Maastrichtian, there is also a clear dominance of flowers with syncarpous gynoecia, which are mainly related to groups of core eudicots.

(vii) *Fruits and seeds*

Fruit types among Early Cretaceous angiosperms are diverse. There are several apocarpous-follicular fruits that have more than one seed per carpel in the Torres Vedras assemblages, but the vast majority of fruits at this level are indehiscent, unilocular nuts or drupes with one or very few seeds. For instance, in the Famalicão mesofossil flora (Late Aptian), seed number could be determined for 18 fruits. Of these, 12 had only a single seed, while the remaining six had two, three or more seeds per fruit. The proportion of fruits with a fleshy outer layer is surprisingly high. In the Famalicão flora, about 25 per cent of the fruits were either drupes or few-seeded berries. This probably indicates the early establishment of animal dispersal among angiosperms (Eriksson *et al.* 2000b). Because of their small size, the fleshy portion of each

fruit was small, but there are several indications that the fruits were borne in dense infructescences. Collectively, the amount of fleshy tissue may have been sufficient for attracting animal dispersers.

Early Cretaceous angiosperms typically have anatropous ovules, but rare orthotropous ovules are also known from the earliest mesofossil floras including the Torres Vedras flora. Campylotropous ovules are known from the Late Aptian flora of Famalicão. Most early angiosperm seeds are apparently formed from bitegmic ovules. Most are exotegmic with a hard outer seed coat (Friis *et al.* 1999).

3. PHYLOGENETIC DIVERSITY OF EARLY ANGIOSPERMS

All angiosperm pollen grains from the earliest phases of the angiosperm diversification described by Hughes (1994) are monocolpate. There are also some records of inaperturate pollen from the Valanginian–Hauterivian of Israel (Brenner 1996), but these need further documentation. Among extant angiosperms, monoaperturate pollen, in which the aperture is generally colpate, is exclusively produced by angiosperms at the ANITA grade (the earliest diverging lineages of extant angiosperms including *Amborella*, *Nymphaeaceae*, *Illicium*, *Trimeniaceae* and *Austrobaileyaceae sensu Qiu (1999)*) as well as by *Chloranthaceae*, monocots and eumagnoliids. Within these groups, some families and genera have very distinctive pollen features and can be identified based on isolated pollen alone. However, despite the very extensive record of dispersed angiosperm pollen from the Early Cretaceous, very few of these grains can be assigned confidently to extant lineages at the order, family or generic level. Recent discoveries of fossil flowers and other angiosperm reproductive organs allow much more detailed evaluation of the phylogenetic relationships of early angiosperms to extant plants. These fossils show that although angiosperms are already diverse by the Barremian–Aptian, this diversity is restricted to early diverging lineages of extant angiosperms, as well as other lineages that appear to be extinct.

(a) ANITA lineages

(i) *Nymphaeales*

Fossil remains of *Nymphaeales* are very well represented in Palaeogene and Neogene floras. *Nymphaealean* seeds are particularly common and easily recognized by their distinct bitegmic, exotestal organization, the presence of a micropylar lid and the often strongly undulating anticlinal walls of the cells on the surface of the exotesta. The Cretaceous fossil record of *Nymphaeales* is much more meagre. Dispersed *Nymphaea*-like pollen, described as *Zonosulcites scollardensis* and *Zonosulcites parvus*, is known from the Maastrichtian of Canada (Srivastava 1969; Muller 1981) and unequivocal *nymphaealean* seeds, described as *Symphaenale futabensis*, are known from the Late Cretaceous (Early Santonian) Gokurakuzawa locality of northeastern Honshu, Japan (Takahashi *et al.* 2007). The *nymphaealean* affinity suggested for flowers of *Microvictoria*, described from

the Turonian of New Jersey, USA (Gandolfo *et al.* 2004), has been questioned (Endress 2008).

Despite their sparse Late Cretaceous record, and even though the extant genera may not have diversified until the Cenozoic, *Nymphaeales* were clearly present at an early stage in angiosperm evolution. A key early record of *Nymphaeales* is the flower of *Monetianthus mirus*, from the Late Aptian–Early Albian flora of Vale de Agua (Friis *et al.* 2001, 2009b). *Monetianthus* provides unequivocal evidence of crown group *Nymphaeales*, even though it cannot be accommodated in any extant genus.

The *Monetianthus* flower is perigynous, about 3 mm long and 2 mm in diameter, with remains of perianth, androecium and gynoecium. The gynoecium is particularly informative, with a whorl of 12 carpels that are fused for most of their length and free only in the apical part. There is a small central projection of the floral axis between the carpels. Each carpel contains many small ovules, which do not fill out the locules completely. Placentation is laminar. The combined characters of the gynoecium are unique for *Nymphaeaceae*, and phylogenetic analysis suggests a position of *Monetianthus* at the root of the *Barclaya* + *Nymphaeoidae* clade (Friis *et al.* 2009b).

