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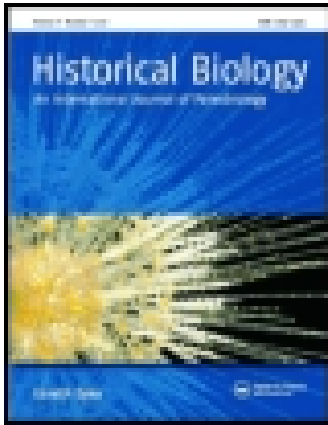2015-04-03

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Recognising angiosperm clades in the Early Cretaceous fossil record

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Studies of the earliest Cretaceous angiosperms in the 1970s made only broad comparisons with living taxa, but discoveries of fossil flowers and increasingly robust molecular phylogenies of living angiosperms allow more secure recognition of extant clades. The middle to late Albian rise of tricolpate pollen and the first local dominance of angiosperm leaves mark the influx of near-basal lines of eudicots. Associated flowers indicate that palmately lobed 'platanoids' and *Sapindopsis* are both stem relatives of *Platanus*, while *Nelumbites* was related to *Nelumbo* (also Proteales) and *Spanomera* to Buxaceae. Monocots are attested by Aptian *Liliacidites* pollen and *Acaciaephyllum* leaves and Albian araceous inflorescences. Several Albian–Cenomanian fossils belong to Magnoliidae in the revised monophyletic sense, including *Archaeanthus* in Magnoliales and *Virginianthus* and *Mauldinia* in Laurales, while late Barremian pollen tetrads (*Walkeripollis*) are related to Winteraceae. In the basal ANITA grade, Nymphaeales are represented by Aptian and Albian flowers and whole plants (*Monetianthus*, *Carpestella* and *Pluricarpellatia*). Epidermal similarities of lower Potomac leaves to woody members of the ANITA grade are consistent with Albian flowers assignable to Austrobaileyales (*Anacostia*). Aptian to Cenomanian mesofossils represent both crown group Chloranthaceae (*Asteropollis* plant) and stem relatives of Chloranthaceae and/or *Ceratophyllum* (*Canrightia*, *Zlatkocarpus*, *Pennipollis* plant and possibly *Appomattoxia*).

Keywords: angiosperms; Cretaceous; palaeobotany; palynology; phylogeny

1. Introduction

The past five decades have seen a dramatic reawakening of interest in the early fossil record of angiosperms, which with some notable exceptions (e.g. Teixeira 1948; Vakhrameev 1952) had been neglected following the first studies of Early Cretaceous floras around the turn of the last century. A major question in this field is what living clades are represented among the oldest unquestioned angiosperms. Early palaeobotanists such as Fontaine (1889) and Berry (1911), working on the Potomac Group of the Atlantic Coastal Plain of the United States (Aptian to early Cenomanian, Virginia and Maryland), did not hesitate to assign angiosperm leaves to living genera, such as *Ficus* or *Sassafras*, or to fossil genera with names intended to suggest affinities with living taxa, such as *Ficophyllum*, *Proteaephyllum*, *Vitiphyllum* and *Sapindopsis*. However, serious doubt was cast on these identifications in the 1960s and 1970s. This was partly due to palynological studies on Cretaceous rocks (e.g. Brenner 1963; Pacltová 1966; Muller 1968), which showed that the first recognisable angiosperm pollen was much less diverse and modern than implied by the old leaf identifications and showed a progressive increase in the diversity of morphological types from the Barremian to the Cenomanian – first monosulcate, then tricolpate, tricolporate and finally triporate (Figure 1). As this pattern paralleled the sequence of pollen evolution inferred from comparative morphological studies of

modern plants, it was taken by Doyle (1969) and Muller (1970) as evidence that the main radiation of angiosperms was going on during this interval, and as support for existing ideas on the evolution of angiosperm pollen and the related 'magnoliid' theory of angiosperm evolution. This was considered evidence against the older view that angiosperms originated and began to diversify much earlier and were simply invading lowland basins of deposition in the Early Cretaceous (e.g. Axelrod 1952, 1970).

In the 1970s, reinvestigations of the Potomac Group angiosperm leaf record (Wolfe et al. 1975; Doyle and Hickey 1976; Hickey and Doyle 1977) showed that early angiosperm leaves were also less modern than previously thought and showed a pattern of temporal diversification similar to that seen in the pollen record (Figure 1). In general, Doyle and Hickey (1976) avoided comparing these leaves with living taxa, except to show that morphological features seen in the fossil leaves occur in living taxa that have pollen types known at the same level, but Hickey and Doyle (1977) did make some broad comparisons with major angiosperm groups. For example, palmately lobed 'platanoid' fossils from the middle and late Albian (Figure 1(p)) resemble leaves of *Platanus*, which has reticulate tricolpate pollen of the type that was becoming abundant at that time. In the lower Potomac (Aptian?), there are leaves with monocot-like venation and monosulcate pollen with monocot-like sculpture (Doyle
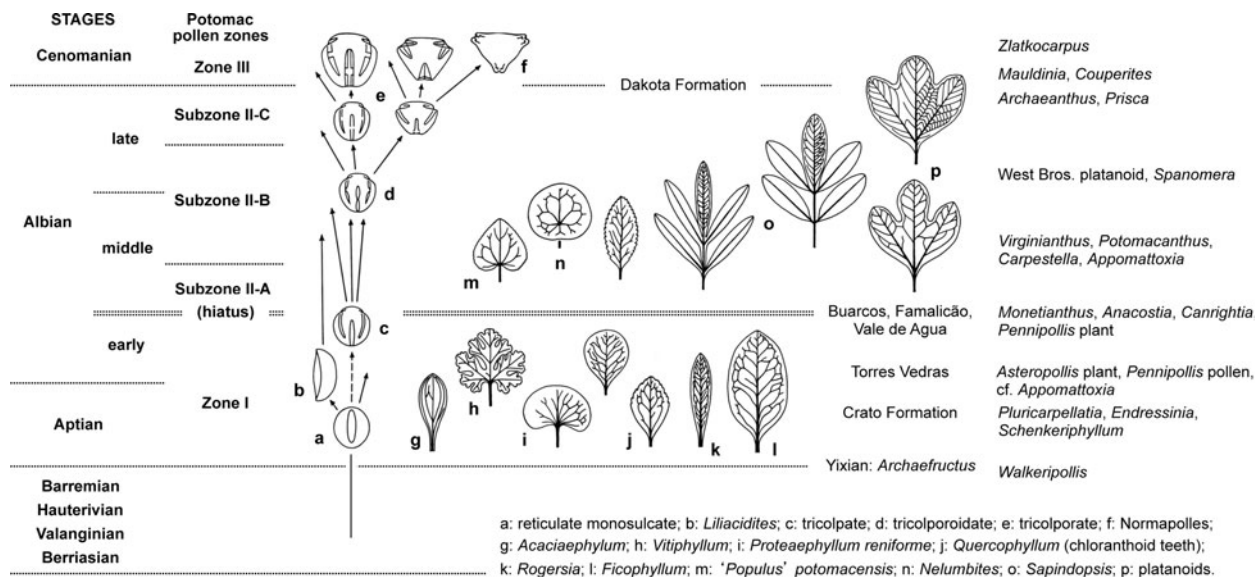
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Figure 1.   Stratigraphic sequence of major angiosperm pollen and leaf types in the Potomac Group of eastern North America (modified from Doyle and Hickey 1976), with correlations of plant localities in other geographic areas and stratigraphic positions of other pollen and floral fossils.

1973; Figure 1(b,g)). Wolfe et al. (1975), Doyle and Hickey (1976) and Hickey and Doyle (1977) argued that most of the earliest leaves had features found in what were then called 'magnoliids', in the paraphyletic sense of Takhtajan (1969) and others, meaning those 'dicots' that retain monosulcate and related pollen types. These included several leaf types (e.g. *Ficophyllum*; Figure 1 (l)) with pinnate venation, like 'woody magnoliids' (now assigned to Magnoliales, Laurales, Canellales and more basal groups such as *Amborella* and Austrobaileyales), and a few with palmate venation (e.g. *Proteaephyllum reniforme*; Figure 1(i)), like 'herbaceous magnoliids' (now placed in Nymphaeales and Piperales).

