UC Davis
UC Davis Previously Published Works

Title
Angiosperm Clades in the Potomac Group: What Have We Learned since 1977?

Permalink

Journal

ISSN

Authors
Doyle, James A
Upchurch, Garland R Jr

Publication Date
2014

DOI

Peer reviewed

Angiosperm Clades in the Potomac Group:
What Have We Learned since 1977?

James A. Doyle[1] and Garland R. Upchurch, Jr.[2]

[1] *Corresponding author:* Department of Evolution and Ecology, University of California, Davis CA 95616 USA
—*email:* jadoyle@ucdavis.edu

[2] Department of Biology, Texas State University, San Marcos TX 78666 USA
—*email:* gu01@txstate.edu

ABSTRACT

In their 1977 study on Potomac Group angiosperms, Hickey and Doyle made only broad comparisons with living taxa. Newer data, especially discoveries of fossil flowers in the Potomac and coeval deposits and increasingly robust molecular phylogenies of living angiosperms, allow more precise phylogenetic placement of fossils. Hickey and Doyle compared most early Potomac leaves (Aptian–early Albian) with "magnoliids," a paraphyletic group as then defined, but several clades can now be recognized. Leaves and dispersed cuticles share epidermal features with woody members of the basal ANITA grade, and in some cases crown group Austrobaileyales, whose presence is confirmed by flowers called *Anacostia*. Aptian–Albian flowers (*Monetianthus*, *Carpestella*) and whole plants (*Pluricarpellatia*) are nested in crown group Nymphaeales; Potomac reniform leaves could belong to this clade. Several Potomac leaves have chloranthoid teeth, venation, and opposite phyllotaxis consistent with Chloranthaceae, while Aptian to Cenomanian flowers reveal the presence of both crown group Chloranthaceae (*Asteropollis* plant, near *Hedyosmum*) and stem relatives of this family and/or *Ceratophyllum* (*Canrightia*, *Zlatkocarpus*, *Pennipollis* plant, possibly *Appomattoxia*). Phylogenetic analyses confirm interpretations of Aptian *Liliacidites* pollen and *Acaciaephyllum* as monocots. Ternately lobed leaves such as *Vitiphyllum* may represent basal eudicots, in or below Ranunculales. In the late Potomac (middle to late Albian), the rise of tricolpate pollen and local dominance of angiosperm leaves mark the influx of near-basal eudicot clades. Associated floral receptacles confirm that *Nelumbites* leaves were related to *Nelumbo* (Proteales), while heads of unisexual flowers indicate that both palmately lobed "platanoid" and pinnatifid *Sapindopsis* leaves (previously compared with rosids) were stem relatives of *Platanus* (also Proteales). Flowers called *Spanomera* are related to Buxaceae. Several Albian and early Cenomanian flowers belong to Magnoliidae in the new monophyletic sense, including *Archaeanthus* in Magnoliales and *Virginianthus* and *Mauldinia* in Laurales; Laurales are common in the late Albian leaf record.

KEYWORDS

Cretaceous, paleobotany, phylogeny, Austrobaileyales, Nymphaeales, Chloranthaceae, Laurales, monocots, eudicots, Proteales

Introduction

In their studies of angiosperm leaves in the Potomac Group of the eastern United States (Figure 1), the main goal of Doyle and Hickey (1976) and Hickey and Doyle (1977) was to test whether the leaf record showed a pattern of morphological diversification through time similar to that observed in the pollen record, with the successive appearance of reticulate-columellar monosulcate, tricolpate, tricolporate, and triporate pollen types (Doyle 1969; Muller 1970), and to explore implications for early angiosperm evolution. By this time identifications of Cretaceous leaves with extant genera and families (e.g., Fontaine 1889; Berry 1911) had been called into question by recognition that the extant taxa differ significantly from the fossils in leaf architecture (Wolfe et al. 1975) or produce pollen types not found in the same beds (Pacltová 1961; Pierce 1961; Brenner
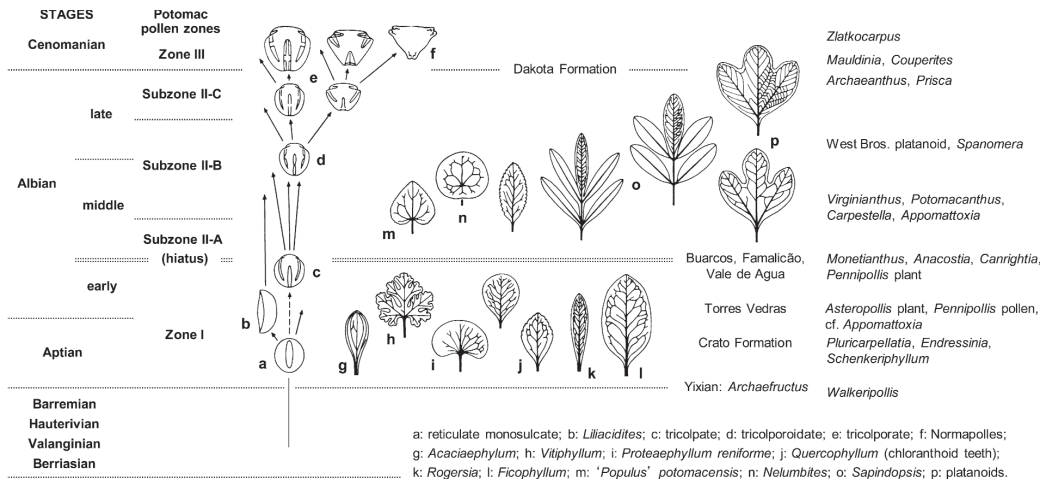
FIGURE 1. Major angiosperm pollen and leaf types in the Potomac Group of eastern North America (modified from Hickey and Doyle 1977), with correlations of plant-bearing localities in other geographic areas and stratigraphic positions of other fossils to the right.

1963). For this reason, Doyle and Hickey (1976) undertook to analyze the Potomac leaf record independent of comparisons with modern taxa, except to show that leaf characters observed at particular levels were consistent with the systematic distribution of pollen characters at the same level, or to make functional-ecological comparisons. Hickey and Doyle (1977) proposed more explicit relationships of Potomac leaves to modern taxa, but at a very broad scale. For example, they argued that most leaves from the lower Potomac had features found in groups then called Magnoliidae (Takhtajan 1969), or those "dicots" that retain monosulcate pollen, the predominant angiosperm pollen type in this interval. In the upper Potomac, they noted that palmately lobed "platanoid" leaves resemble *Platanus*, which has tricolpate pollen of the type that was proliferating at the same time, suggesting presence of what were then called lower hamamelids, where *Platanus* and many other tricolpate groups were assigned.

Since 1977, several major advances have allowed more secure recognition of early angiosperm lines in the Potomac Group and coeval deposits. The main progress with the leaves has come from analysis of cuticular anatomy, often in conjunction with new observations on leaf architecture (Upchurch 1984a, 1984b; Upchurch and Dilcher 1990). The most striking

paleobotanical advance has been the discovery of Cretaceous fossil flowers (Dilcher 1979; Dilcher and Crane 1984; Crane et al. 1986, 1994; Friis et al. 1986, 2011; Friis et al. 1994), mostly preserved as lignite or charcoal and falling in the millimeter size range (mesofossils), which provide a wealth of additional characters for systematic purposes. At the same time, understanding of relationships among living angiosperms has been revolutionized by the development of phylogenetic methods, applied first to morphological characters (e.g., Dahlgren and Bremer 1985; Donoghue and Doyle 1989), then to a vast flood of molecular data (DNA sequences). Molecular phylogenetic analyses have provided an unprecedented, statistically robust picture of how modern groups are related to each other, formalized in the APG (1998, 2003, 2009) classification. Since the first studies of several genes combined (Parkinson et al. 1999; Qiu et al. 1999; Soltis et al. 2000), these results have been remarkably stable with addition of many more genes (see Soltis et al. 2005). The angiosperm phylogenetic tree is rooted among the three "ANITA" lines: *Amborella* (a shrub endemic to New Caledonia), Nymphaeales (water lilies), and Austrobaileyales (woody plants including *Illicium*, or star anise). The remaining 99.9% of angiosperm species form a clade called *Mesangiospermae* (Cantino et al. 2007), which consists of five

strongly supported clades—eudicots, with tricolpate and derived pollen; monocots; Magnoliidae in a restricted sense (Magnoliales, Laurales, Canellales, Piperales); the rootless aquatic *Ceratophyllum*; and Chloranthaceae, which have extremely simple flowers. Relationships among these five clades are more weakly supported, and they vary from one study to another (e.g., Jansen et al. 2007; Moore et al. 2007; Qiu et al. 2006; Qiu et al. 2010).

In this review we summarize current understanding of the presence of living angiosperm clades in the Potomac Group, considering leaf, pollen, and floral data from both the Potomac Group and correlative deposits elsewhere. Many of these results are from a project that began with a morphological data set of Doyle and Endress (2000) for "basal" angiosperms (including basal eudicots and monocots), which has been expanded and refined and used as a framework for analyses of the position of published Early and mid-Cretaceous fossils (Doyle et al. 2008; Endress and Doyle 2009; Friis et al. 2009; Doyle and Endress 2010, 2014; Friis and Pedersen 2011). These analyses used a "molecular scaffold" approach (Springer et al. 2001), in which a morphological data set including living and fossil taxa is analyzed with a parsimony program with the arrangement of living taxa fixed to a backbone constraint tree based on molecular data. This method essentially asks what the morphologically best-supported positions of the fossils are if the molecular relationships are correct. It does not address the possibility that addition of fossils would change inferred relationships among living taxa, but this may be unlikely in most cases in view of the strong statistical support for most molecular relationships and the small number of potentially conflicting characters in fossils.

An alternative total evidence approach (Kluge 1989; Hermsen and Hendricks 2008), combining morphological data on both living and fossil taxa with molecular data on the living taxa, might be theoretically preferable. However, it would require resolution of intractable problems of disparate taxon sampling with the two sorts of data (clades as opposed to exemplar species) and compilation of an appropriate molecular data set (sampling of genes across taxa is highly variable). Both approaches can identify not only members of a crown group (the living representatives of a line,

their most recent common ancestor, and extinct derivatives of this common ancestor: Jefferies 1979; Doyle and Donoghue 1993) but also stem relatives (extinct forms on or attached to the stem lineage leading to a crown group) with a "mosaic" of ancestral and derived character states.

In order to address the uncertainties that still exist in molecular trees, particularly concerning relationships among the five mesangiosperm clades, the molecular scaffold analyses done so far have used two backbone trees, chosen to cover the range of current hypotheses. These differ most significantly in the positions of Chloranthaceae and *Ceratophyllum*. In the J/M backbone, based on nearly complete chloroplast genomes (Jansen et al. 2007; Moore et al. 2007), Chloranthaceae are the sister group of magnoliids and *Ceratophyllum* is sister to eudicots. In the D&E backbone, Chloranthaceae and *Ceratophyllum* form a clade, as inferred from morphology (Endress and Doyle 2009), chloroplast ITS sequences (Antonov et al. 2000), mitochondrial genes (Duvall et al. 2006; Duvall et al. 2008; Qiu et al. 2010), chloroplast genes with many informative sites but low substitution rates (Moore et al. 2011), and low-copy nuclear genes (Zhang et al. 2012); this clade is sister to the remaining mesangiosperms, as in the combined morphological and molecular analysis of Doyle and Endress (2000). Fossils were added to the backbone trees one at a time and sometimes in putatively related groups. In most cases, use of the two backbone trees gave similar results, with the exception of fossils that may be related to Chloranthaceae.

Many of the phylogenetic results presented here (summarized in Figure 2) are also discussed in Doyle (2014), but here we concentrate on the Potomac Group record and the impact of new data on hypotheses and conclusions of Doyle and Hickey (1976) and Hickey and Doyle (1977). Except for some taxa related to Nymphaeaceae and Chloranthaceae, the fossils considered here do not appear to be crown group members of any living family; instead, they appear to be stem relatives of one or more families. In order to treat the phylogenetic position of Potomac fossils in sufficient detail, we do not attempt a comprehensive review of progress in understanding other aspects of the early record of angiosperms, such as their ecology or reasons for their success, but we do mention some recent advances in these areas.
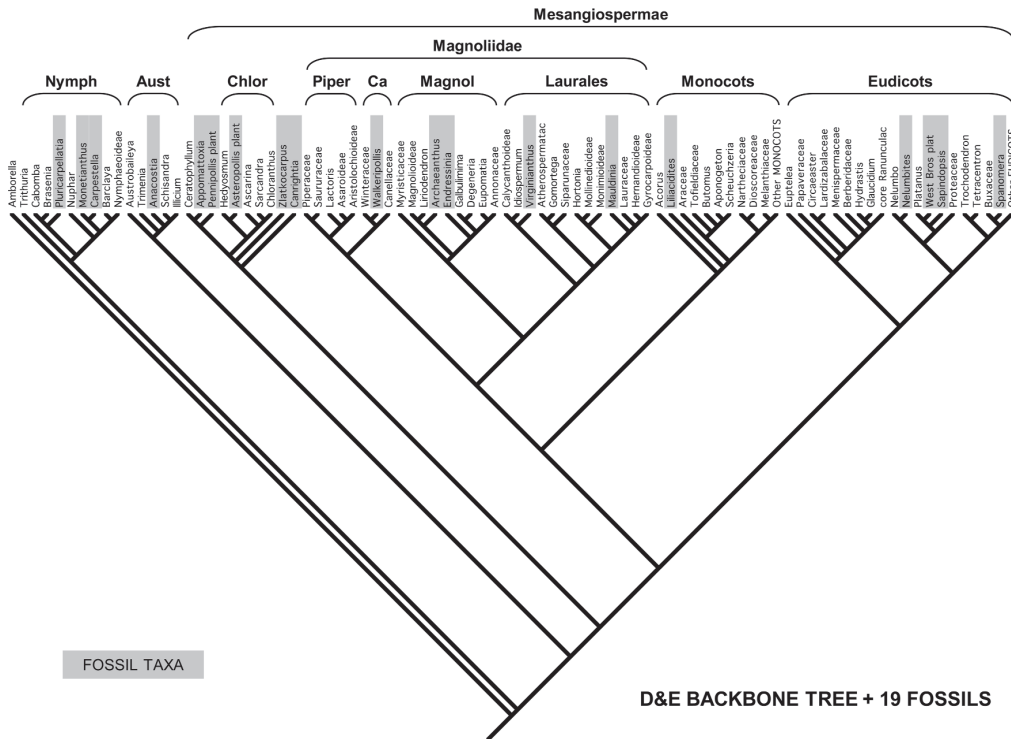
FIGURE 2. Most parsimonious positions of 19 Early Cretaceous and Cenomanian fossil taxa discussed in the text (marked with gray background) on the D&E phylogeny of living angiosperms (Doyle et al. 2008; Endress and Doyle 2009; Friis et al. 2009, 2011; Doyle and Endress 2010, 2014). When a fossil has 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. *Abbreviations:* Aust,Austrobaileyales; Ca,Canellales; Chlor,Chloranthaceae; Magnol,Magnoliales; Nymph,Nymphaeales; Piper,Piperales; plat,platanoid.