Pluricarpellatia peltata from the Early Cretaceous (Late Aptian–Early Albian) of Brazil also provides evidence of Early Cretaceous *Nymphaeales*. It is a fruiting structure preserved in organic connection with peltate *nymphaealean* leaves (Mohr *et al.* 2007). Other Early Cretaceous leaf fossils with distinct *nymphaealean* features also support the presence and diversity of the group early in angiosperm history. Among these are *Brasenia*-like leaves from the Early Cretaceous (Late Aptian or Early Albian) flora of Buarcos-para-Tavarede, Portugal, assigned to the fossil genus *Braseniopsis* (Saporta 1894), and *Scutifolium jordanicum* from the Early Cretaceous (Albian) of Jordan, which was assigned to the *Cabombaceae* (Taylor *et al.* 2008). There are also many seeds with distinct *nymphaealean* features among the Early Cretaceous mesofossils from Portugal and eastern North America. Their first occurrences are in the Late Barremian–Early Aptian Torres Vedras flora, as well as in the more or less contemporaneous mesofossil flora from Drewry's Bluff, Virginia (Friis *et al.* 1999, 2006a).

Carpestella lacunata from the Early–Middle Albian Puddledock flora of Virginia, USA (von Balthazar *et al.* 2008) is another Early Cretaceous flower probably related to ANITA grade angiosperms. The fossil is a small fragmentary gynoecium, about 0.65 mm long and 0.45 mm in diameter, that shows many helically arranged scars from detached floral organs. The gynoecium is syncarpous, consisting of 13 carpels arranged radially around a central column in a star-shaped pattern, as is seen in extant *Nymphaeaceae* and *Illicium* (*Schisandraceae*). The presence of septal slits suggests a link between the fossil and extant *Nymphaeaceae*, but the precise position of *Carpestella* cannot be established securely with the information currently available (von Balthazar *et al.* 2008).

There are other fossils of putative relationship with ANITA grade angiosperms from Early Cretaceous mesofossil floras (Friis *et al.* 1999), but none can be attributed to an extant family. They probably represent extinct lineages that diverged close to the base of the angiosperm phylogenetic tree.

(b) *Chloranthaceae*

Asteropollis is a genus of distinctive early angiosperm pollen grains that is closely comparable with pollen of the extant genus *Hedyosmum* (Chloranthaceae) (Walker & Walker 1984). *Asteropollis* includes species characterized by their star-shaped distal aperture, reticulate pollen wall and muri that have beaded ornamentation. In addition, some species of *Clavatipollenites*, which have a monocolpate or trichotomocolpate aperture and reticulate pollen wall with beaded muri, are very similar to grains of extant *Ascarina* (Chloranthaceae) (Couper 1960; Walker & Walker 1984).

Studies of mesofossils confirm indications from dispersed pollen that Chloranthaceae entered the angiosperm fossil record very early. The family was probably already diverse in the earliest mesofossil floras (Friis *et al.* 2006a). In the Torres Vedras mesofossil flora (Late Barremian–Early Aptian) inflorescences, fruits, dispersed stamens and coprolites suggest the presence of several different species of Chloranthaceae. *Hedyosmum*-like staminate inflorescences often associated with *Hedyosmum*-like fruits are also known from several of the Aptian–Early Albian floras from Portugal (Friis *et al.* 2006a). *Hedyosmum*-like fruits with adhering *Asteropollis* pollen have also been recorded from the Early–Middle Albian Puddledock flora (Friis *et al.* 1997). Unequivocal androecia of *Chloranthus*-like plants are known from Late Cretaceous mesofossil floras (Crane *et al.* 1989; Eklund *et al.* 1997).

(c) *Eumagnoliids*

Eumagnoliids are well known in the Cenozoic fossil record where they are represented extensively by wood, leaves, fruits and seeds. There is also a growing record of well-preserved eumagnoliid flowers from the Cretaceous (e.g. Friis *et al.* 1997). Cenozoic fossils are generally easily assigned to extant genera, but all Cretaceous eumagnoliids appear to represent extinct genera. The Early Cretaceous record consists mainly of taxa with smaller flowers, and lauralean taxa are especially prominent (e.g. *Virginianthus*, *Potomacanthus*, see below). Larger, multipartite flowers similar to those of extant Magnoliaceae, which were previously believed to be archaic in angiosperms, first enter the fossil record in the Late Albian at the very end of the Early Cretaceous (Dilcher & Crane 1984).

(i) *Magnoliales*

Dispersed permanent tetrads of pollen described as *Walkeripollis* (Doyle *et al.* 1990) probably represent stem-group Winteraceae. The earliest flower of probable Magnoliales is *Endressinia brasiliensis* from the Crato Formation (Late Aptian–Early Albian) of Brazil (Mohr & Bernardes-de-Oliveira 2004). It is

particularly similar to extant Eupomatiaceae and Himantandraceae, but cannot be placed in any extant family and may represent an extinct lineage. *Archaeanthus linnenbergeri* from latest Albian–earliest Cenomanian Dakota Formation is very similar in floral structure to extant Magnoliaceae, but the fruits differ from all extant taxa in producing many small seeds (Dilcher & Crane 1984). *Archaeanthus* possibly represents stem-group Magnoliaceae. Flowers of crown group Annonaceae are known from the Early Coniacian of Japan (Takahashi *et al.* 2008).