Since 1977, there have been several major advances that allow more secure identification of early angiosperm lines. First was the discovery of fossil flowers, preserved as charcoal or lignite, by Friis, Crane and others, working first on the Potomac Group and later on Cretaceous sediments in Portugal (Crane et al. 1986; Friis et al. 1986, 2011; Friis, Pedersen, et al. 1994). Many of these flowers are in the millimetre or 'mesofossil' size range. Not only do flowers usually have more characters than pollen and leaves, they can often be connected with the dispersed pollen record through pollen in stamens or adhering to stigmas. Second was the development of cladistic methods for the analysis of phylogenetic relationships, and third was the application of these and related methods to DNA sequence data, which has resulted in a vast flood of new information on relationships among living angiosperms. Since the first large-scale analyses of sequences from several genes combined (Mathews and Donoghue 1999; Parkinson et al. 1999; Qiu et al. 1999; Soltis et al. 1999),

the results have held up remarkably well with studies of many more genes (Soltis et al. 2005; Jansen et al. 2007; Moore et al. 2007; APG III 2009). These analyses have resolved many long-standing problems, such as where the angiosperm phylogenetic tree is 'rooted', or which living lines branched off first at the base of the tree: the New Caledonian genus *Amborella*, Nymphaeales (water lilies) and Austrobaileyales, all classified as magnoliids in older systems, informally designated the 'ANITA grade'. The remaining 99.9% of angiosperm species, named *Mesangiospermae* (Cantino et al. 2007), belong to five major clades: eudicots, including all groups with tricolpate and derived types of pollen; monocots; a clade including most traditional magnoliids, designated *Magnoliidae* in a new sense (Cantino et al. 2007); the rootless aquatic genus *Ceratophyllum*; and Chloranthaceae, which are characterised by unusually simple flowers. All five clades and orders within them have strong statistical support, as measured by bootstrap analysis, but relationships among them are less strongly supported, and they vary from analysis to analysis (Soltis et al. 2005; Qiu et al. 2010).

Recent studies have attempted to clarify the phylogenetic position of early angiosperms by integrating mesofossil and molecular evidence through phylogenetic analysis. The ideal procedure might be to combine morphological and molecular data in a 'total evidence' analysis, with fossils scored as unknown for molecular characters, but this has not been attempted because of problems in representation of living taxa in molecular and morphological data-sets (by species and by a mixture of species and higher taxa, respectively) and choice of molecular data. Instead, Doyle et al. (2008), Endress and

Doyle (2009) and Doyle and Endress (2010, 2014) have used a 'molecular scaffold' approach (Springer et al. 2001; Hermsen and Hendricks 2008), where a morphological data-set of living and fossil taxa is analysed with the arrangement of living taxa fixed to a 'backbone tree' based on molecular data. In the case of angiosperms, this may be an acceptable approach, as many relationships are so strongly supported by molecular data that they are highly unlikely to be overturned by morphological data from fossils. Variously modified versions of the same morphological data-set have been used in similar analyses by other authors (von Balthazar et al. 2008; Friis et al. 2009; Friis and Pedersen 2011; Mohr et al. 2013).

Because the arrangement of the five mesangiosperm clades is more uncertain, these studies used two backbone trees that cover the range of current hypotheses, which differ most significantly in the position of *Ceratophyllum* and Chloranthaceae. In the J/M backbone tree, based on analyses of nearly complete chloroplast genomes by Jansen et al. (2007) and Moore et al. (2007), *Cerato-phyllum* is linked with eudicots and Chloranthaceae with the magnoliids. In the D&E backbone tree, based on combined analyses of morphological and molecular data by Doyle and Endress (2000) and Endress and Doyle (2009), *Ceratophyllum* and Chloranthaceae are linked with each other and sister to the remaining mesangiosperms. The *Ceratophyllum*–Chloranthaceae clade has also been found in analyses of mitochondrial genes (Duvall et al. 2006; Qiu et al. 2010); slowly evolving chloroplast genes (Moore et al. 2011), which should be most reliable for detecting ancient splits; and low-copy nuclear genes (Zhang et al. 2012).

The purpose of the present article is to review the results of these analyses, beginning not with the oldest taxa but with eudicots from the middle and late Albian, for which the results are clearest, and ending with taxa that pose more problems but are equally or more interesting. Most parsimonious positions of most of the fossils on the D&E backbone tree are shown in Figure 2; where a fossil has several most parsimonious positions, one has been
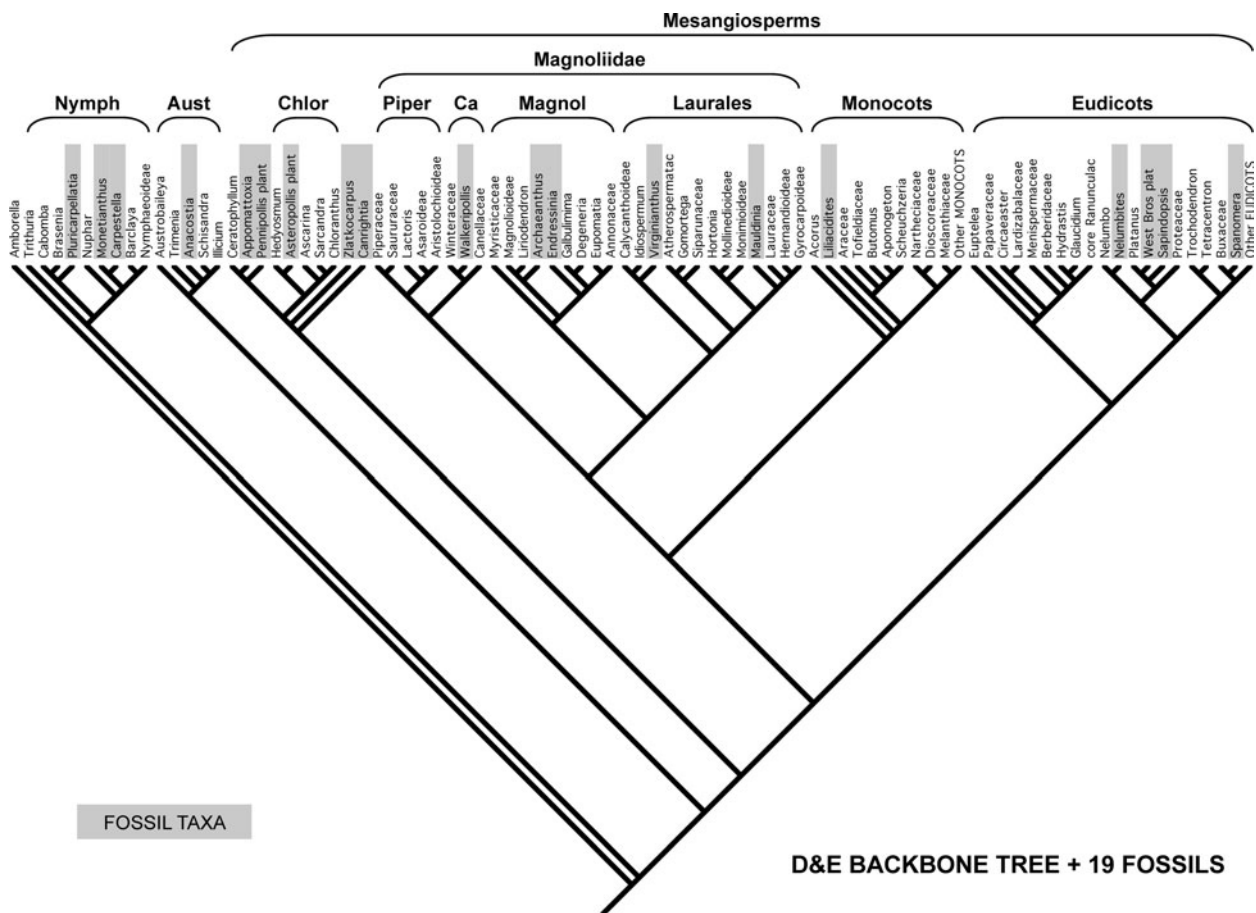
Figure 2. Most parsimonious positions of Early Cretaceous and Cenomanian fossils on a phylogeny of living angiosperms (Doyle et al. 2008; Endress and Doyle 2009; Friis et al. 2009, 2011; Doyle and Endress 2010, 2014). When a fossil has more than one most parsimonious position, one of these has been selected for purposes of discussion. *Couperites* and *Archaefructus* not included because of their excessively uncertain phylogenetic positions. Nymph, Nymphaeales; Aust, Austrobaileyales; Chlor, Chloranthaceae; Piper, Piperales; Ca, Canellales; Magnol, Magnoliales; plat, platanoid.

selected for purposes of discussion. Ages of the localities containing these fossils are discussed critically in Doyle et al. (2008), Doyle and Endress (2010, 2014) and Massoni et al. (in press). Many of these results are also discussed in Doyle and Upchurch (in press), but with special emphasis on progress in understanding the Potomac Group leaf record.