In this article we also document more recent observations on leaf architecture and cuticular anatomy of Potomac Group angiosperms with photographs of representative leaf megafossils and cuticles, using both previously illustrated and unpublished specimens. Many of our images are enhanced by digital photographic techniques, such as image stacking, to document features that were difficult to illustrate with conventional photography or poorly reproduced in print publications. Illustrated specimens are from the paleobotanical collections of the U.S. National Museum of Natural History (USNM) and the University of Michigan Museum of Paleontology (UMMP).

Potomac Zone I
(Aptian to Early Albian)

The lower part of the Potomac sequence (including the Patuxent Formation and Arundel Clay where these units can be recognized) corresponds to palynological Zone I of Brenner (1963) and Doyle and Robbins (1977), in which most angiosperm pollen is monosulcate, with the addition of two or three reticulate tricolpate types in the upper part. This upper part of Zone I has been correlated palynologically with the well-dated marine early Albian of England (Kemp 1968) and Portugal (Heimhofer et al. 2007; Hochuli et al. 2006), which also contains one or two types of reticulate tricolpates and the distinctive reticulate monosulcate *Clavatipollenites rotundus* (often identified as or compared with *Retimonocolpites dividuus*). The later early Albian of Portugal also includes striate tricolpates, which are not known in the Potomac until Zone II of Brenner (1963) and Doyle and Robbins (1977). As argued by Hochuli et al. (2006) and Doyle and Endress (2014), this interval in Portugal, where monosulcates were still more diverse than tricolpates,

probably corresponds to a significant hiatus between Zones I and II in the Potomac sequence (see below). The Portuguese data refute the placement of the Zone I/II boundary within the Aptian by Doyle (1992); they agree more with Doyle and Hickey (1976) and Doyle and Robbins (1977), who dated upper Zone I as either late Aptian or early Albian. Although Brenner (1963) proposed that Zone I began in the Barremian, its base is probably Aptian, as argued by Doyle (1992), on the basis of the presence of *Pennipollis* (*Peromonolites peroreticulatus* and *P. reticulatus* of Brenner 1963), a group of monosulcates with an unusually coarse reticulum and no columellae, which appears just above base of the dated Aptian in England and Portugal (Penny 1988a; Hughes 1994; Hochuli et al. 2006; Heimhofer et al. 2007; Doyle and Endress 2014).

Although monosulcate angiosperm pollen is present at low percentages throughout Zone I, angiosperm leaves are rare and known from only a few localities. Mesofossil reproductive structures are known but have not been studied in detail (Friis et al. 2011). However, angiosperm mesofossils of similar or slightly younger age are known from localities in Portugal (Friis, Pedersen et al. 1994; Friis, Crane et al. 2011). Most of these are probably early Albian, in the missing interval between Zones I and II, but two (Torres Vedras, Catefica) may be either earliest Albian or Aptian (Heimhofer et al. 2007; Doyle and Endress 2014; Massoni et al. 2014). Complete plants and leafy stems with flowers or fruits are known from lake deposits in Brazil (Mohr and Friis 2000), which are probably late Aptian (Heimhofer and Hochuli 2010). These floras provide a check on the plausibility of suggested relationships of lower Potomac pollen and leaves with living clades.

ANITA Lines and Magnoliids

Some of the most-discussed Zone I angiosperm fossils are entire-margined, pinnately veined leaves with unusually irregular "first rank" venation—variably spaced and branching secondaries, which form multiple (festooned) brochidodromous loops and are poorly differentiated from intersecondaries, and random-reticulate higher order venation with poorly differentiated vein orders. Such leaves are most common at the upper Zone I Fredericksburg locality in Virginia. Fontaine (1889) gave these leaves names such as *Ficus*, *Fico-*

phyllum, and *Proteaephyllum* that indicate or suggest relationships with derived groups such as Moraceae, although both he and Ward (1888) noted the irregular venation and described it as "archaic." Wolfe et al. (1975) showed that these fossils differ markedly from the modern taxa to which they were compared and are instead similar to groups then placed in Magnoliales, including Winteraceae (now in Canellales). Doyle and Hickey (1976) and Hickey and Doyle (1977) reaffirmed these similarities but considered them probable shared ancestral states that need not reflect a close relationship with the living taxa that retain them.

Additional evidence on the affinities of these leaves came from cuticle studies by Upchurch (1984a, 1984b), who showed that several Zone I leaf types, including specimens compared with *Ficophyllum*, have unusually varied stomatal structure, especially in numbers and positioning of subsidiary cells. These features may be illustrated by dispersed cuticles from localities of Doyle and Hickey (1976) and Upchurch (1984b) on the south side of Dutch Gap Canal (Aptian) and at Drewry's Bluff (early Albian), Virginia (Figure 3A–C). Upchurch (1984a) compared many living taxa with Zone I leaves and found the most similar stomatal features in *Amborella* and *Austrobaileya*. In a more recent survey of epidermal characters in basal angiosperms, Carpenter (2005, 2006) reaffirmed the similarity of Zone I leaves to these taxa. *Amborella* and Austrobaileyales also have low-rank venation of the type seen in Zone I leaves, Magnoliales, and Winteraceae, consistent with the view that this is a basic angiosperm feature and not evidence for the magnoliid clade. Both the venational and epidermal similarities, which include a thin cuticle in most species, are consistent with an ecology like that of the modern ANITA lines (except Nymphaeales), which grow in wet, shaded understory habitats, an environment that Feild and colleagues (Feild et al. 2004; Feild et al. 2009; Feild, Brodribb et al. 2011; Feild, Upchurch et al. 2011) reconstructed as ancestral for angiosperms. Leaves with an intramarginal vein called *Eucalyptophyllum* represent an important exception, since they have thicker cuticle and sunken stomata (Upchurch 1984b) and may represent trees of sunny habitats (Upchurch and Wolfe 1987). In general, leaves of Zone I angiosperms differ from those of most
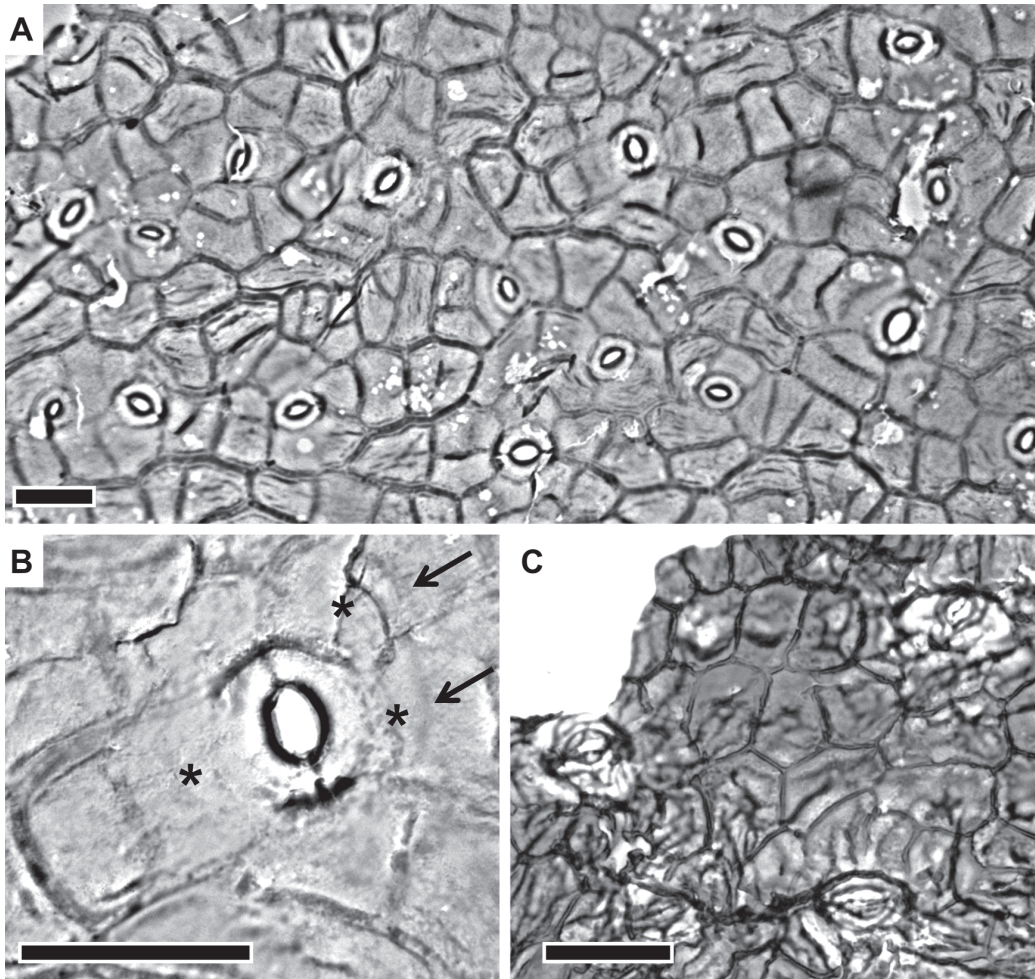
FIGURE 3. Dispersed cuticles of probable Austrobaileyales from Zone I of the Potomac Group. **A,** Dispersed cuticle #1 of Upchurch (1984a) from the Dutch Gap locality of Doyle and Hickey (1976). Note the regions of striate surface sculpture, and stomata that show variable subsidiary cell arrangement and development of T-pieces. UMMP 65125-G153, slide 3. Scale bar equals 50 μm. **B,** Close-up of stomatal complex from A showing T-pieces and irregularly laterocytic subsidiary cell arrangement. Subsidiary cells are marked with asterisks; arrows show thin cuticular flanges on the tangential walls of subsidiary cells. Subsidiaries are poorly differentiated from surrounding epidermal cells. In this species, only the crossbar of the T-piece is well developed. UMMP 65125-G153, slide 3. Scale bar equals 50 μm. **C,** Dispersed cuticle #3 from the Drewry's Bluff locality of Upchurch (1984a). This species shows combined striate and papillate surface sculpture, and T-pieces with both the upright and crossbar. UMMP 65126-56. Scale bar equals 50 μm.

extant angiosperms in having the low vein densities and calculated maximum carbon assimilation rates characteristic of ferns, gymnosperms, ANITA-grade angiosperms, Chloranthaceae, and many magnoliids (Boyce et al. 2009; Feild, Brodribb et al. 2011; Feild, Upchurch et al. 2011).

Because most of the leaf traits discussed so far may be plesiomorphic, they are only consistent with the presence of plants at the ANITA grade and do not support a relationship with any particular clade. However, the dispersed cuticle record at Dutch Gap and Drewry's Bluff indicates the presence of crown group Austrobaileyales. Two cuticle types (Figure 3A–C) have a combination of features found in this order, including elliptic to round guard cell pairs, striate surface sculpture, and a variable pattern of subsidiary cell arrangement (Upchurch 1984a, 1984b; Carpenter 2005, 2006). The polarity of these characters is uncertain, although Carpenter (2006) proposed
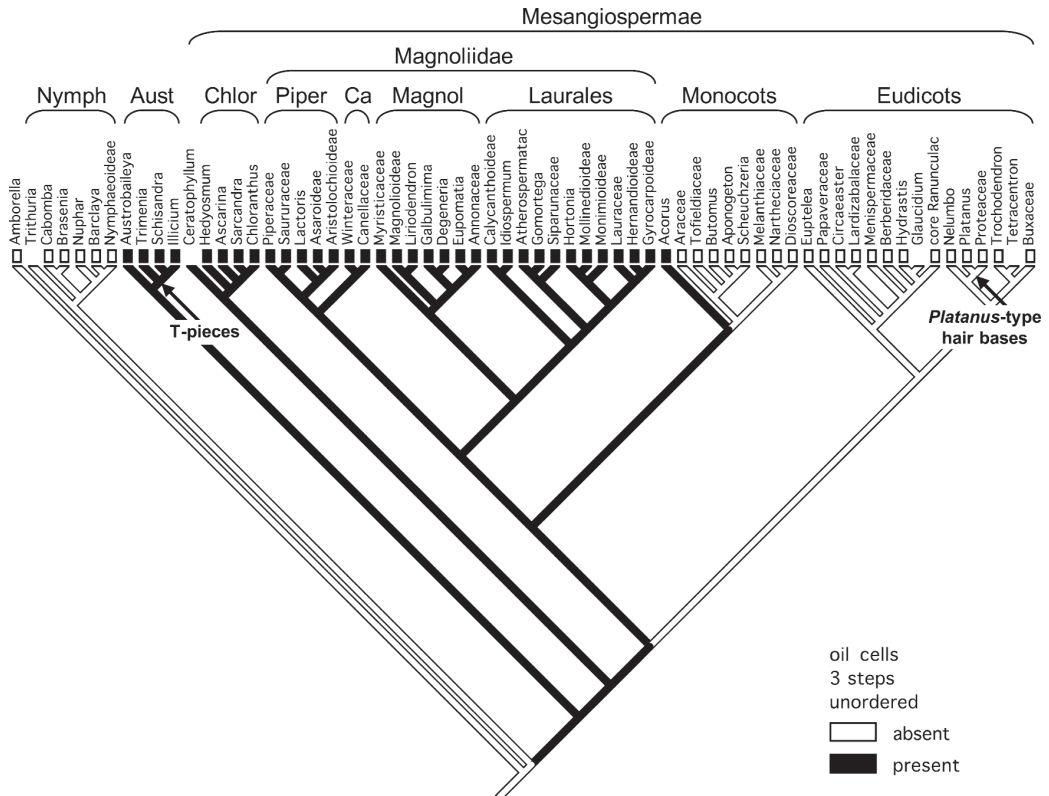
FIGURE 4. Cladogram of extant angiosperms with relationships as in Figure 2, showing the phylogenetic distribution of three characters important for placement of Potomac leaves: oil cells in the mesophyll, T-pieces at the stomatal poles, and *Platanus*-type hair bases. *Trithuria* (=Hydatellaceae) and *Ceratophyllum* are scored as unknown for oil cells because of the possibility that their lack of oil cells is a functional consequence of their submerged aquatic habitat, and because *Ceratophyllum* has tanniferous cells that could be modified oil cells (Doyle and Endress 2010). *Abbreviations:* Aust, Austrobaileyales; Ca, Canellales; Chlor, Chloranthaceae; Magnol, Magnoliales; Nymph, Nymphaeales; Piper, Piperales.

that striations may be a synapomorphy of Austrobaileyales and mesangiosperms. However, the fossils also have T-pieces at the stomatal poles, a feature developed to varying degrees in *Trimenia* and Schisandraceae (sensu APG 2009), especially *Illicium*, but not reported in the basal genus *Austrobaileya*, other ANITA-grade taxa, Chloranthaceae, and magnoliids, indicating a position nested within Austrobaileyales (Figure 4).