(ii) *Laurales*

Laurales have an extensive Cenozoic fossil record and are becoming increasingly well documented from the Cretaceous based on numerous remains of flowers and inflorescences (e.g. Drinnan *et al.* 1990; Eklund 2000; Takahashi *et al.* 2001). The first of these fossils to be described was *Mauldinia mirabilis* from the Mauldin Mountain flora of Maryland (Early Cenomanian) (Drinnan *et al.* 1990). *Mauldinia* and similar genera have since been recognized from several fossil floras in Europe and Central Asia (Eklund & Kvaček 1998; Frumin *et al.* 2004; Viehofen *et al.* 2008), and *Mauldinia* currently includes four distinct species.

In the Early Cretaceous, lauralean flowers are known only from the Puddledock flora (Early–Middle Albian) of Virginia, USA. Laurales known from this flora are the calycanthaceous flower *Virginianthus* (Friis *et al.* 1994), the lauraceous flower *Potomacanthus lobatus* (von Balthazar *et al.* 2007) and several other undescribed forms. The fossil flower *Lovelleya wintonensis*, described by Dettmann *et al.* (2009) from the mid-Cretaceous of Western Australia, is another Early Cretaceous lauralean element. Its closest similarities are to extant Gomortegaceae and Monimiaceae, but its precise position among Laurales remains to be established (Dettmann *et al.* 2009).

(iii) *Piperales*

Several dispersed pollen grains from the Early Cretaceous, such as species assigned to the pollen genera *Tucanopollis* and *Transitoripollis*, are monoaperturate with a continuous tectum. In these features they are very similar to pollen grains of extant Piperales. This kind of pollen has been found on fruits (Friis *et al.* 1995) from the Puddledock flora (Early–Middle Albian). The same kind of pollen has also been found on fruits as well as in stamens and in coprolites from the Torres Vedras locality (Late Barremian–Early Aptian) (Friis *et al.* 2006a). The combined fruit, seed and pollen characters suggest a relationship to extant Piperales, but other features of the plants are unknown and the putative relationship to Piperales remains to be established more securely.

(d) *Eudicots*

The earliest record of triaperturate pollen is a single grain from Zone 4 of Hughes (Late Barremian–Early Aptian; Hughes & McDougall 1990; Hughes 1994). Above this level in the Wealden succession of southern England, triaperturate pollen becomes more common.

In palynofloras from other areas tricolpate pollen also enters the fossil record around the Barremian–Aptian boundary. Tricolpate grains remain rare until later in the Aptian (e.g. Doyle *et al.* 1977; Penny 1991) and first dominate palynofloras in the Late Albian where they include tricolpate as well as tricolporoidate forms (Doyle & Hickey 1976). Tricolpate pollen grains are also known from flowers and dispersed stamens in many Early Cretaceous mesofossil floras. In the Late Barremian–Early Aptian Torres Vedras flora, tricolpate pollen has not so far been found in flowers or on the surface of carpels or fruits. Nor has it been observed in the dispersed palynoflora from the same samples. However, two different kinds of tricolpate pollen were found in a coprolite and in a stamen. Similarly, in the Late Aptian flora of Famalicão, no tricolpate pollen grains have been observed *in situ*. In the younger Early–Middle Albian Puddledock flora, a rough estimate of distribution of angiosperm pollen types *in situ* shows that about one-third are triaperturate.

All Early Cretaceous floral structures with tricolpate pollen *in situ* that have been placed systematically have relationships to groups of eudicots that diverged very early from the lineage that gave rise to the bulk of eudicot diversity. Currently, Early Cretaceous floral structures related to Ranunculales, Buxales and Proteales have been identified. Probable Ranunculales are represented by a single staminate flower, *Teixeiraea lusitanicum*, from the Vale de Agua flora (Late Aptian–Early Albian) (von Balthazar *et al.* 2005). Also from the Vale de Agua flora are four different kinds of pistillate structures (*Aguacarpus hirsutus*, *Lusicarpus planatus*, *Silucarpus camptostylus*, *Valecarpus petiolatus*) and one kind of staminate flower (*Lusistemon striatus*) that are related to the Buxales (Pedersen *et al.* 2007). Unequivocal buxalean flowers and inflorescence fragments are also known from the Potomac Group. *Spanomera marylandensis* is from the Late Albian West Brothers locality and *Spanomera mauldinensis* is from the Early Cenomanian Mauldin Mountain locality (Drinnan *et al.* 1991), both in Maryland, USA.

Proteales are known from several Potomac Group mesofossil floras. Especially common are a variety of flowers and inflorescences of platanoid affinity. These include pistillate flowers and inflorescences of *Friisicarpus brookensis* and the associated staminate material of *Aquia brookensis* from the Early–Middle Albian Bank near Brooke locality in Virginia (Crane *et al.* 1993), as well as pistillate *Friisicarpus marylandensis* and associated staminate *Platananthus potomacensis* from the Late Albian West Brothers locality (Friis *et al.* 1988).

The presence of Proteales in the Early Cretaceous is further supported by the occurrence of *Nelumbo*-like leaves described as *Nelumbites* from the Bank near Brooke (Early–Middle Albian) and the Quantico localities (Late Albian) (Doyle & Hickey 1976; Upchurch *et al.* 1994), both from Virginia, USA.