2. Eudicots

One of the first major findings of molecular systematics was that plants with tricolpate and derived pollen types, which include nearly 75% of angiosperm species, form a clade called eudicots (Doyle and Hotton 1991; Magallón et al. 1999; Cantino et al. 2007). This conclusion contrasts with the older view that such plants were polyphyletic (e.g. Takhtajan 1969) but was anticipated by some morphological cladistic analyses (Dahlgren and Bremer 1985; Donoghue and Doyle 1989). This means that the oldest known tricolpate pollen, for example from the late Barremian of England (Hughes and McDougall 1990) and Africa (Doyle et al. 1977; Doyle 1992), is evidence for the existence of this clade or the stem lineage leading to it. Furthermore, studies of fossil flowers confirm and extend earlier suggestions that many of the first common angiosperm leaf types in the middle and late Albian belong to lines that diverge near the base of the eudicots in molecular trees, below the vast bulk of eudicots, which typically have pentamerous flowers and well-differentiated sepals and petals and have been called core eudicots or *Pentapetalae* (Cantino et al. 2007).

A widespread Albian leaf type is *Nelumbites* (Figures 1(n) and 3(a)), assigned by some earlier authors to *Menispermites*, which resembled leaves of modern *Nelumbo* (= Nelumbonaceae, lotus) in being peltate and palmately veined but differed in being smaller and having less regular venation (Berry 1911; Vakhrameev 1952; Hickey and Doyle 1977; Upchurch et al. 1994). In many pre-molecular classifications, *Nelumbo* was placed in Nymphaeales, because of its aquatic habit and multiparted flowers, but it has tricolpate pollen, and molecular data indicate that it belongs to Proteales, a clade that diverges one or two nodes above the base of the eudicots. Upchurch et al. (1994) reported moulds of floral receptacles in a bed dominated by *Nelumbites* that resembled those of *Nelumbo* in being covered with pits for the carpels but differed in being round rather than flat-topped. An analysis by Doyle and Endress (2010; Figure 2) confirmed that *Nelumbites* was most closely related to *Nelumbo*, but it was almost as parsimonious to place it in Nymphaeales with *Brasenia*, which also has peltate leaves. This uncertainty is largely a function of the small number of characters preserved. A character not used by Doyle and Endress (2010) that would favour a relationship of *Nelumbites* to *Nelumbo* is the

shape of the leaf blade, which is like that of *Nelumbo* in varying from round to wider than long, whereas the blade in *Brasenia* is longer than wide (cf. Wang and Dilcher 2006).

Significantly, the two most common Potomac angiosperm leaf types are related to another member of Proteales, namely *Platanus* (= Platanaceae, sycamore or plane tree). These include the palmately lobed platanoid leaves already mentioned (Figure 1(p)), which are a conspicuous feature of late Albian and Cenomanian floras around the Northern Hemisphere, including the classic Dakota flora of Kansas (Lesquereux 1892) and similar floras in Kazakhstan (Vakhrameev 1952). Their platanaceous affinity was suspected based on similarities in venation and co-occurrence with inflorescence axes bearing *Platanus*-like heads (e.g. Hickey and Doyle 1977). Subsequently, Crane et al. (1986), Friis et al. (1988) and Pedersen et al. (1994) showed that the heads were like those of *Platanus* in consisting of unisexual flowers with peltate stamens and free carpels, but apparently more primitive (most notably in having a better-developed perianth). A more surprising result was the discovery of Crane et al. (1993) that pinnately dissected (nearly compound) leaves known as *Sapindopsis* (Figure 1(o)) were from plants with heads made up of similar flowers (Figure 3(b)). There had been suggestions that *Sapindopsis* and the platanoids were related, based on similarities in leaf architecture (Hickey and Wolfe 1975; Doyle and Hickey 1976) and cuticle anatomy (Upchurch 1984a) and the presence of heads in the same beds (Hickey and Doyle 1977). However, Hickey and Wolfe (1975) and Hickey and Doyle (1977) had compared *Sapindopsis* with Rosidae, where pinnately compound leaves are most common, and argued that this supported a common origin of the now-defunct subclass Hamamelididae (to which *Platanus* was assigned) and Rosidae. This hypothesis would be inconsistent with the finding that *Sapindopsis* had heads of unisexual flowers, which would not be expected on the line leading to Rosidae. The analysis of Doyle and Endress (2010) strongly confirmed that both *Sapindopsis* and the platanoids were extinct relatives of the *Platanus*, either as two successive outgroups (with *Sapindopsis* diverging first) or a sister clade.

According to molecular analyses, the sister group of *Platanus* is the Southern Hemisphere family Proteaceae, which has triporate pollen of a type that appears in the Cenomanian of Africa and Brazil (*Triorites africaensis*: Jardiné and Magloire 1965; Ward and Doyle 1994; Dettmann and Jarzen 1996; Sauquet et al. 2009). As the two other lines in Proteales occur in the middle Albian, the tree implies that the line leading to Proteaceae also existed by this time, but presumably it still had tricolpate pollen.

Another eudicot line is represented by *Spanomera*, from the late Albian and early Cenomanian of Maryland (Drinnan et al. 1991), which had reduced unisexual flowers
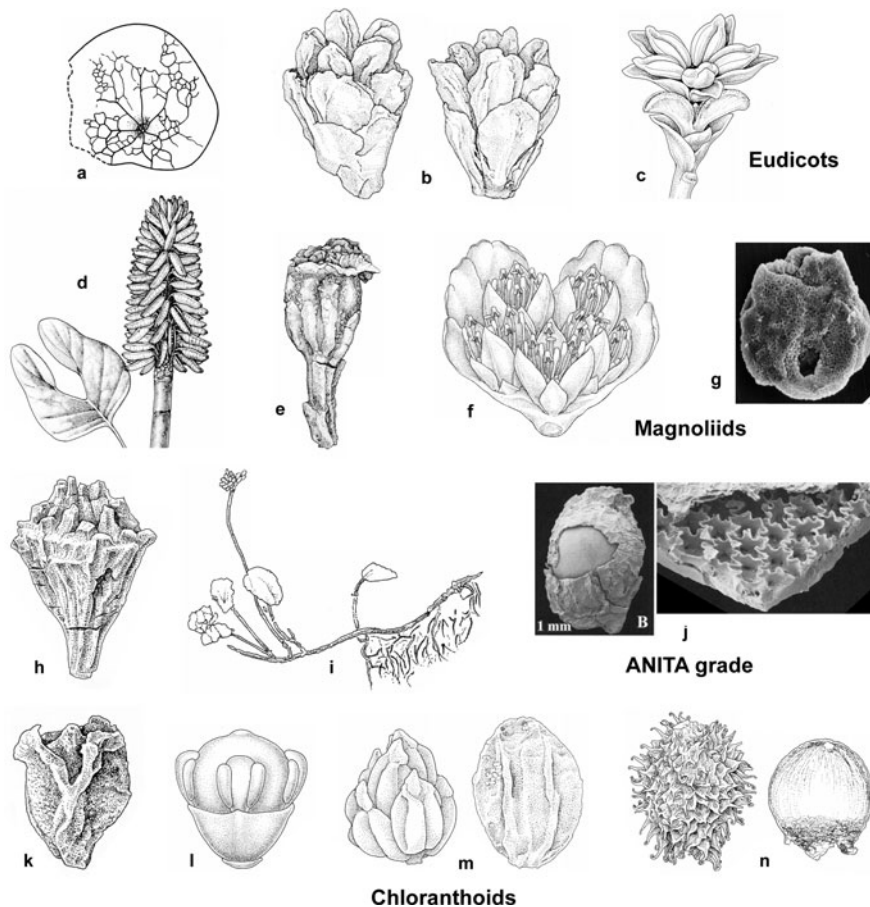
Figure 3.   Cretaceous angiosperm fossils discussed in the text (images reproduced with permission from the publications cited). (a) *Nelumbites extenuinervis*, leaf (Doyle and Hickey 1976); (b) *Friisicarpus brookensis*, female flowers associated with *Sapindopsis variabilis* leaves (Friis et al. 2011); (c) *Spanomera mauldinensis*, reconstruction of inflorescence with lateral male flower above and terminal female flower below (Friis et al. 2011); (d) *Archaeanthus linnenbergeri*, reconstruction of leaf and flower in fruit stage (Dilcher and Crane 1984); (e) *Virginianthus calycanthoides*, flower (Friis et al. 2011); (f) *Mauldinia mirabilis*, reconstruction of inflorescence unit with five flowers (Friis et al. 2011); (g) *Walkeripollis gabonensis*, pollen tetrad, SEM (Doyle et al. 1990); (h) *Monetianthus mirus*, flower (Friis et al. 2011); (i) *Pluricarpellatia peltata*, rhizome with roots, leaves and flower in fruit stage (Friis et al. 2011); (j) *Anacostia teixeiri*, carpel with enclosed seed and broken portion of seed coat, SEM (Friis et al. 2011); (k) *Asteropollis* plant, female flower (Friis et al. 2011); (l) *Canrightia resinifera*, reconstruction of flower (Friis et al. 2011); (m) *Pennipollis* plant: *Pennistemon portugallicus*, fragment of male inflorescence, and *Pennicarpus tenuis*, carpel (Friis et al. 2011); (n) *Appomattoxia ancistrophora*, carpel and seed (Friis et al. 2011).