The existence of crown Austrobaileyales at this time is confirmed by uniovulate fruits and floral axes called *Anacostia* from the early Albian of Portugal and the middle Albian (lower Subzone IIB) Kenilworth and Puddledock localities in Maryland and Virginia (Friis et al. 1997; for age, see Massoni et al. 2014). Phylogenetic analyses (Doyle et al. 2008; Doyle and Endress 2014) nest *Anacostia* within Austrobaileyales, as the sis-

ter group of *Illicium* and *Schisandra* or of *Schisandra* alone, supported by the distinctive seed coat anatomy, with an outer palisade exotesta and a sclerotic mesotesta layer. Pollen of the associated *Similipollis* type extends down into Zone I (e.g., *Liliacidites* sp. B of Doyle and Robbins 1977).

These data do not rule out the possibility that some pinnately veined lower Potomac leaves belong to the magnoliid clade, which is known to have been diversifying at this time. Ward et al. (1989) compared large monosulcate pollen grains with granular infratectal sculpture from lower Zone I, named *Lethomasites*, with Magnoliales, many of which have such structure. Granular or related "atectate" structure was once thought to be primitive in angiosperms (Van Campo and Lugardon 1973; Doyle et al. 1975; Walker and Skvarla 1975; Walker 1976) but is now inferred to

have evolved within Magnoliales and many other groups (Doyle 2009). However, it would be premature to draw conclusions from fossils with so few characters. Wolfe et al. (1975) compared the venation of "*Sapindopsis*" *elliptica* (not to be confused with true *Sapindopsis* from Zone II) to that of extant Winteraceae, but better evidence is needed to determine whether the similarities are apomorphic or plesiomorphic. More convincingly, phylogenetic analyses have placed leafy stems and flowers named *Endressinia* (Mohr and Bernardes-de-Oliveira 2004) and *Schenkeriphyllum* (Mohr et al. 2012) from the late Aptian Crato Formation of Brazil in Magnoliales, although different analyses have given inconsistent results on their position within the order (Doyle and Endress 2010; Mohr et al. 2012; Massoni et al. 2014). Phylogenetic analysis (Doyle and Endress 2010) has linked monoporate tetrad pollen called *Walkeripollis* from the late Barremian of Gabon (Doyle et al. 1990) with Winteraceae, in the Canellales. Similar pollen with sculpture more like that of living Winteraceae is known from the mid-Cretaceous of Israel (Walker et al. 1983; Schrank 2013) and Argentina (Barreda and Archangelsky 2006). Evidence for Magnoliales and Laurales in the later Albian and Cenomanian is discussed below.

Another important lower Potomac leaf type is *Proteaephyllum reniforme*, which has a reniform blade, three-stranded midrib, and basally crowded or palmate major venation. Judging from current phylogenetic trees, palmate venation is a derived condition that evolved from pinnate venation more than once in "basal" angiosperms (Doyle 2007). Hickey and Doyle (1977) compared *P. reniforme* with palmately veined cordate and peltate leaves in the upper Potomac, which they associated with Nymphaeales, then thought to include *Nelumbo*. However, it is equally suggestive of other "herbaceous magnoliids" with palmate venation, which are now grouped as Piperales (including Aristolochiaceae). In the morphological cladistic analysis of Donoghue and Doyle (1989), Nymphaeales and Piperales (plus monocots) formed a clade called "paleoherbs," but the two orders are well separated in molecular analyses, with Nymphaeales in the ANITA grade and Piperales in the magnoliid clade.

It is not clear which (if either) of these groups is represented by the lower Potomac reniform

leaves, but there is an increasing number of fossils that confirm the early presence of Nymphaeales. The most conclusive is *Monetianthus* (Friis et al. 2001; Friis et al. 2009), a flower with numerous tepals and stamens and 12 fused carpels with laminar placentation from the early Albian of Portugal. Morphological cladistic analyses using a molecular backbone (Friis et al. 2009; Doyle and Endress 2014) placed *Monetianthus* within Nymphaeaceae, one of the three families of Nymphaeales, above *Nuphar* and below or in the clade consisting of *Barclaya* and Nymphaeoideae. Von Balthazar et al. (2008) described a similar but less well preserved flower from the middle Albian Puddledock locality in Virginia as *Carpestella*; their phylogenetic analysis gave ambiguous results, but Doyle and Endress (2014) placed it in the same most parsimonious positions as *Monetianthus*. Whole plants with cordate to peltate leaves and flowers attached to rhizomes from the late Aptian lacustrine Crato Formation of Brazil, *Pluricarpellatia* (Mohr et al. 2008), give direct evidence for an aquatic habit, but phylogenetic analyses (Mohr et al. 2008; Taylor 2008; Doyle and Endress 2014) have not resolved whether they were more closely related to Nymphaeaceae or the sister family Cabombaceae. Plants with a short rhizome, roots, and attached actinodromous leaves were figured from the Crato Formation by Mohr and Friis (2000) and placed phylogenetically in Nymphaeaceae by Coiffard et al. (2013b). The fact that these and other fossils contradict molecular dating of crown group Nymphaeales as Tertiary (Yoo et al. 2005) has been emphasized by Nixon (2008), Coiffard et al. (2013b), and Doyle and Endress (2014).

So far, there is no secure evidence for Piperales in Zone I time. Middle Albian fruits (*Appomattoxia*) associated with *Tucanopollis* pollen, which extends back to the Barremian, have been related to Piperales by Friis et al. (1995) and Friis et al. (2011), but as discussed below phylogenetic analyses suggest that these belong near the base of angiosperms or Chloranthaceae. The divergence of Piperales by this time can be inferred from the occurrence of *Walkeripollis*, in its sister group Canellales, in the late Barremian. A specimen collected from lower Zone I at Dutch Gap (Figure 5A) has obovate, entire-margined leaves with low-angle pinnate venation and sheathing bases that are borne along a zigzag stem, suggesting sympodial branching, a
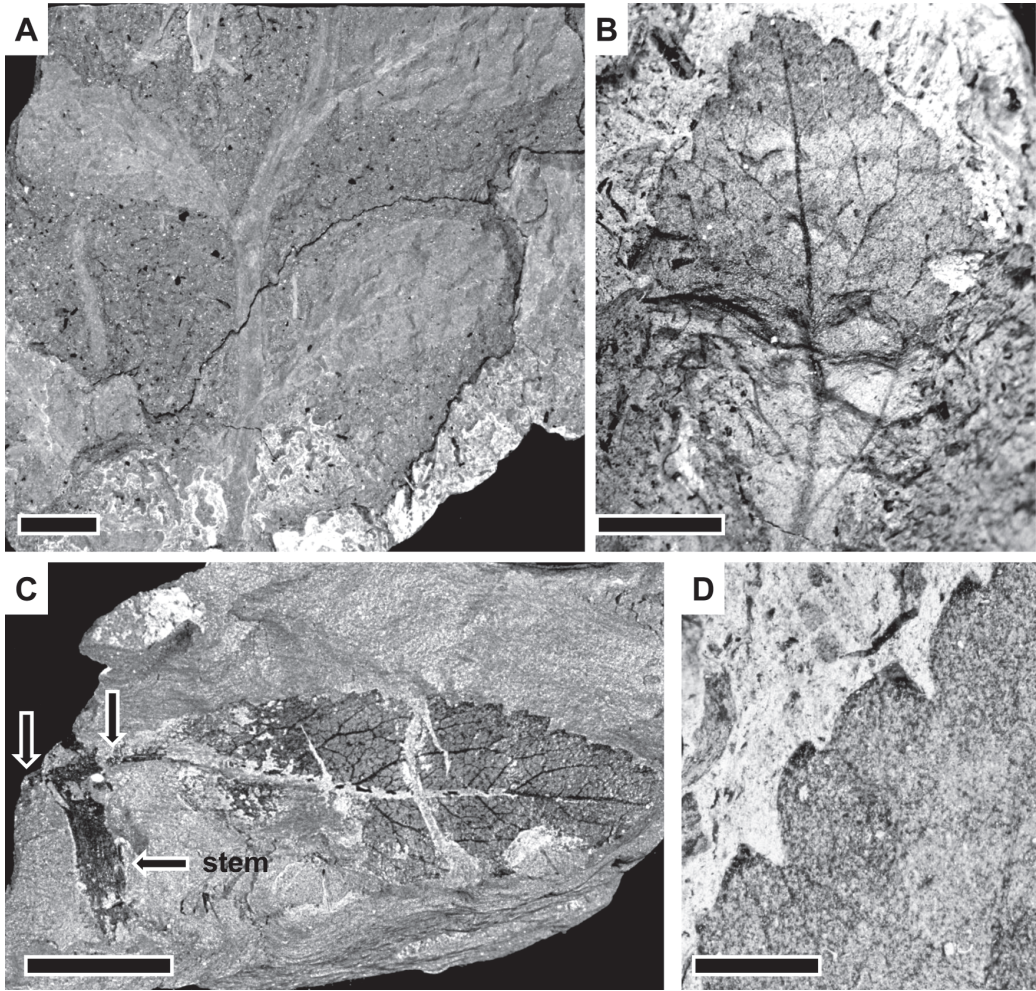
FIGURE 5. Leaves and leaf-bearing shoots from lower Zone I of the Potomac Group. **A,** Possible piperalean shoot showing zigzag (probably sympodial) stem bearing obovate leaves with sheathing bases. Dutch Gap locality of Doyle and Hickey (1976), UMMP 64900. Scale bar equals 1 cm. **B,** Chloranthoid leaf identified as *Quercophyllum tenuinerve* by Hickey and Doyle (1977), showing irregular festooned craspedodromous secondary venation in which each secondary vein gives off one or more low-angle inner branches and curves apically to enter a tooth. The small dark dots in the lamina are presumed to be remains of oil cells. Dutch Gap, UMMP 64896. Scale bar equals 5 mm. **C,** Chloranthoid leaf identified as *Celastrophyllum* sp. by Upchurch (1984a), showing attachment of the leaf to a stem (right-hand arrow). Left-hand arrow indicates the probable attachment of a second leaf at the same node. Drewry's Bluff locality, UMMP 64892. Scale bar equals 1 cm. **D,** Chloranthoid leaf, close-up of counterpart of B showing weakly biserrate margin with small chloranthoid teeth. UMMP 64896. Scale bar equals 2 mm.

presumably derived feature of many Piperales. However, the venation is too poorly preserved to rule out a relationship to broad-leafed monocots, where sympodial branching is also common.

Chloranthoids

Since Couper (1958) described the reticulate-columellar monosulcate pollen genus *Clavatipollen-*

ites from the Wealden of England and compared it with pollen of the living chloranthaceous genus *Ascarina*, it has been suggested that Chloranthaceae, one of the five mesangiosperm clades, were an important early angiosperm group. This led to speculation that the extremely simple flowers of Chloranthaceae, with one carpel and usually one stamen, provide an alternative model for the

ancestral flower (Meeuse 1972; Burger 1977; Leroy 1983; Nixon et al. 1994; Hickey and Taylor 1996). However, their position in the mesangiosperm clade implies that their floral simplicity is the result of very early reduction (Endress and Doyle 2009). The large number of fossils that appear to be related to Chloranthaceae is consistent with the hypothesis of Feild et al. (2004) that Chloranthaceae were among the first angiosperms to "break out" of the wet understory niche of the first angiosperms into more open, sunny habitats.

In the lower Potomac, leaves variously assigned to *Proteaephyllum dentatum*, *Celastrophyllum*, and *Quercophyllum* (Figures 5B–D) resemble Chloranthaceae in having pinnate venation and marginal teeth. Hickey and Doyle (1977) did not relate these leaves to Chloranthaceae, but Upchurch (1984b) showed that they have chloranthoid teeth (Hickey and Wolfe 1975), with three veins forming a tripod at or below an apical gland (Figure 5D), and share cuticle features with Chloranthaceae. Chloranthoid teeth alone do not necessarily imply a relationship to Chloranthaceae, since they also occur in *Amborella*, Austrobaileyales (*Trimenia*, *Schisandra*), and basal eudicots, and have been inferred to be ancestral in angiosperms (Doyle 2007). However, many Potomac chloranthoid leaves resemble leaves of *Ascarina* and some *Hedyosmum* species in having festooned craspedodromous secondary venation, a presumed derived condition in which each secondary vein forms an inner low-angle branch that connects with the superjacent secondary vein, and a thicker outer branch that curves apically and enters a tooth. In this respect, younger leaves named *Crassidenticulum* from the late Albian Rose Creek locality in the Dakota Formation of Nebraska are even more like leaves of extant Chloranthaceae in having more regular venation and more strongly developed craspedodromy (Upchurch and Dilcher 1990).

Potomac Group chloranthoid leaves have additional derived features that support a relationship with Chloranthaceae over other possibilities. These include secretory cells in the lamina (Figure 5B), presumably equivalent to the oil cells of modern taxa, which according to parsimony optimization (Figure 4) arose in the common ancestor of Austrobaileyales and mesangiosperms and persisted in Chloranthaceae and magnoliids, but were lost in monocots (above the basal genus

Acorus) and eudicots. Two specimens representing different species from Drewry's Bluff appear to show opposite attachment of leaves to stems (Figure 5C). Opposite phyllotaxis may be a synapomorphy of Chloranthaceae, or of Chloranthaceae and *Ceratophyllum* (which has whorled leaves, lumped with the opposite state in Doyle and Endress 2014) if the two are sister groups, as in the D&E tree. However, with the D&E tree, where Chloranthaceae and *Ceratophyllum* are basal in mesangiosperms, it is equally parsimonious to assume that their opposite leaves are homologous with those of Austrobaileyales (*Austrobaileya*, *Trimenia*) and were lost in the remaining mesangiosperms. In any case, opposite phyllotaxis originated independently in many other clades, most notably Laurales.

Mesofossils from Portugal, many of them associated with pollen types known in the lower Potomac, confirm the presence of Chloranthaceae and related lines (stem relatives) by the early Albian. If *Ceratophyllum* is sister to Chloranthaceae, as indicated by morphological and some molecular analyses, some of these fossils may be more closely related to this enigmatic aquatic plant.

Ironically, the first mesofossils to be associated with pollen of the *Clavatipollenites* type, namely fruits called *Couperites* from the early Cenomanian of Maryland (Pedersen et al. 1991), may not be chloranthaceous. Like Chloranthaceae they have one apical seed, but the seed is anatropous rather than orthotropous and has different seed coat anatomy. In analyses by Doyle and Endress (2014) with the J/M chloroplast backbone tree, where Chloranthaceae and *Ceratophyllum* are well separated, *Couperites* is sister to Chloranthaceae; but with the D&E tree, where Chloranthaceae and *Ceratophyllum* form a clade, it has several most parsimonious positions in and around Chloranthaceae and sister to mesangiosperms, and many other positions are only one step less parsimonious. These results do not necessarily apply to other dispersed pollen identified as *Clavatipollenites*. The pollen associated with *Couperites*, compared to *Clavatipollenites rotundus* (Kemp 1968) and *Retimonocolpites dividuus* (Pierce 1961), is only one of many assigned to *Clavatipollenites*, which may be systematically heterogeneous, especially considering that most of its characters are plesiomorphic.