(e) Monocotyledons

Fossil remains of monocotyledons are common in Cenozoic floras where they are represented by many different organs, including stems, leaves, rhizomes,

flowers, fruits, seeds, pollen and phytoliths. There are also reliable monocot fossils from the Late Cretaceous, including stems, fruits, seeds and pollen (e.g. Herendeen & Crane 1995). However, the record of monocotyledons is much less extensive in the Cretaceous than in the Cenozoic. It is also interesting that some of the key monocotyledons of present day wetland communities, which are well represented in the Cenozoic, are absent in the Cretaceous. For example, Cyperaceae have fruits that fossilize well, are easily recognizable and that are extremely common in Palaeogene and Neogene fossil assemblages, but they have not yet been documented from the Cretaceous.

Until now, the Early Cretaceous record of monocots has been especially meagre and, according to Gandolfo *et al.* (2000), all Early Cretaceous records of monocotyledons are ambiguous.

Recognizing the pollen of monocots among the monocolpate grains of early angiosperms has been a particular challenge because the morphological and structural features that potentially distinguish monocot pollen from that of other angiosperms are relatively subtle. Walker & Walker (1984) listed seven features of potential importance for assigning dispersed monocolpate grains to monocots. These include: (i) reticulate sculpturing differentiated into coarse and fine areas (graded reticulum), (ii) smooth muri, (iii) lumina of different sizes, (iv) ‘frilled’ muri caused by laterally extended columellae, (v) regular and clearly polygonal lumina, (vi) a thin pollen wall combined with a very thin non-apertural nexine and (vii) absence of endexine.

While there are many exceptions to these generalizations, among extant angiosperms monoaperturate pollen with a graded reticulum is known only for monocots. The reticulum may have lumina decreasing in size either towards the polar areas (e.g. some palms) or towards restricted areas of the equatorial region (e.g. some Liliales and Asparagales), but there are also other variations. Based on these features, Walker & Walker (1984) suggested that many of the dispersed pollen grains from the Early Cretaceous that are assigned to extinct pollen genera, such as *Retimonocolpites* and *Liliacidites*, were produced by monocots. Support for a monocot affinity of some *Liliacidites* grains was also inferred by Doyle *et al.* (2008) from a recent phylogenetic analysis.

Another character that, as far as we are aware, is restricted to monocot pollen is acolumellate-reticulate wall structure, in which the reticulum is only loosely attached to the foot layer and where the infratectal layer is reduced to an ultrathin granular layer. This kind of wall structure is particularly common among extant Alismatales (Grayum 1990). It may reflect an evolutionary transition to the predominantly atectate condition seen in extant aroid and other monocots. In the fossil record, transitional states between columellate and acolumellate grains reported for *Pennistemon*-type pollen (Penny 1988a) have also been observed for various *Retimonocolpites*-type pollen grains.

(i) Alismatales–Araceae

Mayoa portugallica is a small fragment of lignitized plant tissue with masses of striate (polypligate) pollen

adhering to its irregular surface (Friis *et al.* 2004). The pollen grains are inaperturate and elliptical in outline. They have a finely striate tectum composed of closely spaced, straight ribs that cross each other in a characteristic way. The tectum is supported by a very thin granular or weakly columellate infratectal layer and the endexine is extremely thin and granular. These distinctive pollen grains are closely similar to those of extant *Holochlamys* in every respect. Although other information on the *Mayoa* plant has not yet been discovered, the unique pollen morphology combined with the unusual wall ultrastructure strongly suggests a close relationship of the fossil to the subfamily Monsteroideae, and this supports the presence of crown group Araceae in the Early Cretaceous. Flowers of extant Monsteroideae are bisexual and have a perianth.

In contrast to *Mayoa*, several new fossils from a new Early Cretaceous locality in Portugal (Vila Verde 2, northeast of Figueira da Foz, Figueira da Foz Formation, Late Aptian–Early Albian) are known from much more complete material. These fossils, which comprise inflorescence axes (spadices) and flowers with pollen *in situ*, can also be assigned to Araceae.

One of these araceous fossils, here informally referred to as ‘Araceae fossil sp. A’ (figures 1*a–f* and 2*a,b*) is known from many small inflorescence fragments bearing simple flowers that are densely packed in a low spiral. Most of the specimens are charcoalified and have retained their original three-dimensional shape. The flowers are unisexual (staminate) and lack a perianth (in aroid terminology: aperigonate). Each consists of one or two free stamens. The anthers are tetrasporangiate, basifixed and almost sessile, with a short, inconspicuous filament. Anthers are also bulky, broad and almost square apically. They appear to have been fleshy with a very extensively thickened connective between the four small and widely spaced pollen sacs. The thecae are placed opposite each other and the pollen sacs placed along the four edges of the anther. The surface of the anthers usually has distinctive bulges, indicating the presence of densely spaced secretory cells. In many specimens, the apical part of the connective shows the remains of an abundant secretion, and we infer that the anther connective was odour producing (osmophoric). Pollen grains found in the stamens are clustered in elongated strands. Pollen is monocolpate with a long extended colpus and a semitectate-reticulate pollen wall. The reticulum is coarse with dimorphic lumina. Muri are psilate towards the outside and almost granular towards the inside. The reticulum is supported only by a few columellae. The columellae are uneven in length and shape. They detach easily from the main body of the grain, leaving scattered scars on the outer surface of the foot layer.