grouped into bisexual inflorescences (Figure 3(c)), as in living Buxaceae, and striate tricolpate pollen (*Striatopollis paraneus* and *Striatopollis vermimurus*). Similar but more fragmentary remains are known from the early Albian of Portugal (Pedersen et al. 2007). The analysis of Doyle and Endress (2010) confirmed that *Spanomera* was related to Buxaceae, although it could almost as well be located a node lower. These results also fit the view that the oldest known eudicots belonged to lines that diverged near the beginning of the radiation of the clade. *Spanomera* has not been associated with leaves, but by plotting leaf characters in the Doyle and Endress (2010) data-set on the tree, we can predict that it had ovate leaves with palmate venation and chloranthoid teeth, like '*Populus*' *potomacensis* (Figure 1(m)) in the middle–late Albian part of the Potomac Group.

Dissected leaves such as *Vitiphyllum* (Figure 1(h)) and *Potomacapnos* (Jud and Hickey 2013) from the lower Potomac Group (Zone I, Aptian to early Albian?), *Leefructus* from the Barremian–Aptian Yixian Formation of NE China (Sun et al. 2011) and morphotype 'LC-Microphyll trifoliate' from the Aptian of Argentina (Puebla 2009) are suggestive of Ranunculales, the sister group of all other eudicots, in their ternate organisation, a feature of many members of this order (Hickey and Wolfe 1975; Doyle 2007). However, similar but more finally dissected leaves also occur in *Archaefructus*, an aquatic plant of highly debated affinities from the Yixian Formation (Sun et al. 1998, 2002; Friis et al. 2003; Endress and Doyle 2009), discussed further below. The fact that *Leefructus* and the Argentine leaves (though not *Vitiphyllum*) predate the appearance of definite tricolpate

pollen in their geographic areas suggests the possibility that they represent either stem relatives of eudicots or some unrelated extinct group(s), as discussed by Doyle (2012). Parsimony analysis implies that dissected leaves arose within the eudicots (Doyle 2007), but a likelihood-based analysis by Geeta et al. (2012) indicated that they were most likely ancestral in the clade.

Core eudicots or *Pentapetalae*, with basically penta-merous flowers, are probably represented among the tricolporate pollen types that appear and begin to diversify in the late Albian. Such pollen appears to be basic for the two main subclades of *Pentapetalae*, Rosidae and Asteridae, although both tricolpate and tricolporate pollen occurs in some of the more basal lines, such as Saxifragales and Caryophyllales (Doyle 2005; Furness et al. 2007). A typical pentamerous flower from the latest Albian Rose Creek locality in the Dakota Formation of Nebraska (Basinger and Dilcher 1984) probably belongs to crown group *Pentapetalae*, but it has not been analysed phylogenetically.

3.   Monocots

The next-largest mesangiosperm clade is the monocots. Two kinds of fossils from the lower Potomac Group (Aptian) have been interpreted as monocots (Doyle 1973; Hickey and Doyle 1977; Walker and Walker 1984): boat-shaped monosulcate pollen of the *Liliacidites* type (Figure 1(b)), with 'graded' reticulate sculpture that is finer at the ends of the grain and coarser in the middle; and *Acaciaephyllum* (Figure 1(g)), best known as a leafy stem bearing narrow leaves with apically fusing venation. These fossils were questioned as monocots by Gandolfo et al. (2000), in part because of cases where the name *Liliacidites* was used for pollen without the typical sculpture pattern and leaf architectural similarities between *Acaciaephyllum* and living and fossil Gnetales, but their relationship to monocots was reaffirmed by phylogenetic analyses of Doyle et al. (2008). Sculpture of the *Liliacidites* type is restricted to monocots today (although far from universal among them), and the combination of spiral phyllotaxis, narrow blade, presence of a median vein, and apically fusing, low-angle secondary veins distinguishes *Acaciaephyllum* both from other angiosperms with palmate venation and from superficially similar leaves in Gnetales.

Although not yet analysed phylogenetically, inflor-escences of sessile, ebracteate and dimerous flowers from the probable early Albian of Portugal (Friis et al. 2010b; Figure 1) provide evidence that monocots had begun to diversify by this time, because the floral features listed are apomorphies of Araceae, in the Alismatales, an order that diverges one node above the base of the monocots (after *Acorus*) in molecular trees. Another probable early

representative of Araceae is *Spixianthus*, based on aroid-like leaves and a stem bearing roots and leaves from the late Aptian Crato Formation of Brazil (Coiffard et al. 2013b).

4.   Magnoliids

All groups of angiosperms other than eudicots and monocots were formerly classified as magnoliids (e.g. Takhtajan 1969), a name no longer used in this sense because it would designate a paraphyletic grade. However, molecular data indicate that most of these plants do belong to one clade, called *Magnoliidae* in a revised sense (Cantino et al. 2007), which includes Magnoliales, Laurales, Canellales and Piperales. An increasing number of these groups have been recognised in the Cretaceous floral record, implying that they were actively radiating alongside early eudicots and monocots.

Several mid-Cretaceous fossils appear to represent Magnoliales. The most securely placed of these is *Archaeanthus* (Figure 3(d)), from the latest Albian or earliest Cenomanian of the Dakota Formation of Kansas (Dilcher et al. 1976; Dilcher and Crane 1984). This plant is known from isolated leaves with a bilobed apex, bracts, tepals, and floral axes bearing numerous carpels and scars that correspond in size and position to the numerous stamens, three whorls of perianth parts and sheathing floral bract in Magnoliaceae. The analysis of Doyle and Endress (2010) strongly associated *Archaeanthus* with Magnolia-ceae, either attached to the stem lineage of the family or nested within it, linked with one or the other of its two subgroups (*Liriodendron* and Magnolioideae = *Magnolia* s.l.). A recent analysis by Romanov and Dilcher (2013) placed *Archaeanthus* in the crown group of Magnoliaceae, as the sister group of *Liriodendron*. However, this analysis treated lobation of the leaf apex and the leaf blade as two characters, when they represent only one change from the ancestral unlobed leaf, and it incorrectly identified the whorled perianth phyllotaxis of *Archaeanthus* and *Liriodendron* as a synapomorphy because it used the distantly related genus *Illicium* (Austrobaileyales) as outgroup rather than other Magnoliales, most of which also have a whorled perianth (Massoni et al. in press).

Older fossils that probably belong to Magnoliales but are less precisely located within the order are *Endressinia* (Mohr and Bernardes-de-Oliveira 2004) and *Schenker-iphyllum* (Mohr et al. 2013) from the late Aptian Crato flora of NE Brazil, both represented by stems with leaves and incompletely preserved flowers. Doyle and Endress (2010) placed *Endressinia* below or within the clade consisting of *Degeneria*, *Galbulimima*, *Eupomatia* and Annonaceae, supported in part by similar inner staminodes in these taxa, but an analysis by Mohr et al. (2013) associated *Endressinia* and *Schenkeriphyllum* with each

other as the sister group of Magnoliaceae, based on their sheathing leaf bases and dry fruit. These conflicting results have not been resolved, but the two studies agree in indicating the existence of crown group Magnoliales in the late Aptian. Two Potomac Group fossils that have been compared with Magnoliales are large, boat-shaped monosulcate pollen grains with granular infratectal structure (*Lethomasites*, Aptian: Ward et al. 1989) and laminar stamens containing smooth, boat-shaped mono-sulcate pollen (dispersed stamen type 1, Albian: Crane et al. 1994), but these comparisons are speculative given the small number of characters involved.