Better evidence for Chloranthaceae comes from flowers from the early Albian of Portugal with pollen of the *Asteropollis* type (Friis et al. 1999, 2006; Friis et al. 2011; Eklund et al. 2004), which is like *Clavatipollenites* except that the sulcus has four or five branches, as in the living genus *Hedyosmum*. The female flowers have three reduced tepals on top, also as in *Hedyosmum*. Analyses of Eklund et al. (2004) and Doyle and Endress (2014) linked these fossils with *Hedyosmum*, indicating that crown group Chloranthaceae had originated by the early Albian. Some authors have used *Asteropollis* for pollen with a three-armed (trichotomosulcate) sulcus, which extends down into the Aptian, but the oldest well-dated grains with a four- or five-armed sulcus are early Albian (see Doyle and Endress 2014); in the Potomac they are not known until Zone II.

Another flower from the early Albian of Portugal, *Canrightia* (Friis and Pedersen 2011), is linked with Chloranthaceae but notably more primitive. It resembles Chloranthaceae in having one orthotropous ovule per carpel, but it is bisexual and has a reduced perianth and four or so stamens and carpels. Analyses by Friis and Pedersen (2011) and Doyle and Endress (2014) placed it on the stem lineage of Chloranthaceae (plus *Ceratophyllum* with the D&E tree). Its pollen is of an open reticulate type with smooth muri often assigned to *Retimonocolpites*, which occurs throughout the Potomac.

Another chloranthoid group is known from uniovulate carpels, male flowers consisting of one stamen, and coarsely reticulate monosulcate pollen called *Pennipollis* (Friis et al. 2000), one of the most common angiosperm pollen types in Zone I and Aptian beds elsewhere (Penny 1988a). As discussed above, such pollen was first described by Brenner (1963) as *Peromonolites* and provides evidence for an Aptian age of the basal Potomac. Friis et al. (2000) and Friis et al. (2011) argued that the *Pennipollis* plant was a monocot in the near-basal order Alismatales, in which some members have pollen that resembles *Pennipollis* in having a reticulate tectum and granular infratectal structure. However, Doyle et al. (2008) and Doyle and Endress (2014) found that it was much more parsimonious to place the *Pennipollis* plant on the stem lineage of Chloranthaceae (J/M), Chloranthaceae plus *Ceratophyllum*, or *Ceratophyllum* (D&E). *Appomattoxia* (Friis et al.

1995) is based on spiny fruits from the middle Albian of Virginia and associated pollen of the *Tucanopollis* type, which extends down to the Barremian in Northern Gondwana (Doyle et al. 1977; Regali 1989). Friis, Pedersen et al. (1995) and Friis, Crane et al. (2011) argued that *Appomattoxia* was related to Piperales, on the basis of its sclerotic tegmen in the seed coat, but analyses of Doyle and Endress (2014) placed it either near the base of the angiosperm tree or with Chloranthaceae and/or *Ceratophyllum*. Mid-Cretaceous megafossils from other regions that could represent stem relatives of *Ceratophyllum*, such as *Pseudoasterophyllites*, associated with *Tucanopollis*-like pollen by Kvacek et al. (2012), are discussed in Doyle and Endress (2014).

Monocots

The second-largest mesangiosperm clade is the monocots. Two lower Potomac fossil types that Doyle (1973), Doyle and Hickey (1976), and Hickey and Doyle (1977) interpreted as monocots are *Liliacidites*, comprising monosulcate pollen with reticulate sculpture that grades from fine at the ends of the grain to coarse in the middle, and *Acaciaephyllum*, best known as a stem bearing leaves with apically fusing veins. *Acaciaephyllum* is from the "Fishing hut above Dutch Gap Canal" locality of Fontaine (1889), not to be confused with the previously mentioned locality of Doyle and Hickey (1976) and Upchurch (1984b) on the south side of Dutch Gap Canal, which is about 1.5 km downstream but apparently of similar age (early Zone I, probably Aptian).

The monocot affinities of these fossils were questioned by Gandolfo et al. (2000) but reaffirmed by Doyle et al. (2008) on the basis of closer examination of characters and phylogenetic analyses. The case of *Liliacidites* had been confused by assignment of pollen with different patterns of grading or a non-graded reticulum to this genus, some of which has been associated with non-monocotyledonous mesofossils (including *Anacostia*). However, the specific pattern of grading seen in typical *Liliacidites* (fine at the ends, coarse in the middle) is not known outside monocots. *Acaciaephyllum* has alternate phyllotaxis, a midvein, and major veins that fuse successively toward the apex (Figures 6A, B, arrows). These features occur in most monocots but contrast with character states in the most similar non-angiospermous
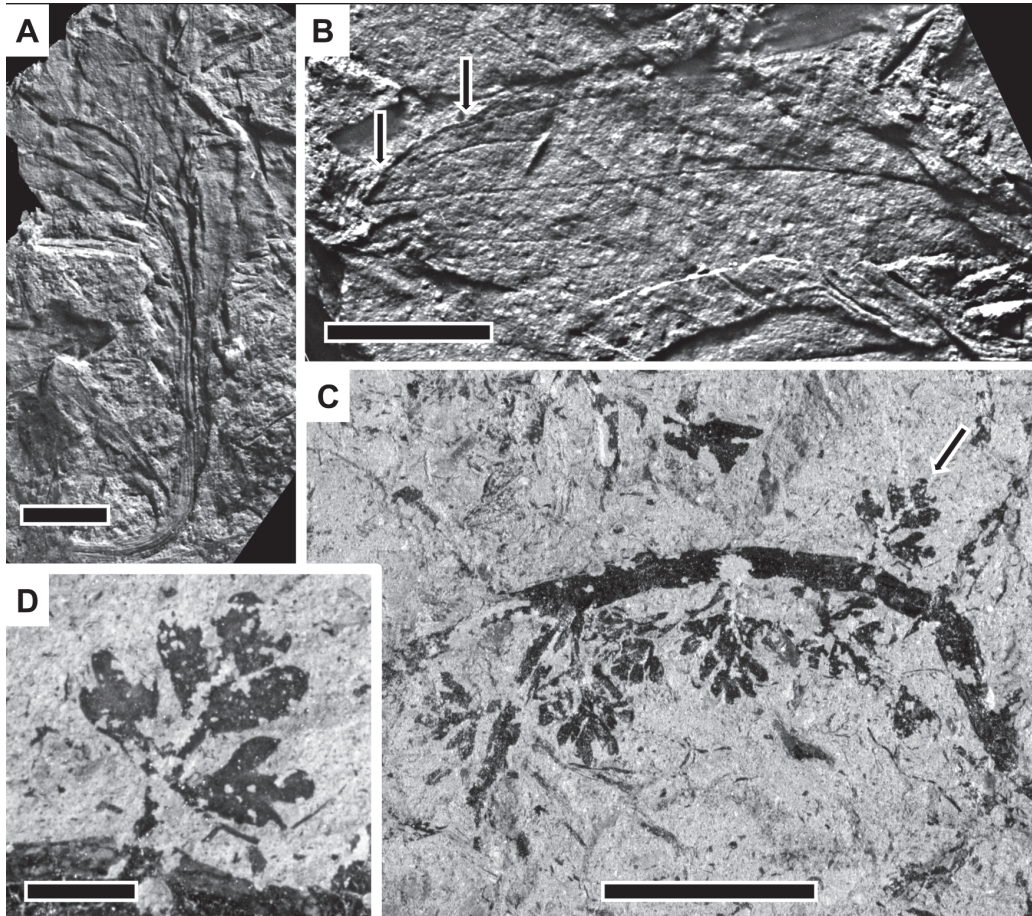
FIGURE 6. Leaf-bearing shoots of a monocot and possible eudicot from lower Zone I of the Potomac Group. **A, B,** *Acaciaephyllum spatulatum* from the Fishing hut above Dutch Gap Canal locality of Fontaine (1889). USNM 175802A. **A,** General shot. Scale bar equals 5 mm. **B,** Close-up of leaf showing successive fusion of longitudinal parallel veins toward the apex (arrows). Scale bar equals 5 mm. **C, D,** Leaf-bearing shoot with similarities to *Vitiphyllum parvifolium*, from the basal bed at the Dutch Gap locality of Doyle and Hickey (1976). USNM 455017. **C,** General shot showing herbaceous stem bearing small leaves and axillary branches. Arrow points to leaf illustrated in D. Scale bar equals 1 cm. **D,** Close-up of basalmost leaf of shoot. Note ternate lobation. Scale bar equals 2 mm.

seed plants, which are some fossil and Recent Gnetales (Doyle et al. 2008). The idea that monocots had begun to diversify by the Albian is confirmed by inflorescences from the early Albian of Portugal (Friis et al. 2010) that resemble Araceae, in Alismatales, the second branch above the base of the monocots in molecular phylogenies, and stems with aroid-like leaves (*Spixiarum*) from the late Aptian of Brazil (Coiffard et al. 2013a).

Eudicots

Plants with tricolpate and derived pollen form a clade, the eudicots (Doyle and Hotton 1991;

Cantino et al. 2007), which was first suggested by morphological cladistic analyses (Dahlgren and Bremer 1985; Donoghue and Doyle 1989) and conclusively established by molecular analyses (Chase et al. 1993). Rare tricolpate pollen appears consistently in upper Zone I and the early Albian of England and Portugal (Kemp 1968; Laing 1975; Heimhofer et al. 2007), indicating the presence of eudicots. However, these are not the oldest evidence for eudicots, as tricolpate pollen extends back to the late Barremian in Northern Gondwana (Doyle et al. 1977; Regali and Viana 1989; Doyle 1992),

and a few isolated grains have been reported in the Barremian and Aptian of England (Hughes and McDougall 1990; Hughes 1994) and the lower part of Potomac Zone I (Doyle 1992).

These observations raise the question of whether any lower Potomac leaves are related to eudicots. Fossils known as *Vitiphyllum* from an upper Zone I flora at Baltimore, Maryland, resemble leaves of the basal eudicot order Ranunculales in their ternately lobed organization (Doyle 2001), a clearly derived condition (Doyle 2007). A small leafy shoot (Figure 6C and D) from the south side of Dutch Gap Canal (probably Aptian) has similarities to *Vitiphyllum parvifolium* of Fontaine (1889). Jud and Hickey (2013) described another ternately organized leaf, *Potomacapnos*, from the same locality and presented a phylogenetic analysis that nested it within the ranunculalean family Papaveraceae, although they cautioned that this was based on a relatively small number of characters. *Leefructus*, from the Barremian-Aptian Yixian Formation of China (Sun et al. 2011), had ternate leaves and a 5-carpellate fruit, as in Ranunculaceae.

A complicating factor is that these fossils also show similarities to the controversial aquatic plant *Archaefructus* from the Yixian Formation (Sun et al. 1998; Sun et al. 2002). This had herbaceous stems bearing more finely dissected but ternately organized leaves and reproductive axes with paired stamens and carpels, which have been variously interpreted as pre-flowers (Sun et al. 2002) or inflorescences of highly reduced flowers (Friis et al. 2003). Different phylogenetic analyses have interpreted *Archaefructus* as a stem relative of angiosperms (Sun et al. 2002), a member of Nymphaeales near the highly reduced Hydatellaceae, or a eudicot (Endress and Doyle 2009).

Except for *Vitiphyllum* from Baltimore, all of these fossils predate the consistent presence of tricolpate pollen in their respective areas, although as noted exceedingly rare tricolpate grains of similar age are known in England and the Potomac. This conflict could be resolved if the leaf fossils were stem relatives of eudicots in which tricolpate pollen had not yet evolved. In terms of parsimony the ancestor of eudicots had simple leaves and ternate dissection evolved in Ranunculales (Doyle 2007), but a likelihood-based analysis by Geeta et al. (2012) inferred that dissection probably evolved earlier, on the eudicot stem lineage. Interestingly,

some leaves of *Vitiphyllum* from Baltimore have what appear to be mesophyll secretory cells, which would support a position outside crown group eudicots, which lack such cells (Figure 4). These problems were explored in greater detail in Doyle (2012).

Potomac Zone II (Middle to Late Albian)

In the palynological record, Zone II corresponds to the proliferation of tricolpate eudicot pollen. The fact that tricolpates are more diverse than angiospermous monosulcates from the base of the zone is consistent with the view of Hochuli et al. (2006) that there was a significant hiatus between Zones I and II. However, their suggestion that almost all of Zone II is late Albian or Cenomanian is not supported by correlations with well-dated middle and late Albian floras in Oklahoma and the U.S. Western Interior (Massoni et al. 2014).

Eudicots

The most conspicuous feature of the Zone II leaf record is the appearance of peltate, palmately lobed, pinnatifid, and pinnately compound angiosperm leaves, which are dominant at some localities, particularly in stream-margin facies (Doyle and Hickey 1976; Hickey and Doyle 1977). As argued by Hickey and Doyle (1977), many of these leaves are of types seen in eudicots with tricolpate pollen, and affinities with such "basal" eudicots have been confirmed by discoveries of fossil flowers (Crane et al. 1986; Crane et al. 1993; Drinnan et al. 1991). All Albian eudicots that have been analyzed phylogenetically (Doyle and Endress 2010) belong to lines that branch off below the huge "core eudicot" clade, named Pentapetalae by Cantino et al. (2007), where we find typical pentamerous flowers with distinct sepals and petals. The oldest known flowers of this type were reported by Basinger and Dilcher (1984) from what are now known to be latest Albian beds at the Rose Creek locality in the Dakota Formation of Nebraska (Gröcke et al. 2006). Pentapetalae may also be represented by the first typical tricolporates, the basic pollen type for the rosid and asterid clades of the Pentapetalae, which appear near the Albian-Cenomanian boundary.

Many authors (Berry 1911; Vakhrameev 1952; Samylina 1968; Hickey and Doyle 1977)

compared peltate leaves with actinodromous venation from the upper Potomac and the Albian of other areas with the aquatic genus *Nelumbo*. *Nelumbo* was formerly assigned to Nymphaeales but has tricolpate pollen, and molecular data place it in the near-basal eudicot order Proteales, where it is sister to *Platanus* plus Proteaceae. The Albian leaves have been identified as *Nelumbites* (the correct name according to Upchurch et al. 1994) or *Menispermites*. Doyle and Hickey (1976) and Hickey and Doyle (1977) adduced evidence that the *Nelumbites* plant was aquatic from the functional morphology of the leaves and their abundance in pond facies, for example at Quantico, Virginia. A relationship to *Nelumbo* was strengthened by the discovery at Quantico of floral receptacles with pits where the carpels were presumably borne, as in *Nelumbo* (Upchurch et al. 1994; Figure 7C). However, the fossils are more plesiomorphic than modern *Nelumbo*: the receptacles are round rather than flat-topped, and the leaves are smaller and have fewer primary veins and more irregular venation.