An isolated stamen from the Catefica locality (Late Barremian–Aptian) with very bulky anthers and a connective that was probably also osmophoric may belong to the same taxon as the Villa Verde aroid, indicating a wider occurrence of this kind of plant. Dispersed pollen grains very similar to the pollen grains *in situ* within the stamens from Villa Verde 2 are common in Early Cretaceous palynofloras. They are typically

assigned to *Retimonocolpites* or occasionally to *Liliacidites*. Both of these genera include a variety of different dispersed grains that vary in colpus configuration as well as in the pattern of the reticulum and the ornamentation of the muri. We infer that these other forms of *Retimonocolpites* and *Liliacidites* are probably also monocotyledons as suggested previously by Walker & Walker (1984), although they most likely belong to different taxa at generic or higher levels.

All characters of the new fossil strongly support a close relationship with the true aroids, subfamily Aroideae, which are characterized by their unisexual, perianth-less flowers (Cabrera *et al.* 2008). They therefore support earlier inferences based on *Mayoa* and provide further evidence of crown group Araceae in the Early Cretaceous. Most extant Aroideae have inaperturate and atectate pollen. However, *Calla*, which under some analyses is the sister genus to all other true aroids (Cabrera *et al.* 2008), has aperturate, tectate pollen. Tectate–semitectate pollen, sometimes with extended colpi, is also a characteristic of the closely related Lasioideae and Zamioculcadoideae and is most likely plesiomorphic within the family. Reduction of columellae as seen in the new fossil may be a step towards loss of tectum characterizing most aroids.

Another araceous fossil from the Vila Verde 2 locality, here informally referred to as ‘Araceae fossil sp. B’ (figure 1*g–i*), consists of a single inflorescence with numerous, densely spaced flowers that are borne in a spiral arrangement. The fossil is lignitic and slightly compressed, which impedes a full understanding of the floral organization. Nevertheless, it is clear that the flowers have a perianth (in aroid terminology, perigonate). Scars left by the flowers, and the organization of the surface of the inflorescence, show that there were four tepals. It is unclear whether they were in opposite pairs or in a whorl. The flowers appear bisexual, with a massive central gynoecium surrounded by free stamens. The stamens consist of a long anther and a short, indistinct filament. The apical, exposed surface of the gynoecium is rhomboidal.

Pollen grains preserved *in situ* are periporate and semitectate–reticulate. The reticulum is coarse with homogeneous lumina. Muri are smooth with a sharp triangular profile. The tectum is supported by scattered, long columellae. The pores are scattered over the surface of the pollen and the aperture membranes are covered with densely spaced granules. We are not aware that similar grains have been described from dispersed Early Cretaceous palynofloras. However, from the Famalicão locality (Late Aptian), Portugal, similar periporate grains have been observed *in situ* in a tetrasporangiate anther (Friis *et al.* 1999). This pollen differs in having more densely spaced columellae.

The characters of this fossil indicate a phylogenetic relationship to subfamily Pothoideae. It thus provides further evidence of crown group Araceae in the Early Cretaceous. Extant Pothoideae is the only extant group of Araceae that has perigonate, bisexual flowers with periporate semitectate–reticulate pollen.