Laurales are represented in the Albian–Cenomanian by several floral types, which correspond to both relatively plesiomorphic and more derived morphologies in the order. *Virginianthus*, from the middle Albian of the Potomac Group (Figure 3(e)), was assigned by Friis, Eklund et al. (1994) to 'stem group Calycanthaceae' because it had a deep floral cup with numerous spiral tepals, stamens, and staminodes on the rim and numerous carpels inside, as in Calycanthaceae, the sister group of the remaining Laurales, but monosulcate rather than dis-ulculate pollen. In the analysis of Doyle et al. (2008), *Virginianthus* was sister to Calycanthaceae in one most parsimonious tree, but in the other it was attached to the line to the remaining Laurales. At the other extreme is *Mauldinia* (Drinnan et al. 1990; Figure 3(f)), known from inflorescences made up of dichasial cymes of trimerous flowers with one carpel and stamens with paired basal glands and flap dehiscence, as in Lauraceae, and associated wood (*Paraphyllanthoxylon*: Herendeen 1991), from the early Cenomanian of Maryland. Fossils named *Prisca* from the Dakota Formation of Kansas (latest Albian or early Cenomanian) that Retallack and Dilcher (1981) interpreted as elongate floral axes are probably inflorescences of similar or identical plants. Despite the nearly lauraceous floral morphology, the analysis of Doyle and Endress (2010) indicated that *Mauldinia* did not belong to Lauraceae but was instead an extinct sister group of Lauraceae and the related family Hernandiaceae, based on its retention of ancestral features such as a more differentiated perianth and endosperm in the mature seed. Similar but less complete flowers from Virginia, *Potomacanthus* and *Cohongarootonia* (von Balthazar et al. 2007, 2011), appear to extend this line back to the middle Albian. Leaves assigned to Laurales by Upchurch and Dilcher (1990) are common in the late Albian of the Dakota Formation, including both simple, pinnately veined leaves (*Pandemophyllum*) and palmately lobed leaves (*Pabiania*), formerly confused with platanoids, which are superficially similar to *Sassafras* but more plesiomorphic than extant Laurales in their fine venation (Doyle and Upchurch in press).

The third magnoliid order, Canellales, includes Winteraceae, which are famous for their vesselless wood, and the small tropical family Canellaceae. This clade is represented by tetrads of monoporate grains that closely resemble pollen of living Winteraceae in their aperture and exine structure but have finer sculpture, from the late Barremian to Cenomanian of Gabon, Israel and Argentina (Walker et al. 1983; Doyle et al. 1990; Barreda and Archangelsky 2006; Schrank 2013). The phylogenetic analysis of Doyle and Endress (2010) supported the interpretation of the oldest pollen (*Walkeripollis gabo-nensis*; Figure 3(g)) as representing stem relatives of Winteraceae. These Early Cretaceous fossils were more tropical in their distribution than Late Cretaceous, Tertiary, and living Winteraceae, suggesting a later shift from tropical to temperate climatic preferences (Doyle 2000).

So far no Early Cretaceous fossils have been described that clearly represent the fourth magnoliid order, Piperales. Friis et al. (1995, 2011) suggested that Albian fruits described as *Appomattoxia* were piperalean, but as discussed below phylogenetic analysis indicates that they are more likely related to *Amborella* or Chloranthaceae (Doyle and Endress 2014).

5. ANITA lines

Molecular trees predict that the basal ANITA lines occurred in the Early Cretaceous, and there is increasing fossil evidence that they did. The best-documented line is Nymphaeales, consisting of Cabombaceae, Nymphaea-ceae and the highly reduced Hydatellaceae (*Trithuria*), which until recently were thought to be monocots (Saarela et al. 2007). The phylogenetic position of Nymphaeales, one node above the base of the angiosperms, implies that they are an ancient line that went from the land into the water, but it does not say when this shift occurred – it could have been in the Early Cretaceous, earlier or much later.

The most informative nymphaealean fossil is *Mon-etianthus*, a flower from the early Albian of Portugal (Friis et al. 2009; Figure 3(h)). It had numerous tepals and stamens and a ring of 12 carpels, and X-ray microtomo-graphy showed that the carpels had the typical laminar placentation of Nymphaeales. Using the data-set of Saarela et al. (2007), Friis et al. (2009) concluded that *Monetianthus* was nested within Nymphaeaceae, as the sister group of *Barclaya* and Nymphaeoideae (*Nymphaea*, *Victoria* and *Euryale*), with which it shares an inferior ovary. With a larger data-set, Doyle and Endress (2014) obtained a similar result, with additional most parsimo-nious positions sister to either *Barclaya* or Nymphaeoi-deae. Von Balthazar et al. (2008) described a similar but less well-preserved flower from the middle Albian of Virginia as *Carpestella*. Its position was poorly resolved in their phylogenetic analysis, but Doyle and Endress (2014) found that it had the same three most parsimonious

positions as *Monetianthus*. Because all living Nymphaeales are aquatic (except for an obvious reversal to wet terrestrial habitats in *Barclaya rotundifolia*: Feild et al. 2004), this evidence that Albian fossils were crown group members implies that the nymphaealean line had become aquatic by this time.

More direct evidence for an aquatic habit is seen in *Pluricarpellatia* (Mohr et al. 2008; Figure 3(i)), from the lacustrine Crato Formation of Brazil (late Aptian: Heimhofer and Hochuli 2010), which had cordate to peltate leaves with long petioles attached to an herbaceous rhizome and flowers (in the fruit stage) with several free carpels. An analysis of vegetative characters by Taylor (2008) indicated that *Pluricarpellatia* could be sister to either Cabombaceae or Nymphaeales as a whole (not including *Trithuria*), but Doyle and Endress (2014) found that it could be sister to Cabombaceae, *Brasenia* (one of the two genera of Cabombaceae) or Nymphaeaceae; the ambiguity was due in part to uncertainty on the arrangement of the carpels. An analysis by Coiffard et al. (2013a) concluded that other Crato fossils with stems, roots and palmately veined, cordate leaves but no flowers (*Jaguariba*) were nested within Nymphaeaceae. A variety of other cordate and peltate leaves that probably represent Nymphaeales have been described from the Albian of Jordan (Taylor et al. 2008) and the late Albian or early Cenomanian of Kansas (Wang and Dilcher 2006). It is possible that lower Potomac (Aptian–early Albian) reniform leaves with palmate venation (*Proteaephyllum reniforme*: Figure 1(i)) also represent Nymphaeales.

As several authors have noted (Nixon 2008; Coiffard et al. 2013a; Doyle and Endress 2014), Early Cretaceous Nymphaeales present a case of conflict between the fossil record and molecular dating analyses, which use the divergence of DNA sequences and fossil calibrations to estimate the age of clades. Because these analyses are based on DNA from living taxa, they necessarily provide ages for crown clades only. Such an analysis by Yoo et al. (2005) concluded that the crown group of Nymphaeaceae and Cabombaceae (Hydatellaceae had not yet been associated with the order) was less than a third the age of the angiosperms, or Eocene (44.6 Ma) on the assumption that angiosperms were not much older than the first unquestioned fossil pollen of angiosperms in the Hauterivian. However, the analyses of *Monetianthus*, *Carpestella* and *Pluricarpellatia* imply that this crown group had originated by the end of the Aptian (ca. 112 Ma), which would put the origin of angiosperms in the Carboniferous. This could be taken to mean that angiosperms do go back to the Palaeozoic, or that the fossils are incorrectly placed, but it could also reflect problems of molecular dating methods in dealing with unequal rates of evolution (cf. Nixon 2008).

A more controversial fossil is *Archaefructus*, an aquatic plant with finely dissected leaves and fertile axes bearing loosely spaced stamens and carpels from the Barremian or Aptian Yixian Formation of NE China (Sun et al. 1998, 2002). A phylogenetic analysis by Sun et al. (2002) attached *Archaefructus* to the stem lineage of living angiosperms, but Friis et al. (2003) interpreted the fertile axes as inflorescences of reduced flowers and argued that *Archaefructus* was a crown group angiosperm that had undergone floral reduction during adaptation to an aquatic habitat. An analysis by Endress and Doyle (2009) placed it in Nymphaeales, sister to Hydatellaceae, which show even more extreme floral reduction. Wang and Zheng (2012) reported that ovules of *Archaefructus* were borne on the midrib of the carpel, as in Cabombaceae, which might support this hypothesis. However, the Endress and Doyle (2009) result depended on the interpretation of structures extracted from the stamens as monosulcate pollen grains, which was questioned by Friis et al. (2003, 2011) because of their irregular size and shape. If pollen characters are removed from the Endress and Doyle (2009) analysis, it is more parsimonious to place *Archaefructus* in Ranunculales, near the base of the eudicots, which would be consistent with its ternately dissected leaves. However, as discussed by Doyle (2012), a position in crown eudicots is hard to reconcile with the lack of tricolpate pollen in the Yixian and other floras at the same latitude. Another possibility, mentioned above, is that *Archaefructus* and other ternately dissected Early Cretaceous leaves such as *Vitiphyllum* (Figure 1(h)) represent stem relatives of eudicots.