Consistent with these observations, Doyle and Endress (2010) found that the most parsimonious position for *Nelumbites* is sister to *Nelumbo*. However, it was only one step less parsimonious to link *Nelumbites* with *Brasenia* (Cabombaceae) in the Nymphaeales, probably because relatively few characters in the data matrix could be scored. Some characters not used by Doyle and Endress (2010) may favor a relationship with *Nelumbo* rather than *Brasenia*, such as associated tubers and the fact that the leaf blade tends to be wider than long, as in *Nelumbo*, rather than longer than wide, as in *Brasenia* (cf. Wang and Dilcher 2006).

A characteristic element of mid-Cretaceous floras is palmately lobed and veined "platanoid" leaves. Early authors assigned these leaves to many extant families (e.g., Araliaceae, Lauraceae, Platanaceae, Sterculiaceae: Lesquereux 1892), but they have venational features most typical of modern *Platanus*: palinactinodromous primary venation, percurrent tertiaries, and "stitched intertertiary" veins (formed by branching and fusion of alternating quaternary veins, analogous to composite intersecondary veins of Hickey 1973). *Platanus* was formerly grouped with other wind-pollinated taxa in the now-obsolete subclass Hamamelidae (Cronquist 1968; Takhtajan 1969),

but molecular data place it in Proteales with *Nelumbo* and Proteaceae, where it is sister to the latter family. Platanoid leaves are abundant in channel margin and levee facies in Potomac Subzone II-C (latest Albian), as in the correlative Dakota flora of Kansas (Lesquereux 1892). Leaves with comparable venation (Platanoids #1 and #3 of Upchurch 1984a) extend down into Subzone II-B (middle to late Albian), together with similar leaves with less platanaceous fine venation (Doyle and Hickey 1976; Hickey and Doyle 1977). Several authors noted axes bearing numerous "pom-pom-like" heads, which recall the heads of *Platanus* but are smaller, in beds with platanoid leaves, and Hickey and Doyle (1977) interpreted this as evidence for relatives of *Platanus*.

Additional evidence came from cuticle studies (Upchurch 1984a), which showed that some Albian platanoid leaves share important epidermal features with *Platanus*. Most definitive is the presence of *Platanus*-type hair bases, in which the basal cell of the trichome is shaped like a truncate cone and symmetrically placed over the junction of two or more epidermal cells (Figure 7A, B). Such hair bases also occur in Proteaceae and have been considered a synapomorphy of the two taxa (Figure 4) because they are unknown in *Nelumbo*, other basal eudicots, magnoliids, and other basal angiosperms (Carpenter et al. 2005; Upchurch, unpubl. data). An additional epidermal character of platanoid leaves that supports a relationship to *Platanus* is laterocytic stomata (Figure 7A), which are present in both *Platanus* and *Bellendena*, a near-basal genus of Proteaceae, but are absent in more derived Proteaceae and *Nelumbo*, which have paracytic and anomocytic stomata, respectively.

The view that heads from the upper Potomac of Maryland were from relatives of *Platanus* was confirmed by Crane et al. (1986), Friis et al. (1988), and Pedersen et al. (1994), who showed that the flowers making up the heads were unisexual, with reticulate tricolpate pollen in the stamens, as in *Platanus*, but had larger perianth parts, five stamens or five carpels, and other more plesiomorphic features. However, although inflorescences from Bull Mountain (Subzone II-C; Pedersen et al. 1994) were in beds dominated by typical palmately lobed platanoid leaves, those at the West Brothers locality (upper Subzone II-B; Crane et al. 1986; Friis et al. 1988) co-occurred with both platanoid
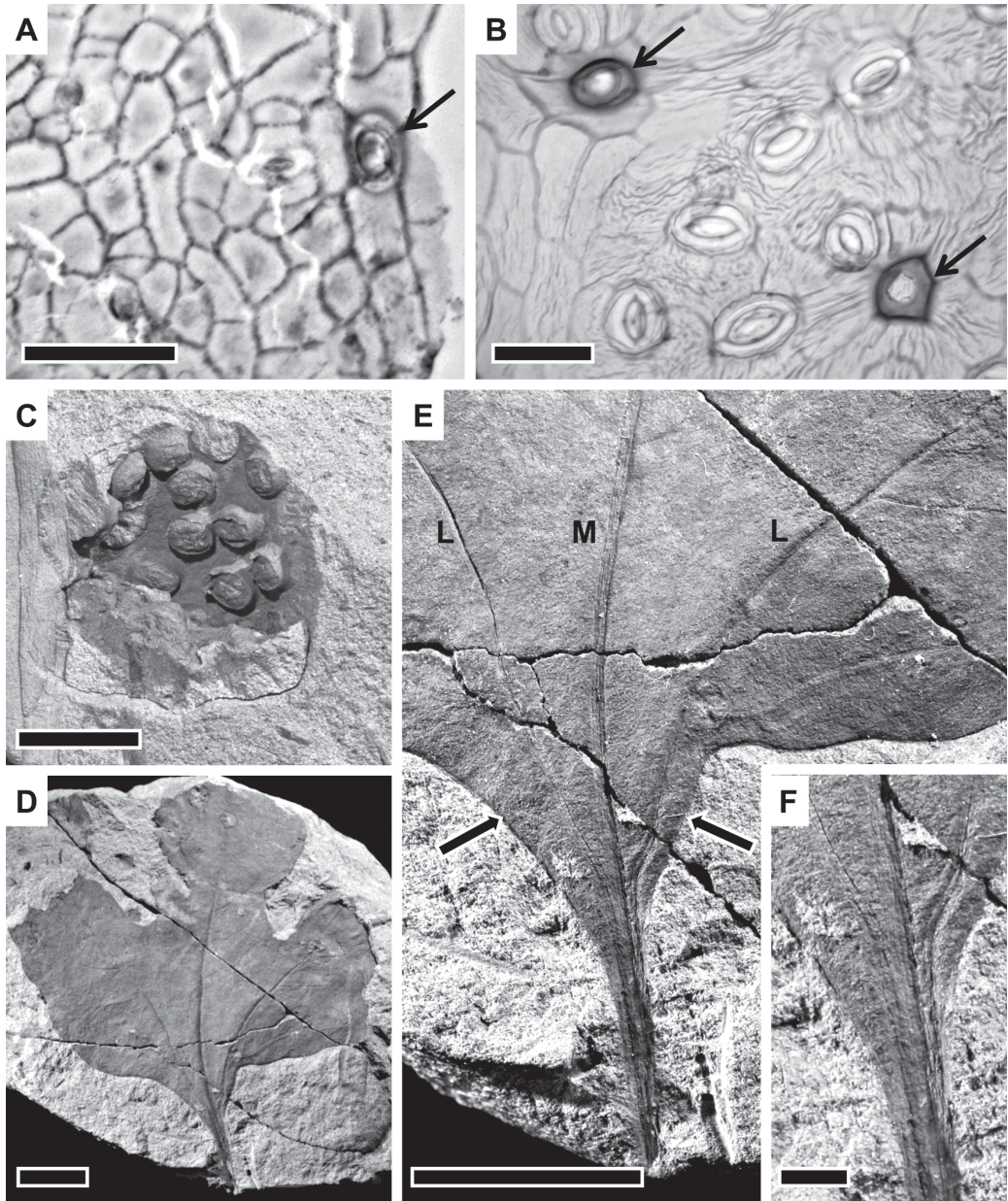
FIGURE 7. Proteales and Laurales from Subzone II-B of the Potomac Group. **A,** Platanoid #3 of Upchurch (1984a) from Stump Neck, abaxial cuticle showing *Platanus*-type hair base (arrow) and two laterocytic stomata. UMMP 65103. Scale bar equals 50 μm. **B,** Extant *Platanus occidentalis*, abaxial cuticle showing two hair bases (arrows) and several stomata. Texas State University Modern Cuticle Reference Collection GU59. Scale bar equals 50 μm. **C,** Mold of a floral receptacle from Quantico illustrated by Upchurch et al. (1994), found in association with *Nelumbites* leaves and tepal-like structures. The large inward-directed protuberances are interpreted as infilled carpel-bearing pits in the floral receptacle. UMMP 446045a. Scale bar equals 5 mm. **D–F,** Leaf of aff. *Pabiania* from Quantico illustrated by Upchurch et al. (1994). UMMP 66621. **D,** General shot of trilobed leaf. Scale bar equals 1 cm. **E,** Basal half of leaf showing midvein (M), lateral primary veins (L), and basilaminar secondary veins (arrows). Scale bar equals 1 cm. **F,** Close-up of blade-petiole junction showing lateral primary veins that are decurrent onto the midvein. Scale bar equals 2 mm.

leaves and pinnately compound leaves of the *Sapindopsis* type (cf. Upchurch 1984a), and it is not known which leaves belonged with the inflorescences. In any case, the analyses of Doyle and Endress (2010) strongly linked the West Brothers inflorescences with *Platanus*, as a stem relative of the living genus.

Sapindopsis includes pinnately divided leaves that range from deeply pinnatifid, with lobes connected by a decurrent wing of laminar tissue, to truly compound, with leaflets attached to the rachis by distinct petiolules. Pinnatifid leaves occur at Fontaine's (1889) lower Subzone II-B locality near Brooke, Virginia, while truly compound leaves dominate at upper Subzone II-B localities, such as West Brothers and Red Point in Maryland. Leaves similar to Potomac Group *Sapindopsis* occur in the early late Albian Cheyenne Sandstone of Kansas (Berry 1922), the Albian of Israel (Krassilov and Schrank 2011) and Spain (Sender et al. 2013), and the Cenomanian of Lebanon (Dilcher and Basson 1990; Krassilov and Bacchia 2000). Hickey and Wolfe (1975) and Hickey and Doyle (1977) suggested that *Sapindopsis* and the platanoids were related, on the basis of similar teeth in some members of the two groups, the resemblance of the lobed terminal leaflet in some *Sapindopsis* leaves to a platanoid leaf (cf. Crane 1989), and the presence of similar heads at localities with the two leaf types; this view was strengthened by cuticle similarities documented by Upchurch (1984a). Hickey and Wolfe (1975) and Hickey and Doyle (1977) proposed that *Sapindopsis* was on the line leading to rosids, the angiosperm group where compound leaves are most prevalent, while the platanoids were "lower hamamelids," and they took the similarities as evidence that rosids and hamamelids had a close common ancestor.

This situation was greatly clarified by Crane et al. (1993), who conclusively associated *Sapindopsis* at Brooke with heads in the same beds (figured by Hickey and Doyle 1977), on the basis of characters of the cuticle of the inflorescence axes, and showed that these heads consisted of unisexual flowers similar to those associated with platanoid leaves. Phylogenetic analyses by Doyle and Endress (2010) confirmed that *Sapindopsis* was a stem relative of *Platanus*, like the West Brothers platanoid. When both fossils were added to the backbone tree, they formed either a sister clade or

two successive outgroups, with *Sapindopsis* more basal. These results imply that *Sapindopsis* has nothing to do with rosids, since *Platanus* and rosids are separated by many nodes in molecular trees, and heads of unisexual flowers would not be predicted in stem relatives of rosids. It should be noted that not all leaves formerly considered platanoids are basal eudicots related to *Platanus*; as discussed below, some are now known to represent Laurales.

Another basal eudicot line is represented by *Spanomera* (Drinnan et al. 1991), which had unisexual flowers with reduced tepals grouped into bisexual inflorescences, as in Buxaceae. The analysis of Doyle and Endress (2010) indicated that *Spanomera* was sister to Buxaceae, one or two nodes above Proteales on the line leading to Pentapetalae. The presence of relatives of Buxaceae was not suspected from the leaf record, but leaves in this part of the tree can be reconstructed as being ovate and having palmate venation and marginal teeth, like upper Potomac fossils known as "*Populus*" *potomacensis*. *Spanomera* has tricolpate pollen with striate-reticulate exine sculpture, as in some *Buxus* species and Trochodendraceae (*Trochodendron, Tetracentron*), which form a line adjacent to Buxaceae in molecular phylogenies. Such pollen appears above the base of the early Albian in Portugal (Heimhofer et al. 2007), and it has been found in less complete buxoid flowers from the Vale de Agua mesofossil locality (Pedersen et al. 2007). However, similar pollen extends down to the early Aptian in Egypt (Penny 1988b) and other areas in Northern Gondwana (Doyle et al. 1977; Doyle 1992).

Magnoliids

An important result of studies of fossil flowers is recognition that woody members of the magnoliid clade, particularly Magnoliales and Laurales, were radiating in the Albian, alongside the eudicots. We have noted pollen evidence for stem relatives of Winteraceae (Canellales) in the late Barremian through Albian of Gondwana (Walker et al. 1983; Doyle et al. 1990; Barreda and Archangelsky 2006; Schrank 2013). Magnoliales, Laurales, and Canellales have basically pinnately veined, entire-margined leaves, becoming palmately veined in "higher" Laurales. Leaves of the pinnately veined type were mentioned but not illustrated by Doyle and Hickey (1976) and Hickey and Doyle (1977).

However, Upchurch et al. (1994) reported such leaves from Quantico as *Landonia*, a genus that Upchurch and Dilcher (1990) first described from the Dakota Formation of Nebraska and assigned to Laurales, and *Dicotylophyllum ovatodecurrens*.

Confirmed Magnoliales are not known from the Potomac Group. Besides *Lethomasites* from Zone I, the order could be represented by laminar stamens containing monosulcate pollen with a smooth tectum from the middle Albian Puddledock locality in Virginia (Crane et al. 1994, fig. 11a, b). Better evidence for Magnoliales is provided by fossil flowers named *Archaeanthus* and associated bilobed leaves (*Liriophyllum*) described by Dilcher and Crane (1984) from the Dakota Formation at the Linnenberger Ranch in Kansas. Although the age of the published leaf flora from the Rose Creek locality in the Dakota has been refined to latest Albian (Gröcke et al. 2006), like Subzone II-C in the Potomac, an early Cenomanian age for the Linnenberger locality cannot be excluded (Massoni et al. 2014). The flowers are known as floral axes bearing numerous spiral carpels, with scars below that correspond to other floral parts in Magnoliaceae, and detached tepals and stipular bracts. The analysis of Doyle and Endress (2010) strongly associated *Archaeanthus* with Magnoliaceae, either attached to the stem lineage of the family or nested in the crown group. Romanov and Dilcher (2013) presented an analysis that linked *Archaeanthus* exclusively with *Liriodendron*, but this was a result of use of redundant characters and inappropriate outgroups (Massoni et al. 2014).

By contrast, the Potomac mesofossil record provides abundant evidence for Laurales. This includes both one taxon from near the base of the clade and an increasing number from higher within it, which together show two extremes in floral morphology in the order.