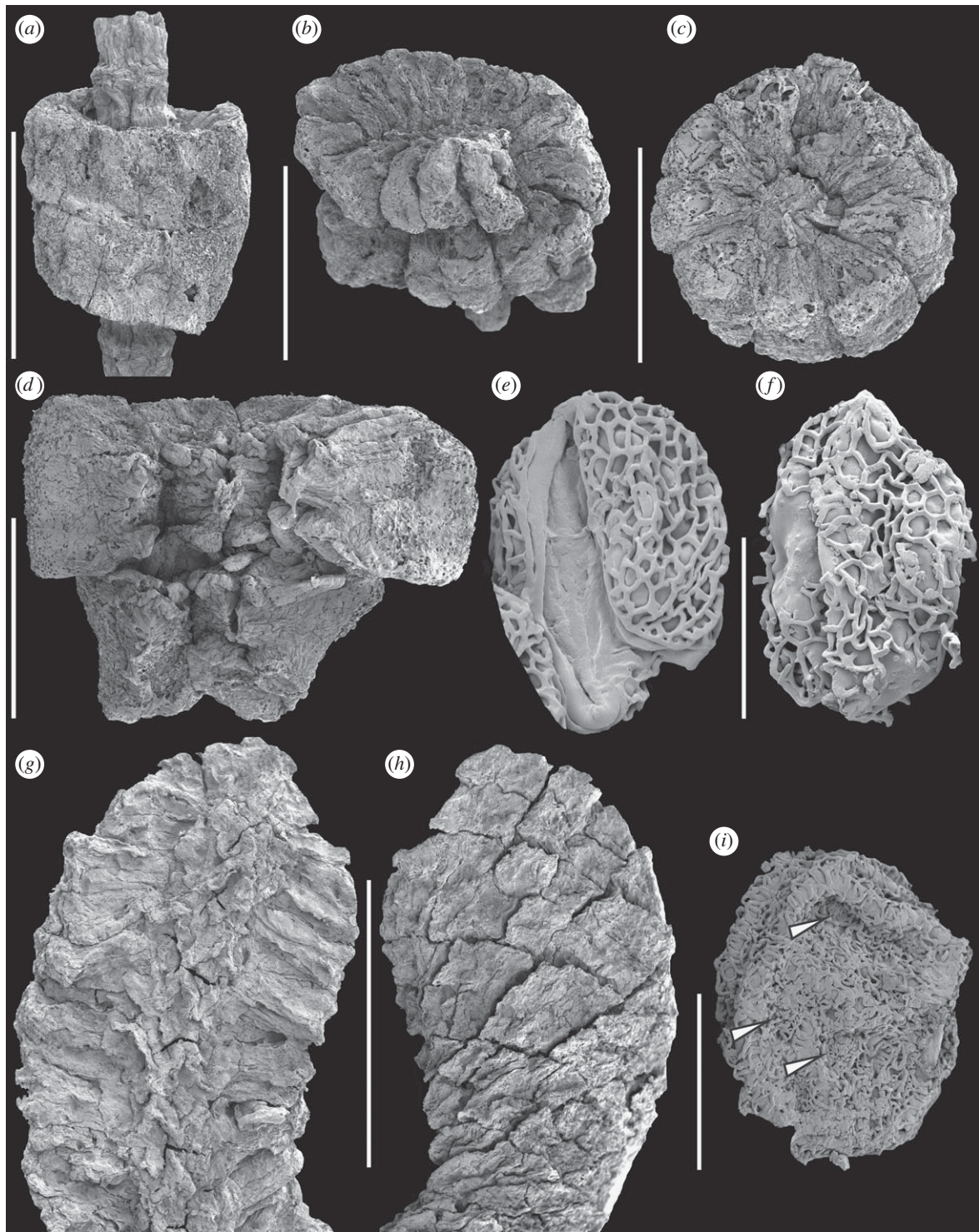


Figure 1. Scanning electron micrographs of fossil inflorescences of Araceae from the Early Cretaceous (Late Aptian–Early Albian) of the Vila Verde 2 locality (sample Vila Verde 2 439), Portugal. (a–f) Araceae fossil sp. A, and *in situ* pollen. (a) Inflorescence fragment with densely spaced and spirally arranged staminate flowers on the central axis; S165015. (b) Inflorescence fragment with many spirally arranged staminate flowers; S165005. (c) Single inflorescence section with 10 stamens; S165002. (d) Inflorescence fragment with several flowers, central axis missing; S165001. (e, f) Pollen grains from staminate flower in inflorescence fragment shown in figure 1c; S165005. (g–i) Araceae fossil sp. B, with densely spaced and spirally arranged flowers and periporate pollen; S165007. (g) Internal view of inflorescence showing axis and attached flowers. (h) External view of inflorescence. (i) Periporate pollen grain from anther; arrows show three of several pores. Scale bars: a = 2 mm; c = 250 μ m; b, d, g, h = 1 mm; e, f = 10 μ m; i = 20 μ m. All specimens housed in the palaeobotanical collections at the Swedish Museum of Natural History (S).

A further Early Cretaceous fossil that may also belong to Pothoideae is a small inflorescence fragment from the Vale de Agua locality (Late Aptian–Early Albian) of Portugal. The fossil is strongly compressed and the organization of the flowers difficult to establish,

but the flowers appear very similar to the Araceae fossil sp. B. The *in situ* pollen are similarly periporate and semitectate–reticulate, but the reticulum is much more dense with very small lumina, and muri have a supracteal ornamentation of minute spinules.