The other two ANITA lines, *Amborella* and Austrobaileyales, are woody plants with pinnate leaf venation. In the lower Potomac Group (Aptian–early Albian), there are pinnately veined leaves such as *Ficophyllum* and *Rogersia* that have unusually irregular venation, with variable spacing, branching and looping of the secondary veins and a continuum of finer vein orders (Figure 1(k,l)). Wolfe et al. (1975), Doyle and Hickey (1976) and Hickey and Doyle (1977) pointed out similar venation in Winteraceae, now known to belong in the magnoliid clade, but it also occurs in ANITA groups such as *Illicium* (Upchurch and Dilcher 1990). In studying cuticle anatomy of the early Potomac leaves, Upchurch (1984b) concluded that the most similar living taxa were *Amborella* and *Austrobaileya*, 15 years before molecular data showed that these were two of the most basal angiosperm lines. Some cuticle types have features that suggest a position nested within Austrobaileyales (Doyle and Upchurch in press). Other leaves from the late Albian of the Dakota Formation may also represent Austrobaileyales (as 'Illiciales': Upchurch and Dilcher 1990).

Reproductive evidence for Austrobaileyales comes from uniovulate fruits and multicarpellate floral axes named *Anacostia* from the early and middle Albian of Portugal and the Potomac Group (Friis et al. 1997; Figure 3(j)). Pollen on the stigmas is of the type called

Similipollis (Góczán and Juhász 1984), which varies between monosulcate and trichotomosulcate and has finer sculpture at the proximal and distal poles; because of the graded sculpture, such pollen was once incorrectly assigned to *Liliacidites* and monocots (Doyle 1973; Walker and Walker 1984). The seed coat has an outer palisade exotesta of thick-walled cells and a sclerotic mesotesta of cells with sinuous walls, an anatomy characteristic of Austrobaileyales, as illustrated in *Illicium* by Oh et al. (2003). Phylogenetic analyses by Doyle et al. (2008) and Doyle and Endress (2014) nested *Anacostia* within Austrobaileyales, sister to *Illicium* and *Schisandra* or to *Schisandra* alone. The possibility that fruits called *Appomattoxia* (Friis et al. 1995) are from relatives of *Amborella* is discussed in the next section.

This evidence for ANITA lines in the Early Cretaceous has an indirect relation to recent discussions on the age of the angiosperms (cf. Doyle 2012). Most molecular dating analyses indicate that crown group angiosperms originated in the Jurassic or Triassic (e.g. Bell et al. 2010; Smith et al. 2010; Clarke et al. 2011), but this raises the question of why they are not seen in the fossil record until the Cretaceous. One hypothesis (Feild et al. 2004, 2009) is based on the fact that the living ANITA lines (except for Nymphaeales, which are derived in being aquatic) are ecologically restricted to wet forest understorey habitats, as in New Caledonia and Queensland today, and low in diversity (only 0.1% of angiosperm species). This suggests that pre-Cretaceous ANITA-grade angiosperms could have escaped detection because wet habitats suitable for them were geographically restricted, because arid and semiarid conditions prevailed across most of the tropics (Rees et al. 2000; Ziegler et al. 2003). The rise of angiosperms observed in the Cretaceous might reflect the origin and radiation of mesangiosperms, assuming that these were able to escape from the original wet understorey niche (as argued by Feild et al. 2004) and had higher rates of diversification (as inferred by Magallón and Sanderson 2001). However, the results summarised here imply that the ANITA lines were also radiating at least modestly in the Early Cretaceous, alongside magnoliids, monocots, primitive eudicots and relatives of Chloranthaceae. This could mean that external environmental factors had inhibited the diversification of angiosperms in general before the Cretaceous, or that angiosperms are not as old as molecular analyses imply.

6. Chloranthaceae and relatives

The last two mesangiosperm clades, Chloranthaceae and *Ceratophyllum*, are remarkable for their extremely simple flowers. Of the four genera of Chloranthaceae (Endress 1987), *Ascarina* has spikes of either male flowers consisting of one stamen (rarely 2–5) or female flowers

consisting of one carpel that contains one ovule. *Hedyosmum* also has unisexual flowers with one stamen or one carpel, but the female flowers have three reduced tepals on top. *Sarcandra* and *Chloranthus* have bizarre bisexual flowers that consist of one carpel and either one stamen or a three-lobed androecium, respectively. In *Ceratophyllum*, a floating aquatic with whorled dichotomous leaves and no roots, the male structures have been variously interpreted as flowers with many stamens or spikes of flowers consisting of one stamen, while the female flowers consist of one uniovulate carpel; sterile organs below the fertile parts are interpreted as bracts (Endress and Doyle 2009). In both groups, the single ovule is apical and orthotropous, with the number of integuments reduced to one in *Ceratophyllum*. In analyses of chloroplast genomes (Jansen et al. 2007; Moore et al. 2007), the two taxa are well separated, with Chloranthaceae sister to magnoliids and *Ceratophyllum* sister to eudicots. However, morphological data indicate that they are sister groups (Endress and Doyle 2009; cf. Figure 2), and this result has also been found in analyses of mitochondrial genes (Duvall et al. 2006; Qiu et al. 2010), slowly evolving chloroplast genes (Moore et al. 2011) and low-copy nuclear genes (Zhang et al. 2012). Essentially, such trees imply that *Ceratophyllum* was derived from Chloranthaceae-like plants that became aquatic.

Before the advent of molecular systematics, there was speculation that Chloranthaceae might provide an alternative model for the first angiosperms (Burger 1977; Leroy 1983; Endress 1987; Taylor and Hickey 1992; Nixon et al. 1994), but this is refuted by molecular data, which uniformly exclude the family from the basal ANITA grade. The combined morphological and molecular analysis of Doyle and Endress (2000), which did not include *Ceratophyllum*, placed Chloranthaceae at the base of the mesangiosperm clade (Figure 2), in part because they retain the ancestral ascidiate carpel typical of the ANITA lines. However, in molecular trees where the two taxa are sister groups, their position is variable.

It has been suggested that Chloranthaceae were an important early angiosperm group since Couper (1958) described the columellar monosulcate pollen genus *Clavatipollenites* from the upper Wealden (Barremian) of England and compared it with pollen of *Ascarina*. This comparison was strengthened by electron microscopic work (Doyle et al. 1975; Walker and Walker 1984), which showed that the living and fossil taxa both have a tectal reticulum with supratectal spinules, a thick nexine made up of foot layer (underlain by endexine below the sulcus) and a sculptured sulcus membrane. Chloranthaceae have pinnately veined, toothed leaves, like some Potomac fossils (Figure 1(j)), and Upchurch (1984b) showed that these fossils resembled Chloranthaceae in cuticle anatomy and chloranthoid tooth structure (Hickey and Wolfe 1975), with median and lateral veins that fuse below an apical

gland. Chloranthoid teeth alone are not diagnostic of Chloranthaceae, because they also occur in some ANITA groups (including *Amborella*) and basal eudicots and may be ancestral in angiosperms (Hickey and Wolfe 1975; Doyle 2007). Other leaf characters suggestive of Chloranthaceae, including apparent opposite attachment of leaves to stems, are discussed by Doyle and Upchurch (in press).

Phylogenetic analyses have associated several meso-fossil taxa with Chloranthaceae, both as crown group members and as branches from the line leading to the family. These analyses often yielded different results with the two backbone trees, as might be expected from the fact that these differ primarily in the positions of Chloranthaceae and *Ceratophyllum*, and with chloranthoid fossils added individually or several at once to the analysis.

Pedersen et al. (1991) associated pollen of the *Clavatipollenites* type with early Cenomanian fruits called *Couperites*, which resemble berries of Chloranthaceae in containing a single pendent seed. However, the seed was unlike that of Chloranthaceae in being anatropous rather than orthotropous, suggesting that *Couperites* was outside crown group Chloranthaceae, and it had a palisade exotesta, as in most ANITA groups but not Chloranthaceae. Analyses by Doyle and Endress (2014) indicated that *Couperites* may or may not be related to Chloranthaceae. With the chloroplast backbone tree (J/M), where Chloranthaceae and *Ceratophyllum* are well separated, *Couperites* was sister to Chloranthaceae, but with the backbone tree where Chloranthaceae and *Ceratophyllum* form a clade (D&E), it had four most parsimonious positions – sister to *Ascarina* or the *Ascarina*–*Sarcandra*–*Chloranthus* (ASC) clade, below both Chloranthaceae and *Ceratophyllum* or sister to mesangiosperms as a whole – and many other positions were only one step less parsimonious. Still more positions within, below and well separated from Chloranthaceae were found when *Couperites* was added together with other chloranthoid fossils. It should be noted that *Clavatipollenites* is a relatively plesiomorphic and variable fossil genus that may well be systematically heterogeneous, and is possible that future associations of pollen and mesofossils will show that other pollen types called *Clavatipollenites* are more convincingly related to Chloranthaceae.