The first extreme is represented by *Virginianthus*, a flower from the middle Albian Puddledock locality (Friis, Eklund et al. 1994). This fossil has a deep floral cup with numerous spiral tepals, stamens, and inner staminodes on the rim and carpels inside, as in Calycanthaceae, the relatively plesiomorphic sister group of the remaining Laurales. However, the pollen is monosulcate with an open reticulum, of a type called *Clavatipollenites minutus*, rather than disulculate with small per-

forations in living Calycanthaceae. Because Walker and Walker (1984) had identified dispersed pollen of this type as "*Liliacidites*" *minutus* and interpreted it as monocotyledonous, Doyle et al. (2008) analyzed *Virginianthus* in their review of Early Cretaceous monocots. This analysis indicated that *Virginianthus* had two most parsimonious positions, one sister to Calycanthaceae, the other sister to the remaining Laurales. The fact that *Virginianthus* has reticulate monosulcate pollen suggests that more dispersed pollen of this common early type was produced by magnoliids than might be assumed on the basis of the numerous living magnoliids with tectate exines.

At the other extreme is *Mauldinia*, described by Drinnan et al. (1990) from Mauldin Mountain, Maryland, near the base of Zone III (early Cenomanian; Massoni et al. 2014). It is known as isolated flowers and inflorescences with curious bilobed flower-bearing lateral units, interpreted as dichasial cymes with fused bracts. The flowers are trimerous, with two whorls of three tepals, stamens with basal glands and flap dehiscence, and one carpel, as in Lauraceae, but the inner tepals are more petaloid than those of Lauraceae and there is endosperm in the seed, whereas endosperm is used up at maturity in Lauraceae. Herendeen (1991) used xylem in the inflorescence axes to associate *Mauldinia* with *Paraphyllanthoxylon*, a widespread mid-Cretaceous wood genus, which is anatomically similar to wood of Lauraceae but more plesiomorphic in lacking well-developed paratracheal parenchyma. Abundant dispersed cuticle with lauraceous features occurs in the same bed (Richey and Upchurch 2011). The superior ovary also contrasts with the inferior ovary of basal Lauraceae, which is reconstructed as ancestral in the family and reversed to superior in derived members (Rohwer and Rudolph 2005). Similar but less complete flowers extend down to the middle Albian at Puddledock (von Balthazar et al. 2007; von Balthazar et al. 2011). Inflorescences similar or identical to *Mauldinia* from the Dakota Formation of Kansas were described by Retallack and Dilcher (1981) as *Prisca*, who misinterpreted the inflorescences as elongate floral axes, the fused bracts as open follicles, and the fruits as seeds.

Despite the close similarity of the flowers to modern Lauraceae, the analysis of Doyle and Endress (2010) indicated that *Mauldinia* was not

uniquely linked to this family but was rather an extinct sister group of Lauraceae plus Hernandiaceae. This suggests that flowers of both Lauraceae and Hernandiaceae (which also have one carpel but a more variable perianth and androecium) were derived from the essentially lauraceous type of *Mauldinia*. A problem is that the arrangement of these two families and the related Monimiaceae is not resolved by molecular data, which usually link Monimiaceae with either Lauraceae or Hernandiaceae (Renner and Chanderbali 2000; Massoni et al. 2014). The sister group relationship of Lauraceae and Hernandiaceae in the Doyle and Endress (2010) backbone tree was based on the combined morphological and molecular analysis of Doyle and Endress (2000). This was the case where morphological data most strongly overruled molecular data; with the Doyle and Endress (2010) data set the two families are united by 17 morphological synapomorphies. When Doyle and Endress (2010) used a backbone tree in which Monimiaceae were linked with Lauraceae, the most parsimonious position of *Mauldinia* was sister to all three modern families, which would imply that the derived features shared by *Mauldinia*, Lauraceae, and Hernandiaceae were reversed in Monimiaceae.

Many Albian-Cenomanian leaves also appear to represent more or less derived Laurales. Some of these have been called "platanoids," which means that leaves of this type do not all form a natural group. These include *Pabiania*, a palmately veined and lobed leaf type that Upchurch and Dilcher (1990) described from the latest Albian Rose Creek locality in the Dakota Formation of Nebraska and identified as occurring in the Potomac Group ("*Sassafras*" *potomacensis* of Hickey and Doyle 1977, figs. 49–51). *Pabiania* differs from *Platanus* in lacking such apomorphies as stitched intertertiaries and *Platanus*-type hair bases and in having mesophyll secretory cells (which were retained from below Austrobaileyales into magnoliids but lost in eudicots: Figure 4), lateral primary veins that are decurrent into the petiole (a feature that occurs in both Laurales and Piperales), basilaminar secondary veins, and sinus bracing by a secondary vein that runs to the sinus and bifurcates, as in extant Laurales with lobate leaves (some Lauraceae, Hernandiaceae). Other lobed Potomac Group leaves, such as aff. *Pabiania* from Quantico (Upchurch et al. 1994;

Figures 7D–F) and Platanoid #2 from Stump Neck, Maryland (Upchurch 1984a), differ from *Pabiania* in their sinus bracing but fit better in Laurales than near *Platanus* because of their secretory cells and/or pattern of primary and tertiary venation. Upchurch and Dilcher (1990) linked *Pabiania* with derived Laurales on the basis of its palmate venation, as in Hernandiaceae, many Lauraceae, and some Monimiaceae (*Hortonia*), but they noted that it is more plesiomorphic than all Lauraceae and some Hernandiaceae (*Gyrocarpus* and *Sparattanthelium*) in having less organized fine venation and numerous freely ending veinlets. Its palmate lobation is therefore purely convergent with that of the temperate lauraceous genera *Sassafras* and *Lindera*, which are located well up in the phylogeny of Lauraceae (Rohwer and Rudolph 2005).

Another lauralean leaf type is *Pandemophyllum*, described by Upchurch and Dilcher (1990) from Rose Creek, which is common at Dakota localities with *Prisca* and occurs abundantly as dispersed cuticle in the bed at Mauldin Mountain, Maryland, that yields *Mauldinia*. Unlike *Pabiania*, *Pandemophyllum* has pinnate venation, and it shares presumably derived features with Lauraceae that are absent from *Pabiania*: more highly organized fine venation, uniformly paracytic stomata, and scale-shaped guard cell lamellae. If *Pandemophyllum* is the leaf of *Prisca* and *Mauldinia*, its "lauraceous" features might conflict with the idea that *Mauldinia* is sister to both Lauraceae and Hernandiaceae. However, evaluating this argument requires better information on epidermal characters in Hernandiaceae. Relatives of Lauraceae have not been reported in the Potomac pollen record, but this is not surprising, since both Lauraceae and Hernandiaceae have inaperturate pollen with a reduced granular exine that is rarely preserved.

Many angiosperms from Zone II and coeval beds, particularly locally abundant types assigned to Proteales (*Sapindopsis*, platanoids) and Laurales (*Pabiania*, *Pandemophyllum*, *Eucalyptolaurus*), have vein densities and inferred maximum assimilation rates higher than those of ferns, gymnosperms, ANITA-grade angiosperms, Chloranthaceae, and basal magnoliids (Feild, Brodribb et al. 2011; Feild, Upchurch et al. 2011). Angiosperms with the still higher vein densities characteristic of extant tropical rainforest trees are not known until

the latest Cretaceous. This trend for increase in vein density has been functionally linked with the diversity and dominance of angiosperms in modern tropical rainforests (Boyce et al. 2009).

Conclusions

With the fossils discussed in this paper placed at most parsimonious positions on the modern tree (see Figure 2), most of the lines that diverged near the base of the molecular tree of angiosperms can be traced back to the early Albian. These include Nymphaeales, Austrobaileyales, Chloranthaceae, magnoliids (Canellales and Magnoliales), monocots, and eudicots. Many of the taxa that appear after the early Albian, such as *Archaeanthus*, *Mauldinia*, the platanoids, and *Spanomera*, are nested higher in the tree, as expected if angiosperms were radiating during this time (Doyle 2012). A significant diversity of angiosperms had evolved by the middle Albian, but it should be noted that there is no clear fossil evidence before the latest Albian for the huge clades of core eudicots (Pentapetalae) or core monocots (Petrosaviidae of Cantino et al. 2007), which make up the vast bulk of modern angiosperms. There is abundant evidence that these core groups were diversifying in the Late Cretaceous (Friis et al. 2011) and were important in the transformation of the vegetation that occurred in this interval (Crane 1987; Upchurch and Wolfe 1987).

Although much has been learned about the systematic relationships of Potomac Group angiosperms since Hickey and Doyle (1977), many areas need additional work. Zone I (Aptian and early Albian) angiosperm mesofossils are virtually undescribed, although they do exist (Friis et al. 2011); they could provide much-needed evidence on the systematic diversity of angiosperms in floras coeval with or older than those in Portugal, or allow us to detect patterns of geographic endemism and dispersal. Evidence on the floral organization of taxa represented by isolated carpels and stamens, such as *Couperites*, *Appomattoxia*, and the *Pennipollis* plant, could resolve ambiguities concerning their phylogenetic placement (cf. Doyle and Endress 2014). More associations of reproductive and vegetative organs, of the sort established for *Nelumbites* and *Sapindopsis*, are desirable in order to reconstruct whole plants and decide between competing systematic hypotheses, such as the monocot versus chloranthaceous affinities of the *Pennipollis* plant. Leaf macrofossils and dispersed cuticles need full taxonomic description and placement in a phylogenetic framework, as done for flowers. More accurate systematic comparisons between the leaf, floral, and pollen records are needed to add the dimensions of vegetative adaptation and ecology to inferences on floral and dispersal biology, and to establish a phylogenetic framework for understanding community- and landscape-scale changes in vegetation during the rise of angiosperms.

Acknowledgments

Literature Cited

Antonov, A.S., A.V. Troitsky, T.K. Samigullin, V.K. Bobrova, K.M. Valiejo-Roman and W. Martin. 2000. Early events in the evolution of angiosperms deduced from cp rDNA ITS 2–4 sequence comparisons. In: Y.-H. Liu, H.-M. Fan, Z.-Y. Chen, Q.-G. Wu and Q.-W. Zeng, eds. Proceedings of the International Symposium on the Family Magnoliaceae. Beijing: Science Press. pp. 210–214.

[APG] Angiosperm Phylogeny Group. 1998. An ordinal classification for the families of flowering plants. Annals of the Missouri Botanical Garden 85:531–553.

—2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. Botanical Journal of the Linnean Society 141: 399–436.

—2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. Botanical Journal of the Linnean Society 161: 105–121.

Barreda, V. and S. Archangelsky. 2006. The southernmost record of tropical pollen grains in the mid-Cretaceous of Patagonia, Argentina. Cretaceous Research 27:778–787.

Basinger, J.F. and D.L. Dilcher. 1984. Ancient bisexual flowers. Science 224:511–513.

Berry, E.W. 1911. Systematic paleontology, Lower Cretaceous, Pteridophyta-Dicotyledonae. In: W.B. Clark, ed. Maryland Geological Survey, Lower Cretaceous. Baltimore: Johns Hopkins Press. pp. 214–508.

—1922. The flora of the Cheyenne Sandstone of Kansas. U.S. Geological Survey Professional Paper 129-I:199–225.

BOYCE, C.K., T.J. BRODRIBB, T.S. FEILD AND M.A. ZWIENIECKI. 2009. Angiosperm leaf vein evolution was physiologically and environmentally transformative. Proceedings of the Royal Society B 276:1771–1776.

BRENNER, G.J. 1963. The spores and pollen of the Potomac Group of Maryland. Maryland Department of Geology, Mines and Water Resources Bulletin 27:1–215.

BURGER, W.C. 1977. The Piperales and the monocots. Alternate hypotheses for the origin of monocotyledonous flowers. Botanical Review 43:345–393.

CANTINO, P.D., J.A. DOYLE, S.W. GRAHAM, W.S. JUDD, R.G. OLMSTEAD, D.E. SOLTIS, P.S. SOLTIS AND M.J. DONOGHUE. 2007. Towards a phylogenetic nomenclature of Tracheophyta. Taxon 56:822–846.

CARPENTER, K.J. 2005. Stomatal architecture and evolution in basal angiosperms. American Journal of Botany 92:1595–1615.

—2006. Specialized structures in the leaf epidermis of basal angiosperms: morphology, distribution, and homology. American Journal of Botany 93:665–681.

CARPENTER, R.J., R.S. HILL AND G.J. JORDAN. 2005. Leaf cuticular morphology links Platanaceae and Proteaceae. International Journal of Plant Sciences 166:843–855.

CHASE, M.W., D.E. SOLTIS, R.G. OLMSTEAD, D. MORGAN, D.H. LES, B.D. MISHLER, M.R. DUVALL, R.A. PRICE, H.G. HILLS, Y.-L. QIU ET AL. 1993. Phylogenetics of seed plants: an analysis of nucleotide sequences from the plastid gene rbcL. Annals of the Missouri Botanical Garden 80:526–580.

COIFFARD, C., B.A.R. MOHR AND M.E.C. BERNARDES-DE-OLIVEIRA. 2013a. The Early Cretaceous Aroid, Spixiarum kipea gen. et sp. nov., and implications on early dispersal and ecology of basal monocots. Taxon 62:997–1008.

—2013b. Jaguariba wiersemana gen. nov. et sp. nov., an Early Cretaceous member of crown group Nymphaeales (Nymphaeaceae) from northern Gondwana. Taxon 62:141–151.

COUPER, R.A. 1958. British Mesozoic microspores and pollen grains. Palaeontographica Abteilung B 103:75–179.

CRANE, P.R. 1987. Vegetational consequences of the angiosperm diversification. In: E.M. Friis, W.G. Chaloner and P.R. Crane, eds. The Origin of Angiosperms and Their Biological Consequences. Cambridge, UK: Cambridge University Press. pp. 107–144.

—1989. Paleobotanical evidence on the early radiation of non-magnoliid dicotyledons. Plant Systematics and Evolution 162:165–191.

CRANE, P.R., E.M. FRIIS AND K.R. PEDERSEN. 1986. Lower Cretaceous angiosperm flowers: fossil evidence on early radiation of dicotyledons. Science 232:852–854.

—1994. Paleobotanical evidence on the early radiation of magnoliid angiosperms. Plant Systematics and Evolution Supplement 8:51–72.

CRANE, P.R., K.R. PEDERSEN, E.M. FRIIS AND A.N. DRINNAN. 1993. Early Cretaceous (early to middle Albian) platanoid inflorescences associated with Sapindopsis leaves from the Potomac Group of eastern North America. Systematic Botany 18:328–344.

CRONQUIST, A. 1968. The Evolution and Classification of Flowering Plants. Boston: Houghton Mifflin. 396 pp.

DAHLGREN, R. AND K. BREMER. 1985. Major clades of angiosperms. Cladistics 1:349–368.

DILCHER, D.L. 1979. Early angiosperm reproduction: an introductory report. Review of Palaeobotany and Palynology 27:291–328.

DILCHER, D.L. AND P.W. BASSON. 1990. Mid-Cretaceous angiosperm leaves from a new fossil locality in Lebanon. Botanical Gazette 151:538–547.

DILCHER, D.L. AND P.R. CRANE. 1984. Archaeanthus: an early angiosperm from the Cenomanian of the Western Interior of North America. Annals of the Missouri Botanical Garden 71:351–383.