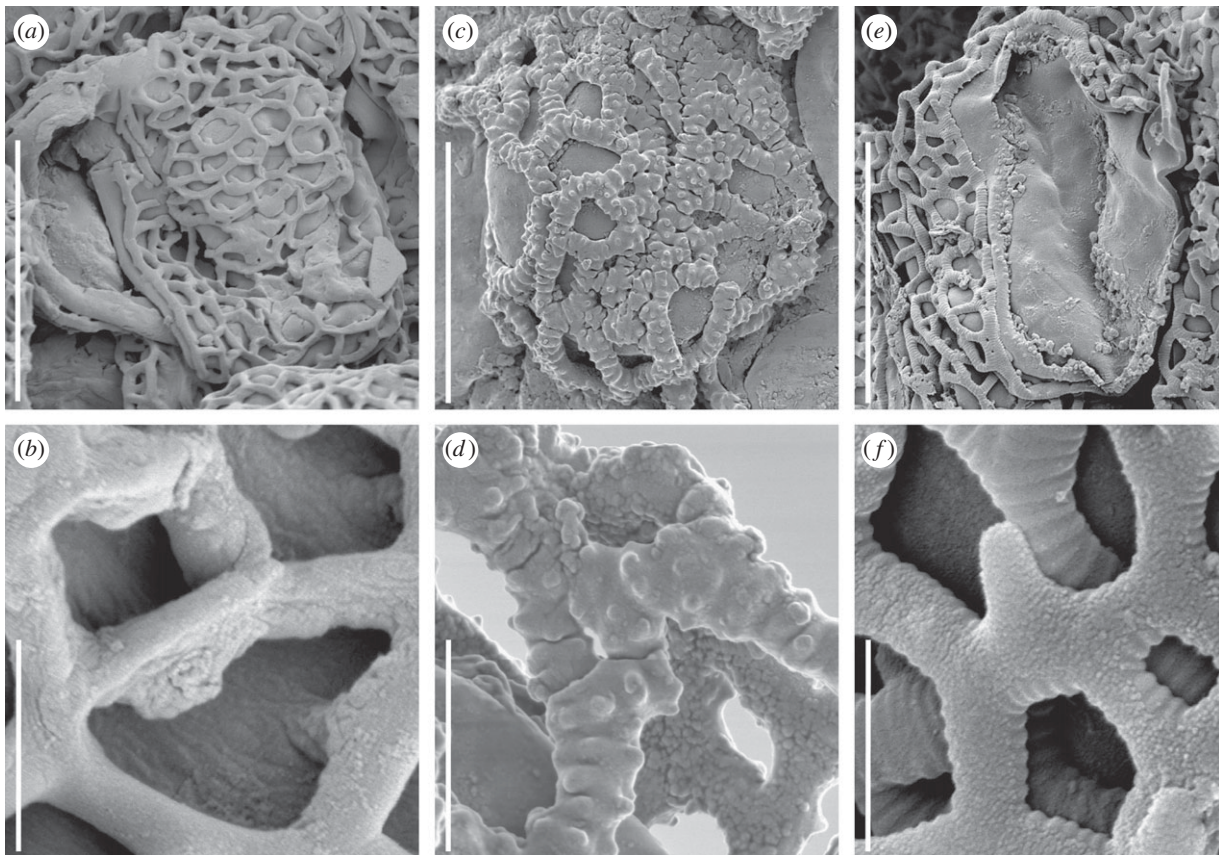


Figure 2. Scanning electron micrographs of *in situ* pollen from Early Cretaceous mesofossil floras from Portugal. (a,b) Pollen from Araceae fossil sp. A shown in figure 1b; S165005 (sample Vila Verde 2 439). (a) Pollen showing long open colpus and coarse, loose reticulum supported by scattered columellae. (b) Detail of wall showing muri without supracteal ornamentation, but with a granular structure on the internal surface and on the columellae. (c,d) *Pennipollis*-type pollen from the Late Aptian–Early Albian Vale de Agua locality (sample Vale de Agua 139); S105603. (c) Pollen showing long colpus and very coarse, loose reticulum with spiny supracteal ornamentation. (d) Detail of reticulum showing spiny supracteal ornamentation externally (above) and granular internal surface of muri (below). (e,f) ‘*Retimoncolpites*’-type pollen from Torres Vedras (sample Torres Vedras 44). (e) Pollen showing long open colpus and coarse, loose reticulum with transverse supracteal striations. (f) Detail of reticulum from two different grains. The upper reticulum is loosed from the main body of the pollen grain and shows the granular inner surface of the muri; the reticulum of the grain below shows the striate supracteal ornamentation of the outside of the muri. Scale bars: a = 10 μm ; b = 1 μm ; c, e = 12 μm ; d = 3 μm ; f = 1.2 μm . All specimens housed in the palaeobotanical collections at the Swedish Museum of Natural History (S).

There are also several fruiting structures in the early mesofossil floras from Portugal that may be linked to Araceae. Some have many fruits borne in a dense spiral along a central inflorescence axis, sometimes with rhombic apical faces, others are isolated fruits with morphological similarities to extant fruits of Araceae and have *Retimoncolpites*-type pollen attached. All these need to be studied in further detail to confirm their systematic affinity.

(ii) Other Alismatales

A general relationship to Alismatales has been suggested for the *Pennistemon/Pennicarpus/Pennipollis* plant (Friis *et al.* 2000). In contrast, an affinity with Chloranthaceae has been suggested by Hesse & Zetter (2007), Doyle *et al.* (2008) and Doyle (2009). Acolumellate pollen with an extremely loose reticulum is widespread in Alismatales and other basal monocotyledons (Grayum 1992), but is not known among extant Chloranthaceae. The finely granular inner lining of the muri seen in pollen of the *Pennistemon/Pennicarpus/Pennipollis* plant (figure 2c,d) is very similar to that seen in the *in situ*

pollen grains from the new Araceae fossil sp. A (figure 2a,b), which supports the possible alismatalean affinity for these fossils. This feature also occurs in many other *Retimoncolpites*-type pollen grains found *in situ* in dispersed stamens that range in age from Late Barremian to Middle Albian (figure 2e,f).