A more secure record of Chloranthaceae consists of female flowers (fruits) and inflorescences of unistaminate male flowers with pollen of the *Asteropollis* type (Hedlund and Norris 1968; Friis et al. 1999; Eklund et al. 2004; Figure 3(k)), from the early Albian and possibly Aptian (Torres Vedras). This pollen resembles *Clavatipollenites* in exine structure but differs in having a four- or five-branched sulcus, like pollen of *Hedyosmum* (Walker and Walker 1984), and the fruits resemble those of *Hedyosmum* in having three tepals on top. Like the study of Eklund et al. (2004) on phylogeny of Chloranthaceae,

which used fewer outgroups, the analysis of Doyle and Endress (2014) associated the *Asteropollis* plant with *Hedyosmum*, and all positions outside the chloranthaceous line were at least six steps worse. These results imply that the crown group of Chloranthaceae had originated by the early Albian. The analysis of Eklund et al. (2004), which included 20 species of *Hedyosmum*, indicated that the *Asteropollis* plant could be either sister to *Hedyosmum* or nested within the basal grade in the genus. A sister group position would be more consistent with evidence from molecular dating that radiation of the crown group was much more recent than origin of the stem lineage (Zhang and Renner 2003; Antonelli and Sanmartín 2011; Zhang et al. 2011), and with the appearance and expansion of *Hedyosmum*-like pollen in the Miocene of South America (Martínez et al. 2013).

Two other fossils are securely linked with Chloranthaceae but differ substantially from all four living genera. *Canrightia*, described by Friis and Pedersen (2011) from the early Albian of Portugal (Figure 3(l)), is significant in showing an intermediate stage in reduction from the ancestral multiparted angiosperm flower. It was like Chloranthaceae as a whole in having one orthotropous ovule per carpel and like *Hedyosmum* in having a reduced perianth, but it was bisexual and had approximately four stamens and two to five fused carpels. Analyses by Friis and Pedersen (2011) and Doyle and Endress (2014) placed *Canrightia* on the stem lineage of Chloranthaceae or the Chloranthaceae–*Ceratophyllum* clade, depending on the backbone tree. As crown group Chloranthaceae existed by the Albian, *Canrightia* must be an extinct side line, and some of its features may be derived (autapomorphies), such as the fused carpels. *Zlatkocarpus*, described by Kvaček and Friis (2010) from the middle Cenomanian of Bohemia, is known as spikes of female flowers that differed from those of *Ascarina* in having a vestigial adnate perianth, plus reticulate monosulcate pollen. In the study of Doyle and Endress (2014), with the backbone tree where Chloranthaceae and *Ceratophyllum* are linked (D&E), *Zlatkocarpus* was nested within Chloranthaceae, sister to the ASC clade, in which the perianth is lost; but with the chloroplast backbone tree (J/M), it was sister to the ASC clade, *Hedyosmum* or the whole family. More basal positions were found when several chloranthoid fossils were included, notably just above *Canrightia* on the stem lineage of Chloranthaceae and *Ceratophyllum* with the D&E backbone tree (Figure 2).

Another fossil, here called the *Pennipollis* plant, was not compared with Chloranthaceae when its parts were associated by Friis et al. (2000; Figure 3(m)). It is known as isolated uniovulate carpels (*Pennicarpus*) and stamens (*Pennistemon*), a fragment of a spike of flowers that consist of one stamen, and pollen of the *Pennipollis* type. *Pennipollis*, variously assigned by earlier workers to *Peromonolites*, *Liliacidites*, *Retimonocolpites* and *Bren-*

neripollis, is one of most common Aptian–Albian angiosperm pollen types (Brenner 1963; Doyle et al. 1975; Penny 1988). It is distinctive in having an unusually coarse reticulum that tends to detach from the nexine, as a result of being underlain by fine granules rather than columellae. Friis et al. (2000, 2011) compared the *Pennipollis* plant with the monocot order Alismatales, in which some members also have a non-columellar reticulum. However, these monocots have a thin nexine, whereas the nexine in *Pennipollis* is unusually thick, as in Chloranthaceae. Instead, the analyses of Doyle et al. (2008) and Doyle and Endress (2014) supported a sister group relationship of the *Pennipollis* plant to Chloranthaceae (with the J/M chloroplast backbone tree) or to Chloranthaceae plus *Ceratophyllum* (with the D&E backbone tree). Its best positions in monocots (linked with *Acorus* and the alismatalean genus *Aponogeton*) were seven to eight steps less parsimonious. Other results raise the intriguing possibility that the *Pennipollis* plant was more closely related to *Ceratophyllum* than to Chloranthaceae. With the D&E backbone tree, it was only one step less parsimonious to link the fossil with *Ceratophyllum*, and this became one of its two most parsimonious positions when it was added to the D&E tree along with the *Asteropollis* plant, *Canrightia* and *Zlatkocarpus*, as well as in two out of four trees found when *Appomattoxia* was added as well (e.g. Figure 2).

Appomattoxia (Figure 3(n)) is based on uniovulate carpels with hooked hairs and adhering monosulcate pollen, first described from the middle Albian of Virginia (Friis et al. 1995) and extended to the Aptian or earliest Albian of Portugal (Friis et al. 2010a). Friis et al. (1995) noted that similar fruits occur in the ranunculalean eudicot *Circaeaster* (which differs in having tricolpate pollen), while the seeds are like those of Piperaceae and Saururaceae (Piperales) in being orthotropous and having a sclerotic inner layer (interpreted as endotegmen) of the seed coat. The pollen is of a type originally described as *Inaperturopollenites crisopolensis* and later renamed *Tucanopollis*, which is one of the most conspicuous angiosperm elements in the Barremian and Aptian of Brazil and Africa (Regali et al. 1974; Doyle et al. 1977; Regali 1989). Similar forms are known from the Albian and Cenomanian of Europe as *Transitoripollis* (Góczán and Juhász 1984). *Tucanopollis* resembles *Clavatipollenites* in having a sculptured sulcus, thick foot layer and supratectal spinules, but the tectum differs in being continuous.

When Doyle and Endress (2014) added *Appomattoxia* to both backbone trees, its four most parsimonious positions were sister to Nymphaeales and on the three branches around the basal node connecting *Amborella* with other angiosperms. However, positions sister to Chloranthaceae or Chloranthaceae plus *Ceratophyllum* were only one step worse. A feature not included by Doyle

and Endress (2014) that might support a relationship with *Amborella* is the low verrucate sculpture of *Appomattoxia* pollen and some dispersed grains assigned to *Tucanopollis*, which could represent a step towards the more prominent dome-like verrucae of *Amborella* (Sampson 1993; Hesse 2001). Given the record of *Tucanopollis*, this might mean that relatives of *Amborella*, which is now endemic to New Caledonia, were among the most common angiosperms in the Barremian–Aptian of Northern Gondwana. However, this may be difficult to accept in view of evidence that most of Northern Gondwana was semiarid or arid in the Early Cretaceous (Brenner 1976; Doyle et al. 1982; Ziegler et al. 2003), whereas *Amborella* and other woody ANITA groups are restricted to wet forest understorey habitats (Feild et al. 2004, 2009).

Another possibility emerged when Doyle and Endress (2014) added *Appomattoxia* and the four most likely fossil relatives of Chloranthaceae to the D&E tree, where Chloranthaceae and *Ceratophyllum* form a clade. In two of the four trees obtained, *Appomattoxia* was sister to Nymphaeales, but in the third it was sister to *Ceratophyllum* and Chloranthaceae, above *Canrightia* and *Zlatkocarpus*, and in the fourth (cf. Figure 2) the *Pennipollis* plant and *Appomattoxia* were successive branches on the line leading to *Ceratophyllum*. One reason such very different hypotheses on the affinities of *Appomattoxia* are possible is that there is no direct evidence on floral organisation of the plants that produced the carpels (this is also true for the *Pennipollis* plant). If the carpels were from a line attached near the base of the angiosperm tree, they would most likely be parts of a multicarpellate flower with numerous tepals (Endress and Doyle 2009), but if they were from close relatives of *Ceratophyllum* or Chloranthaceae, they would probably represent whole female flowers (if they had a perianth, it would have to be free from the carpel, not adnate to it, as in *Canrightia*, *Zlatkocarpus* and *Hedyosmum*). Unfortunately, the pollen of *Ceratophyllum* provides little evidence on relationships with fossils, because it is inaperturate and has an extremely reduced, structureless exine (Takahashi 1995). Information on the vegetative morphology of the plants that produced *Appomattoxia* fruits and *Tucanopollis* pollen could also be decisive.