DONOGHUE, M.J. AND J.A. DOYLE. 1989. Phylogenetic analysis of angiosperms and the relationships of Hamamelidae. In: P.R. Crane and S. Blackmore, eds. Evolution, Systematics, and Fossil History of the Hamamelidae, Volume 1. Oxford: Clarendon Press. pp. 17–45.

DOYLE, J.A. 1969. Cretaceous angiosperm pollen of the Atlantic Coastal Plain and its evolutionary significance. Journal of the Arnold Arboretum 50:1–35.

—1973. Fossil evidence on early evolution of the monocotyledons. Quarterly Review of Biology 48:399–413.

—1992. Revised palynological correlations of the lower Potomac Group (USA) and the Cocobeach sequence of Gabon (Barremian-Aptian). Cretaceous Research 13:337–349.

—2001. Significance of molecular phylogenetic analyses for paleobotanical investigations on the origin of angiosperms. The Palaeobotanist 50:167–188.

—2007. Systematic value and evolution of leaf architecture across the angiosperms in light of molecular phylogenetic analyses. Courier Forschungsinstitut Senckenberg 258: 21–37.

—2009. Evolutionary significance of granular exine structure in the light of phylogenetic analyses. Review of Palaeobotany and Palynology 153:198–210.

—2012. Molecular and fossil evidence on the origin of angiosperms. Annual Review of Earth and Planetary Sciences 40:301–326.

—Recognizing angiosperm clades in the Early Cretaceous fossil record. Historical Biology. In press.

DOYLE, J.A., P. BIENS, A. DOERENKAMP AND S. JARDINÉ. 1977. Angiosperm pollen from the pre-Albian Cretaceous of Equatorial Africa. Bulletin des Centres de Recherches Exploration-Production Elf-Aquitaine 1:451–473.

DOYLE, J.A. AND M.J. DONOGHUE. 1993. Phylogenies and angiosperm diversification. Paleobiology 19:141–167.

DOYLE, J.A. AND P.K. ENDRESS. 2000. Morphological phylogenetic analysis of basal angiosperms: comparison and combination with molecular data. International Journal of Plant Sciences 161(Suppl):S121–S153.

—2010. Integrating Early Cretaceous fossils into the phylogeny of living angiosperms: Magnoliidae and eudicots. Journal of Systematics and Evolution 48:1–35.

—Integrating Early Cretaceous fossils into the phylogeny of living angiosperms: ANITA lines and relatives of Chloranthaceae. International Journal of Plant Sciences 175:555–600.

DOYLE, J.A., P.K. ENDRESS AND G.R. UPCHURCH JR. 2008. Early Cretaceous monocots: a phylogenetic evaluation. Acta Musei Nationalis Pragae, Series B, Historia Naturalis 64(2–4):59–87.

DOYLE, J.A. AND L.J. HICKEY. 1976. Pollen and leaves from the mid-Cretaceous Potomac Group and their bearing on early angiosperm evolution. In: C.B. Beck, ed. Origin and Early Evolution of Angiosperms. New York: Columbia University Press. pp. 139–206.

DOYLE, J.A. AND C.L. HOTTON. 1991. Diversification of early angiosperm pollen in a cladistic context. In: S. Blackmore and S.H. Barnes, eds. Pollen and Spores: Patterns of Diversification. Oxford: Clarendon Press. pp. 169–195.

DOYLE, J.A., C.L. HOTTON AND J.V. WARD. 1990. Early Cretaceous tetrads, zonasulculate pollen, and Winteraceae. I. Taxonomy, morphology, and ultrastructure. American Journal of Botany 77:1544–1557.

DOYLE, J.A. AND E.I. ROBBINS. 1977. Angiosperm pollen zonation of the continental Cretaceous of the Atlantic Coastal Plain and its application to deep wells in the Salisbury Embayment. Palynology 1:43–78.

DOYLE, J.A., M. VAN CAMPO AND B. LUGARDON. 1975. Observations on exine structure of *Eucommiidites* and Lower Cretaceous angiosperm pollen. Pollen et Spores 17:429–486.

DRINNAN, A.N., P.R. CRANE, E.M. FRIIS AND K.R. PEDERSEN. 1990. Lauraceous flowers from the Potomac Group (mid-Cretaceous) of eastern North America. Botanical Gazette 151:370–384.

—1991. Angiosperm flowers and tricolpate pollen of buxaceous affinity from the Potomac Group (mid-Cretaceous) of eastern North America. American Journal of Botany 78:153–176.

DUVALL, M.R., S. MATHEWS, N. MOHAMMAD AND T. RUSSELL. 2006. Placing the monocots: conflicting signal from trigenomic analyses. Aliso 22:79–90.

DUVALL, M.R., J.W. ROBINSON, J.G. MATTSON AND A. MOORE. 2008. Phylogenetic analyses of two mitochondrial metabolic genes sampled in parallel from angiosperms find fundamental interlocus incongruence. American Journal of Botany 95:871–884.

EKLUND, H., J.A. DOYLE AND P.S. HERENDEEN. 2004. Morphological phylogenetic analysis of living and fossil Chloranthaceae. International Journal of Plant Sciences 165:107–151.

ENDRESS, P.K. AND J.A. DOYLE. 2009. Reconstructing the ancestral angiosperm flower and its initial specializations. American Journal of Botany 96:22–66.

FEILD, T.S., N.C. ARENS, J.A. DOYLE, T.E. DAWSON AND M.J. DONOGHUE. 2004. Dark and disturbed: a new image of early angiosperm ecology. Paleobiology 30:82–107.

FEILD, T.S., T.J. BRODRIBB, A. IGLESIAS, D.S. CHATELET, A. BARESCH, G.R. UPCHURCH JR., B. GOMEZ, B.A.R. MOHR, C. COIFFARD, J. KVAČEK AND C. JARAMILLO. 2011. Fossil evidence for Cretaceous escalation in angiosperm leaf vein evolution. Proceedings of the National Academy of Sciences of the USA 108:8363–8366.

FEILD, T.S., D.S. CHATELET AND T.J. BRODRIBB. 2009. Ancestral xerophobia: a hypothesis on the whole plant ecophysiology of early angiosperms. Geobiology 7:237–264.

FEILD, T.S., G.R. UPCHURCH JR., D.S. CHATELET, T.J. BRODRIBB, K.C. GRUBBS, M.-S. SAMAIN AND S. WANKE. 2011. Fossil evidence for low gas exchange capacities for Early Cretaceous angiosperm leaves. Paleobiology 37:195–213.

FONTAINE, W.M. 1889. The Potomac or Younger Mesozoic Flora. Washington, DC: Government Printing Office. 377 pp. (Geological Survey Monographs 15.)

FRIIS, E.M., P.R. CRANE AND K.R. PEDERSEN. 1986. Floral evidence for Cretaceous chloranthoid angiosperms. Nature 320:163–164.

—1988. Reproductive structures of Cretaceous Platanaceae. Copenhagen: Det Kongelige Danske Videnskabernes Selskab. 55 pp. (Biologiske Skrifter 31.)

—1997. *Anacostia*, a new basal angiosperm from the Early Cretaceous of North America and Portugal with trichotomocolpate/monocolpate pollen. Grana 36:225–244.

—2011. Early Flowers and Angiosperm Evolution. Cambridge, UK: Cambridge University Press. 585 pp.

FRIIS, E.M., J.A. DOYLE, P.K. ENDRESS AND Q. LENG. 2003. *Archaefructus*—angiosperm precursor or specialized early angiosperm? Trends in Plant Science 8:369–373.

FRIIS, E.M., H. EKLUND, K.R. PEDERSEN AND P.R. CRANE. 1994. *Virginianthus calycanthoides* gen. et sp. nov.—a calycanthaceous flower from the Potomac Group (Early Cretaceous) of eastern North America. International Journal of Plant Sciences 155:772–785.

FRIIS, E.M. AND K.R. PEDERSEN. 2011. *Canrightia resinifera* gen. et sp. nov., a new extinct angiosperm with *Retimonocolpites*-type pollen from the Early Cretaceous of Portugal: missing link in the eumagnoliid tree? Grana 50:3–29.

FRIIS, E.M., K.R. PEDERSEN AND P.R. CRANE. 1994. Angiosperm floral structures from the Early Cretaceous of Portugal. Plant Systematics and Evolution Supplement 8:31–49.

—1995. *Appomattoxia ancistrophora* gen. et sp. nov., a new Early Cretaceous plant with similarities to *Circaeaster* and extant Magnoliidae. American Journal of Botany 82:933–943.

—1999. Early angiosperm diversification: the diversity of pollen associated with angiosperm reproductive structures in Early Cretaceous floras from Portugal. Annals of the Missouri Botanical Garden 86:259–296.

—2000. Fossil floral structures of a basal angiosperm with monocolpate, reticulate-acolumellate pollen from the Early Cretaceous of Portugal. Grana 39:226–239.

—2001. Fossil evidence of water lilies (Nymphaeales) in the Early Cretaceous. Nature 410:357–360.

—2006. Cretaceous angiosperm flowers: innovation and evolution in plant reproduction. Palaeogeography Palaeoclimatology Palaeoecology 232:251–293.

—2010. Diversity in obscurity: fossil flowers and the early history of angiosperms. Philosophical Transactions of the Royal Society B 365:369–382.

FRIIS, E.M., K.R. PEDERSEN, M. VON BALTHAZAR, G.W. GRIMM AND P.R. CRANE. 2009. *Monetianthus mirus* gen. et sp. nov., a nymphaealean flower from the Early Cretaceous of Portugal. International Journal of Plant Sciences 170:1086–1101.

GANDOLFO, M.A., K.C. NIXON AND W.L. CREPET. 2000. Monocotyledons: a review of their Early Cretaceous record. In: K.L. Wilson and D.A. Morrison, eds. Monocots: Systematics and Evolution. Collingwood, Australia: CSIRO Publishing. pp. 44–51.

GEETA, R., L.M. DÁVALOS, A. LEVY, L. BOHS, M. LAVIN, K. MUMMENHOFF, N. SINHA AND M.F. WOJCIECHOWSKI. 2012. Keeping it simple: flowering plants tend to retain, and revert to, simple leaves. New Phytologist 193:481–493.

GRÖCKE, D.R., G.A. LUDVIGSON, B.L. WITZKE, S.A. ROBINSON, R.M. JOECKEL, D.F. UFNAR AND R.L. RAVN. 2006. Recognizing the Albian-Cenomanian (OAE1d) sequence boundary

using plant carbon isotopes: Dakota Formation, Western Interior Basin, USA. Geology 34:193–196.

HEIMHOFER, U. AND P.A. HOCHULI. 2010. Early Cretaceous angiosperm pollen from a low-latitude succession (Araripe Basin, NE Brazil). Review of Palaeobotany and Palynology 161:105–126.

HEIMHOFER, U., P.A. HOCHULI, S. BURLA AND H. WEISSERT. 2007. New records of Early Cretaceous angiosperm pollen from Portuguese coastal deposits: implications for the timing of the early angiosperm radiation. Review of Palaeobotany and Palynology 144:39–76.

HERENDEEN, P.S. 1991. Lauraceous wood from the mid-Cretaceous Potomac group of eastern North America: *Paraphyllanthoxylon marylandense* sp. nov. Review of Palaeobotany and Palynology 69:277–290.

HERMSEN, E.J. AND J.R. HENDRICKS. 2008. W(h)ither fossils? Studying morphological character evolution in the age of molecular sequences. Annals of the Missouri Botanical Garden 95:72–100.

HICKEY, L.J. 1973. Classification of the architecture of dicotyledonous leaves. American Journal of Botany 60:17–33.

HICKEY, L.J. AND J.A. DOYLE. 1977. Early Cretaceous fossil evidence for angiosperm evolution. Botanical Review 43:1–104.

HICKEY, L.J. AND D.W. TAYLOR. 1996. Origin of the angiosperm flower. In: D.W. Taylor and L.J. Hickey, eds. Flowering Plant Origin, Evolution and Phylogeny. New York: Chapman and Hall. pp. 176–231.

HICKEY, L.J. AND J.A. WOLFE. 1975. The bases of angiosperm phylogeny: vegetative morphology. Annals of the Missouri Botanical Garden 62:538–589.

HOCHULI, P.A., U. HEIMHOFER AND H. WEISSERT. 2006. Timing of early angiosperm radiation: recalibrating the classical succession. Journal of the Geological Society, London 163:587–594.

HUGHES, N.F. 1994. The Enigma of Angiosperm Origins. Cambridge, UK: Cambridge University Press. 303 pp.

HUGHES, N.F. AND A.B. MCDOUGALL. 1990. Barremian-Aptian angiospermid pollen records from southern England. Review of Palaeobotany and Palynology 65:145–151.

JANSEN, R.K., Z. CAI, L.A. RAUBESON, H. DANIELL, C.W. DEPAMPHILIS, J. LEEBENS-MACK, K.F. MÜLLER, M. GUISINGER-BELLIAN, R.C. HABERLE, A.K. HANSEN, T.W. CHUMLEY, S.-B. LEE, R. PEERY, J.R. MCNEAL, J.V. KUEHL AND J.L. BOORE. 2007. Analysis of 81 genes from 64 plastid genomes resolves relationships in angiosperms and identifies genome-scale evolutionary patterns. Proceedings of the National Academy of Sciences of the USA 104(49):19369–19374.

JEFFERIES, R.P.S. 1979. The origin of chordates—a methodological essay. In: M.R. House, ed. The Origin of Major Invertebrate Groups. London: Academic Press. pp. 443–477.

JUD, N.A. AND L J. HICKEY. 2013. *Potomacapnos apeleutheron* gen. et sp. nov., a new Early Cretaceous angiosperm from the Potomac Group and its implications for the evolution of eudicot leaf architecture. American Journal of Botany 100:2437–2449.

KEMP, E.M. 1968. Probable angiosperm pollen from British Barremian to Albian strata. Palaeontology 11:421–434.

KLUGE, A.J. 1989. A concern for evidence and a phylogenetic hypothesis of relationships among Epicrates (Boidae, Serpentes). Systematic Zoology 38:7–25.

KRASSILOV, V.A. AND F. BACCHIA. 2000. Cenomanian florule of Nammoura, Lebanon. Cretaceous Research 21:785–799.

KRASSILOV, V.A. AND E. SCHRANK. 2011. New Albian macro- and palynoflora from the Negev (Israel) with description of a new gymnosperm morphotaxon. Cretaceous Research 32:13–29.

KVACEK, J., B. GOMEZ AND R. ZETTER. 2012. The early angiosperm *Pseudoasterophyllites cretaceus* from Albian-Cenomanian of Czech Republic and France revisited. Acta Palaeontologica Polonica 57:437–443.

LAING, J.F. 1975. Mid-Cretaceous angiosperm pollen from southern England and northern France. Palaeontology 18:775–808.

LEROY, J.-F. 1983. The origin of angiosperms: an unrecognized ancestral dicotyledon, *Hedyosmum* (Chloranthales), with a stroboloid flower is living today. Taxon 32:169–175.