Dispersed pollen grains of *Pennipollis* are diverse and abundant in Early Cretaceous palynological assemblages from southern Laurasia and northern Gondwana, indicating that the *Pennistemon/Pennicarpus/Pennipollis* plants were widespread and probably common in the Barremian–Albian vegetation (Friis *et al.* 2000).

Several other floral structures that are probably related to extant Alismatales are known from the Early Cretaceous mesofossil floras of Portugal. One is a fragmentary bisexual flower with remains of stamens around an apocarpous gynoecium of three or four free follicular carpels. Pollen grains found *in situ* are periporate and tectate with echinate tectum ornamentation and clusters of small spines covering the apertures. These pollen grains are closely similar to grains of Alismataceae, and a systematic position close to Alismataceae is supported also by the general

organization of the flower. We have not seen similar pollen from dispersed palynological assemblages, but comparable periporate, tectate and echinate grains occur in coprolites from the Torres Vedras flora (Late Barremian–Early Aptian).

(iii) *Extinct groups of Early Cretaceous angiosperms*

Notwithstanding the clear presence of chloranthoid, eumagnoliid, eudicot, monocot, nymphaealean and winteroid lineages during the Early Cretaceous, as well as possible Piperales, most of the angiosperm pollen grains, flowers and fruits at this level cannot be linked convincingly to any particular extant angiosperm lineage. From the Famalicão flora for instance, more than 100 taxa of angiosperms are identified, but only a few have currently been placed in extant lineages. The degree to which such fossils reflect the presence of extinct lineages that are relatively independent of extant taxa at this level of angiosperm evolution remains to be determined. However, the relatively few fossil angiosperms in Early Cretaceous floras that can be assigned to extant taxa are strongly suggestive of considerable extinction. Especially, clear cases are those where very distinctive Early Cretaceous pollen types have no counterpart among any group of extant angiosperm (e.g. *Stellatopollis*). Such examples provide unambiguous evidence of extinction, probably at a high taxonomic level.

4. CONCLUSIONS

The extensive and highly informative record of charcoalified and lignitized angiosperm remains from the Cretaceous accumulated over the past 30 years has provided an unexpected picture of the diversity of angiosperms in Early Cretaceous plant communities (e.g. Friis *et al.* 2006a). Flowers, fruits and seeds are mainly small. It has been suggested that Early Cretaceous angiosperms were probably herbaceous on the basis of phylogenetic inferences (Taylor & Hickey 1992) or riparian weeds inferred from leaf architecture (Doyle & Hickey 1976). The identification of diverse monocot flowers in the Early Cretaceous mesofossil floras together with other fossils closely related to extant lineages that comprise predominantly herbaceous or small shrubby plants (Nymphaeaceae, Piperales, Chloranthaceae, Ranunculales, Buxales) supports these ideas. It is also interesting that many of the mesofossil and impression/compression fossils such as *Monetianthus mirus*, *Pluricarpellatia peltata*, the three species of *Archaeofructus* and many isolated leaves suggest an aquatic habitat. The colonization of the freshwater bodies by angiosperms may also have had a considerable impact on aquatic life.

Based on the presence of monoaperturate pollen, both dispersed in palynofloras and *in situ* within floral structures, it is clear that there is a great diversity of forms related to early lineages of angiosperms in the Early Cretaceous. Eudicots do not appear until after the diversification of lineages with monoaperturate pollen is well underway. In the earliest (pre-Albian) phases of the angiosperm radiation, both palynological and floral evidence show that the diversity of non-eudicot angiosperms (ANITA lineages and

Chloranthaceae, eumagnoliids, monocots and other apparently extinct forms) greatly exceeded that of eudicots, but these proportions changed dramatically through the Late Cretaceous as eudicots quickly came to dominate both mesofossil and macrofossil floras as well as most palynofloras.

An important new conclusion from the information presented here is that some of the diversity of angiosperms during the Early Cretaceous included key lineages of early monocotyledons. This had been suspected previously, but until now the early diversity of monocots has been surprisingly cryptic. More monocots may now be recognized as the search image is adjusted in light of these new discoveries. Recognition of Early Cretaceous Araceae raises interesting new questions about the timing of diversification in this family and in monocotyledons as a whole. In addition, the presence of araceous flowers of two very different kinds, together with the considerable diversity of floral form seen in other ancient angiosperms from the Early Cretaceous, highlights the extent of developmental versatility among angiosperm flowers at this very early stage in the evolution of the group.

Improved knowledge of fossil angiosperms from the Early Cretaceous has made some aspects of early angiosperm evolution much less mysterious, but a key remaining issue is the relationship of angiosperms to other seed plants. While this is still very uncertain, new fossils are constantly being added to the fossil record of angiosperms and potentially related seed plants (Friis *et al.* 2009a). These discoveries may ultimately help to clarify the phylogenetic position of angiosperms in the broader context of seed plant evolution. They may also help illuminate how the key features of the angiosperm flower came together, and provide the information needed to better understand the history of pollination and dispersal biology among angiosperms and their relatives.

We thank W. G. Chaloner, London, and an anonymous reviewer for valuable suggestion to this paper. This research was supported by the Swedish Natural Science Research Council (EMF), the Carlsberg Foundation, Denmark (KRP) and the National Science Foundation (PRC).

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