These results raise the question of whether there are any known mid-Cretaceous megafossils that might represent stem relatives of *Ceratophyllum*. Dilcher and Wang (2009) described fruits and leafy stems from near the Albian–Cenomanian boundary in Kansas that resemble *Ceratophyllum*, implying that the *Ceratophyllum* line had diverged by this time, but something less similar to the modern genus could say more about its origin and relationships with other groups. A candidate is *Pseudoasterophyllites*, from the Albian and Cenomanian of France and Bohemia, which Kvaček et al. (2012) suggested was a halophyte. Its leaves are opposite to whorled, as in

Ceratophyllum, but simple and apparently succulent rather than dissected. Remarkably, stamens with similar stomata containing pollen similar (though not identical) to *Tucanopollis* occur in close association, although not in attachment. Another candidate is *Montsechia*, from Barremian lake beds in Spain, which also had reduced whorled or opposite leaves (Martín-Closas 2003; Gomez et al. 2006; Krassilov 2011). It may easier to imagine plants like these growing in local wet or saline habitats in Northern Gondwana than *Amborella* relatives.

7.   Conclusions

Phylogenetic analyses add a more precise and concrete dimension to the broad picture of morphological diversification of angiosperms in the mid-Cretaceous, by identifying specific clades represented in the successive grades of pollen and leaf evolution. General implications of these analyses can be illustrated by placing the fossils discussed here on the modern tree, with the branches

leading to them shaded to indicate how far diversification is inferred to have proceeded in each of three broad stratigraphic intervals (Figure 4). This shows that most of the lines that split near the base of the molecular tree of angiosperms can be recognised by the end of the Albian. However, many of the younger fossils are attached higher in the tree, consistent with the view that the angiosperms were radiating at this time. The total number of phylogenetic lines established by the late Albian may be greater than might be expected based on their relatively uniform reticulate monosulcate and tricolpate pollen. However, similar plesiomorphic pollen types are widely distributed among modern 'basal' lines, and there are none of the glaring inconsistencies noted by early palynologists between old identifications of fossil angiosperm leaves with modern taxa and the level of advancement of pollen types at the same horizons.

Early Cretaceous angiosperm clades include both lines that flourished soon after their appearance but are now relict and others that have been ecologically important
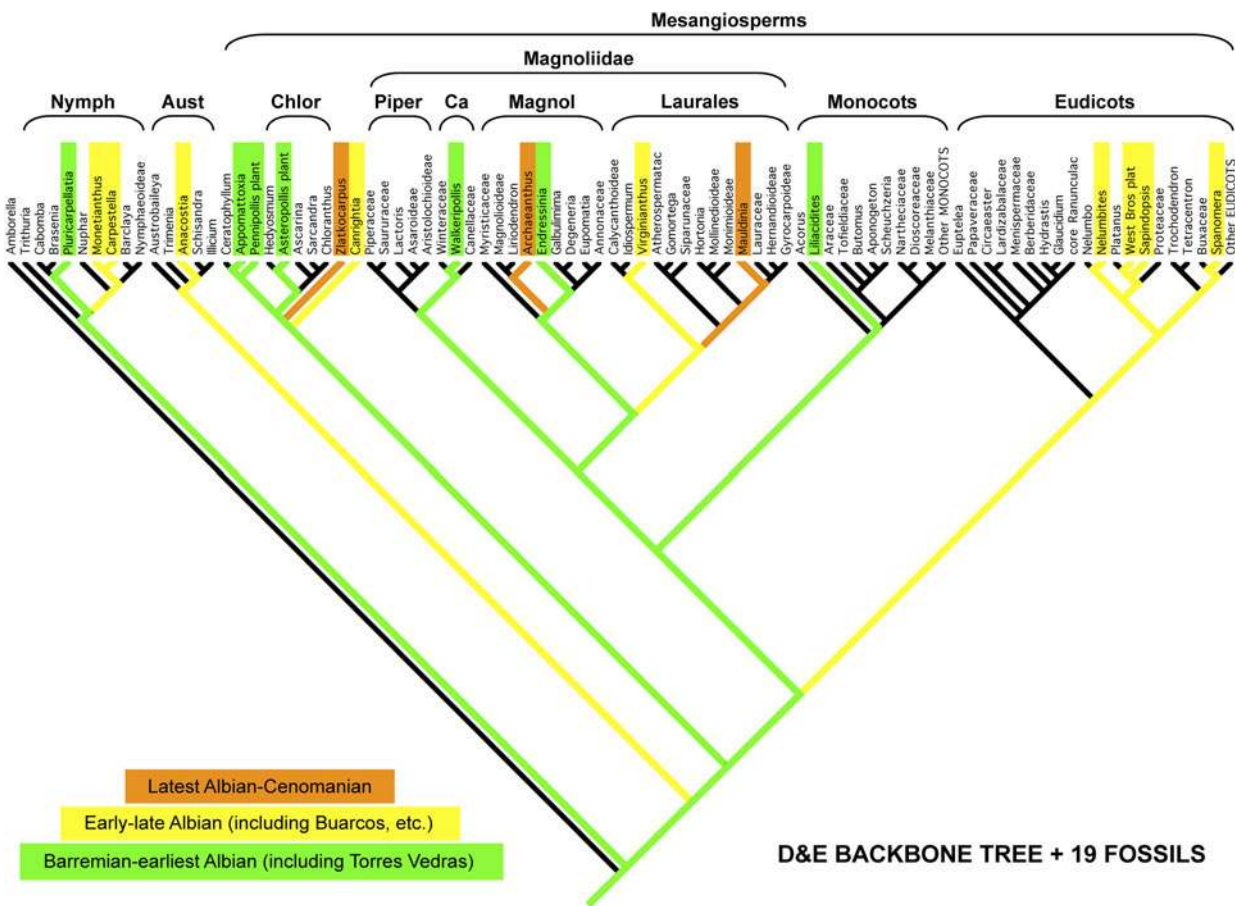

Figure 4.   (Colour online) Tree in Figure 2, with colours indicating stratigraphic horizons where taxa first occur. Subdivisions correspond to palynological zones and subzones I (Aptian–earliest Albian), IIA-B (middle–late Albian) and IIC-IV (latest Albian–Cenomanian) in the Potomac Group and Raritan Formation of the Atlantic Coastal Plain. Barremian floras elsewhere are added to the first interval; presumed later early Albian floras from Portugal, which apparently correlate with a hiatus in the Potomac sequence, are added to the second interval. Abbreviations as in Figure 2.

throughout their history. Although Chloranthaceae and their extinct relatives may be overrepresented in the pollen record because they were wind pollinated, the leaf and mesofossil records suggest that chloranthoids were indeed among the first common angiosperms, consistent with the hypothesis that they were first line to 'break out' of the ancestral wet forest understorey niche (Feild et al. 2004). However, they are now of minor importance, despite the mid-Tertiary resurgence of *Hedyosmum* inferred from molecular dating (Zhang and Renner 2003; Antonelli and Sanmartín 2011) and the fossil pollen record (Martínez et al. 2013). There are intriguing hints that the *Ceratophyllum* line had a similar history. *Platanus* is now just one of many temperate woody taxa, but soon after their appearance, plants related to *Platanus* may have been the most abundant angiosperms, at least in Laurasia, and they continued to be prominent through the Late Cretaceous. Buxales, which produced some if not all of the striate tricolpate pollen in the Aptian–Albian of Northern Gondwana and the Albian–Cenomanian of Laurasia, may be similar. By contrast, groups in the second category include Lauraceae and their stem relatives, which have remained abundant from the late Albian to the present day, and Araceae in the monocots, while Nymphaeales are still important in their specialised aquatic habitat. However, radiation of the huge 'core' clades of eudicots and monocots that dominate the modern flora (*Pentapetalae* and *Petrosaviidae* of Cantino et al. 2007) was apparently a later Cretaceous phenomenon.

Acknowledgements

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