LESQUEREUX, L. 1892. The Flora of the Dakota Group, a posthumous work. F. H. Knowlton, ed. Washington, DC: Government Printing Office. 256 pp., plates. (US Geological Survey Monograph 17.)

MASSONI, J., J.A. DOYLE AND H. SAUQUET. 2014. Fossil calibration of Magnoliidae, an ancient lineage of angiosperms. Palaeontologia Electronica 17.3.2FC; http://palaeo-electronica.org/

MEEUSE, A.D.J. 1972. Facts and fiction in floral morphology with special reference to the Polycarpicae. Acta Botanica Neerlandica 21:113–127, 235–252, 351–365.

MOHR, B.A.R. AND M.E.C. BERNARDES-DE-OLIVEIRA. 2004. *Endressinia brasiliana*, a magnolialean angiosperm from the Lower Cretaceous Crato Formation (Brazil). International Journal of Plant Sciences 165:1121–1133.

MOHR, B.A.R., M.E.C. BERNARDES-DE-OLIVEIRA AND D.W. TAYLOR. 2008. *Pluricarpellatia*, a nymphaealean angiosperm from the Lower Cretaceous of northern Gondwana (Crato Formation, Brazil). Taxon 57:1147–1158.

MOHR, B.A.R., C. COIFFARD AND M.E.C. BERNARDES-DE-OLIVEIRA. 2012. *Schenkeriphyllum glanduliferum*, a new magnolialean angiosperm from the Early Cretaceous of Northern Gondwana and its relationships to fossil and modern Magnoliales. Review of Palaeobotany and Palynology 189:57–72.

MOHR, B.A.R. AND E.M. FRIIS. 2000. Early angiosperms from the Lower Cretaceous Crato Formation (Brazil), a preliminary report. International Journal of Plant Sciences 161(Supp):S155–S167.

MOORE, M.J., C.D. BELL, P.S. SOLTIS AND D.E. SOLTIS. 2007. Using plastid genome-scale data to resolve enigmatic relationships among basal angiosperms. Proceedings of the National Academy of Sciences of the USA 104:19363–19368.

MOORE, M.J., N. HASSAN, M.A. GITZENDANNER, R.A. BRUENN, M. CROLEY, A. VANDEVENTER, J.W. HORN, A. DHINGRA, S.F. BROCKINGTON, M. LATVIS, J. RAMDIAL, R. ALEXANDRE, A. PIEDRAHITA, Z. XI, C.C. DAVIS, P.S. SOLTIS, AND D.E. SOLTIS. 2011. Phylogenetic analysis of the plastid inverted repeat for 244 species: insights into deeper-level angiosperm relationships from a long, slowly evolving sequence region. International Journal of Plant Sciences 172(4):541–558.

MULLER, J. 1970. Palynological evidence on early differentiation of angiosperms. Biological Reviews of the Cambridge Philosophical Society 45:417–450.

NIXON, K.C. 2008. Paleobotany, evidence, and molecular dating: an example from the Nymphaeales. Annals of the Missouri Botanical Garden 95:43–50.

NIXON, K.C., W.L. CREPET, D. STEVENSON AND E.M. FRIIS. 1994. A reevaluation of seed plant phylogeny. Annals of the Missouri Botanical Garden 81:484–533.

PACLTOVÁ, B. 1961. Zur Frage der Gattung Eucalyptus in der böhmischen Kreideformation. Preslia 33:113–129.

PARKINSON, C.L., K L. ADAMS AND J.D. PALMER. 1999. Multigene analyses identify the three earliest lineages of extant flowering plants. Current Biology 9:1485–1488.

PEDERSEN, K.R., P.R. CRANE, A.N. DRINNAN AND E.M. FRIIS. 1991. Fruits from the mid-Cretaceous of North America with pollen grains of the Clavatipollenites type. Grana 30:577–590.

PEDERSEN, K.R., E.M. FRIIS, P.R. CRANE AND A.N. DRINNAN. 1994. Reproductive structures of an extinct platanoid from the Early Cretaceous (latest Albian) of eastern North America. Review of Palaeobotany and Palynology 80:291–303.

PEDERSEN, K.R., M. VON BALTHAZAR, P.R. CRANE AND E.M. FRIIS. 2007. Early Cretaceous floral structures and in situ tricolpate-striate pollen: new early eudicots from Portugal. Grana 46:176–196.

PENNY, J.H.J. 1988a. Early Cretaceous acolumellate semitectate pollen from Egypt. Palaeontology 31:373–418.

—1988b. Early Cretaceous striate tricolpate pollen from the Borehole Mersa Matruh 1, North West Desert, Egypt. Journal of Micropalaeontology 7:201–215.

PIERCE, R.L. 1961. Lower Upper Cretaceous plant microfossils from Minnesota. Minnesota Geological Survey Bulletin 42:1–86.

QIU, Y.-L., J. LEE, F. BERNASCONI-QUADRONI, D.E. SOLTIS, P.S. SOLTIS, M. ZANIS, E.A. ZIMMER, Z. CHEN, V. SAVOLAINEN AND M.W. CHASE. 1999. The earliest angiosperms: evidence from mitochondrial, plastid and nuclear genomes. Nature 402:404–407.

QIU, Y.-L., L. LI, T.A. HENDRY, R. LI, D.W. TAYLOR, M.J. ISSA, A.J. RONEN, M.L. VEKARIA AND A.M. WHITE. 2006. Reconstructing the basal angiosperm phylogeny: evaluating information content of mitochondrial genes. Taxon 55:837–856.

QIU, Y.-L., L. LI, B. WANG, J.-Y. XUE, T.A. HENDRY, R.-Q. LI, J.W. BROWN, Y. LIU, G.T. HUDSON AND Z.-D. CHEN. 2010. Angiosperm phylogeny inferred from sequences of four mitochondrial genes. Journal of Systematics and Evolution 48:391–425.

REGALI, M.S.P. 1989. Tucanopollis, um gênero novo das angiospermas primitivas. Boletim de Geociências da Petrobrás 3:395–402.

REGALI, M.S.P. AND C.F. VIANA. 1989. Late Jurassic–Early Cretaceous in Brazilian Sedimentary Basins: Correlation with the International Standard Scale. Rio de Janeiro: Petrobrás. 95 pp.

RENNER, S.S. AND A.S. CHANDERBALI. 2000. What is the relationship among Hernandiaceae, Lauraceae, and Monimiaceae, and why is this question so difficult to answer? International Journal of Plant Sciences 161(Suppl): S109–S119.

RETALLACK, G. AND D.L. DILCHER. 1981. Early angiosperm reproduction: Prisca reynoldsii, gen. et sp. nov. from mid-Cretaceous coastal deposits in Kansas, U.S.A. Palaeontographica Abteilung B 179:103–137.

RICHEY, J. AND G.R. UPCHURCH. 2011. Inference of pCO$_2$ levels and climate in the Late Cretaceous from fossil Lauraceae. Botany 2011 Abstracts: 122–123.

ROHWER, J.G. AND B. RUDOLPH. 2005. Jumping genera: the phylogenetic positions of Cassytha, Hypodaphnis, and Neocinnamomum (Lauraceae) based on different analyses of trnK intron sequences. Annals of the Missouri Botanical Garden 92:153–178.

ROMANOV, M.S. AND D.L. DILCHER. 2013. Fruit structure in Magnoliaceae s.l. and Archaeanthus and their relationships. American Journal of Botany 100:1494–1508.

SAMYLINA, V.A. 1968. Early Cretaceous angiosperms of the Soviet Union based on leaf and fruit remains. Journal of the Linnean Society (Botany) 61:207–218.

SCHRANK, E. 2013. New taxa of winteraceous pollen from the Lower Cretaceous of Israel. Review of Palaeobotany and Palynology 195:19–25.

SENDER, L.M., U. VILLANUEVA-AMADOZ, D. PONS, J.B. DIEZ, J. FERRER, C. RUBIO, M. GARCÍA ÁVILA, R. SÁNCHEZ-PELLICER AND R. MORENO-DOMÍNGUEZ. 2013. Sapindopsis magnifolia Fontaine emend Berry, 1911 from the Albian of Teruel province (Spain): first occurrence of the genus Sapindopsis in western Eurasia. Paper presented at: 2nd International Conference of Agora Paleobotanica; 9–13 July 2013; Ariño, Teruel, Spain.

SOLTIS, D.E., P.S. SOLTIS, M.W. CHASE, M.E. MORT, D.C. ALBACH, M. ZANIS, V. SAVOLAINEN, W.H. HAHN, S.B. HOOT, M.F. FAY, M. AXTELL, S.M. SWENSEN, L.M. PRINCE, W.J. KRESS, K.C. NIXON AND J.S. FARRIS. 2000. Angiosperm phylogeny inferred from 18S rDNA, rbcL, and atpB sequences. Botanical Journal of the Linnean Society 133(4):381–461.

SOLTIS, D.E., P.S. SOLTIS, P.K. ENDRESS AND M.W. CHASE. 2005. Phylogeny and Evolution of Angiosperms. Sunderland, MA: Sinauer Associates. 370 pp.

SPRINGER, M.S., E.C. TEELING, O. MADSEN, M.J. STANHOPE AND W.W. DE JONG. 2001. Integrated fossil and molecular data reconstruct bat echolocation. Proceedings of the National Academy of Sciences of the USA 98: 6241–6246.

SUN, G., D.L. DILCHER, H. WANG AND Z. CHEN. 2011. A eudicot from the Early Cretaceous of China. Nature 471: 625–628.

SUN, G., D.L. DILCHER, S. ZHENG AND Z. ZHOU. 1998. In search of the first flower: a Jurassic angiosperm, Archaefructus, from northeast China. Science 282:1692–1695.

SUN, G., Q. JI, D.L. DILCHER, S. ZHENG, K.C. NIXON AND X. WANG. 2002. Archaefructaceae, a new basal angiosperm family. Science 296:899–904.

TAKHTAJAN, A.L. 1969. Flowering Plants: Origin and Dispersal. Edinburgh: Oliver and Boyd. 310 pp.

TAYLOR, D.W. 2008. Phylogenetic analysis of Cabombaceae and Nymphaeaceae based on vegetative and leaf architectural characters. Taxon 57:1082–1095.

UPCHURCH, G.R. JR. 1984a. Cuticle evolution in Early Cretaceous angiosperms from the Potomac Group of Virginia and Maryland. Annals of the Missouri Botanical Garden 71:522–550.

—1984b. Cuticular anatomy of angiosperm leaves from the Lower Cretaceous Potomac Group. I. Zone I leaves. American Journal of Botany 71:192–202.

UPCHURCH, G.R. JR., P.R. CRANE AND A.N. DRINNAN. 1994. The megaflora from the Quantico locality (upper Albian), Lower Cretaceous Potomac Group of Virginia. Martinsville, VA: Virginia Museum of Natural History. 57 pp. (Memoir 4.)

UPCHURCH, G.R. JR. AND D.L. DILCHER. 1990. Cenomanian angiosperm leaf megafossils, Dakota Formation, Rose Creek locality, Jefferson County, southeastern Nebraska. Washington, DC: Government Printing Office. 55 pp. (Geological Survey Bulletin 1915.)

UPCHURCH, G.R., JR. AND J.A. WOLFE. 1987. Mid-Cretaceous to Early Tertiary vegetation and climate: evidence from fossil leaves and woods. In: E.M. Friis, W.G. Chaloner and P.R. Crane, eds. The Origin of Angiosperms and Their Biological Consequences. Cambridge, UK: Cambridge University Press. pp. 75–105.

VAKHRAMEEV, V.A. 1952. Stratigrafiya i Iskopaemaya Flora Melovykh Otlozheniy Zapadnogo Kazakhstana (Regional'naya Stratigrafiya SSSR 1). Moscow: Akademiya Nauk SSSR. 340 pp.

VAN CAMPO, M. AND B. LUGARDON. 1973. Structure grenue infratectale de l'ectexine des pollens de quelques Gymnospermes et Angiospermes. Pollen et Spores 15:171–187.

VON BALTHAZAR M., P.R. CRANE, K.R. PEDERSEN AND E.M. FRIIS. 2011. New flowers of Laurales from the Early Cretaceous (Early to Middle Albian) of eastern North America. In: L. Wanntorp and L.P. Ronse De Craene, eds. Flowers on the Tree of Life. Cambridge, UK: Cambridge University Press. pp. 49–87.

VON BALTHAZAR, M., K.R. PEDERSEN, P.R. CRANE AND E.M. FRIIS. 2008. *Carpestella lacunata* gen. et sp. nov., a new basal angiosperm flower from the Early Cretaceous (Early to Middle Albian) of eastern North America. International Journal of Plant Sciences 169:890–898.

VON BALTHAZAR, M., K.R. PEDERSEN, P.R. CRANE, M. STAMPANONI AND E.M. FRIIS. 2007. *Potomacanthus lobatus* gen. et sp. nov., a new flower of probable Lauraceae from the Early Cretaceous (Early to Middle Albian) of eastern North America. American Journal of Botany 94:2041–2053.

WALKER, J.W. 1976. Evolutionary significance of the exine in the pollen of primitive angiosperms. In: I.K. Ferguson and J. Muller, eds. The Evolutionary Significance of the Exine. London: Academic Press. pp. 251–308.

WALKER, J.W., G.J. BRENNER AND A.G. WALKER. 1983. Winteraceous pollen in the Lower Cretaceous of Israel: early evidence of a magnolialean angiosperm family. Science 220:1273–1275.

WALKER, J.W. AND J.J. SKVARLA. 1975. Primitively columellaless pollen: a new concept in the evolutionary morphology of angiosperms. Science 187:445–447.

WALKER, J.W. AND A.G. WALKER. 1984. Ultrastructure of Lower Cretaceous angiosperm pollen and the origin and early evolution of flowering plants. Annals of the Missouri Botanical Garden 71:464–521.

WANG, H. AND D.L. DILCHER. 2006. Aquatic angiosperms from the Dakota Formation (Albian, Lower Cretaceous), Hoisington III locality, Kansas, USA. International Journal of Plant Sciences 167:385–401.

WARD, J.V., J.A. DOYLE AND C.L. HOTTON. 1989. Probable granular magnoliid angiosperm pollen from the Early Cretaceous. Pollen et Spores 33:101–120.

WARD, L.F. 1888. Evidence of the fossil plants as to the age of the Potomac Formation. American Journal of Science, 3rd Series 36:119–131.

WOLFE, J.A., J.A. DOYLE AND V.M. PAGE. 1975. The bases of angiosperm phylogeny: paleobotany. Annals of the Missouri Botanical Garden 62:801–824.

YOO, M.-J., C.D. BELL, P.S. SOLTIS AND D.E. SOLTIS. 2005. Divergence times and historical biogeography of Nymphaeales. Systematic Botany 30:693–704.

ZHANG, N., L. ZENG, H. SHAN AND H. MA. 2012. Highly conserved low-copy nuclear genes as effective markers for phylogenetic analyses in angiosperms. New Phytologist 195:923–937.