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EARLY CRETACEOUS MONOCOTS: A PHYLOGENETIC EVALUATION

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Abstract. Reports of Early Cretaceous monocots have been questioned as being based on invalid systematic criteria and not supported by phylogenetic analyses. Our analyses, using a morphological data set for basal angiosperms and assuming relationships among living taxa derived from morphological and molecular data, support a monocot affinity for *Liliacidites*, i.e., boat-shaped monosulcate pollen with graded sculpture that becomes finer at the ends of the grain. However, pollen with finer sculpture at the poles, originally assigned to *Liliacidites* but segregated as *Similipollis*, has been associated with floral parts called *Anacostia*, which our analysis places in Austrobaileyales. Pollen identified as "*Liliacidites*" *minutus* was produced by *Virginianthus*, near the base of Laurales. Masses of striate pollen called *Mayoa* share unique derived characters with some Araceae, but the coarsely reticulate pollen genus *Pennipollis* and associated floral remains, also compared with Alismatales, are more likely related to Chloranthaceae (with or without *Ceratophyllum*). Addition of *Acaciaephyllum*, a shoot bearing leaves with apically fused major venation, to a seed plant data set supports a relationship with monocots rather than superficially similar living and fossil Gnetales. Late Albian-early Cenomanian leaf fragments from Australia have derived features supportive of a relationship to monocots.

■ Monocots, Cretaceous, paleobotany, palynology, phylogeny, leaf architecture, *Liliacidites, Similipollis, Anacostia, Virginianthus, Mayoa, Pennipollis, Acaciaephyllum*

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Introduction

In the past two decades, studies of Early Cretaceous angiosperm fossils, particularly flower and fruit mesofossils, have confirmed earlier comparisons of pollen and leaves with the basal monosulcate grade of angiosperms – i.e., "magnoliid dicots" in the sense of Takhtajan (1980), including the clade named *Magnoliidae* by Cantino et al. (2007) and more basal groups – and with tricolpate taxa now recognized as basal eudicots (Crane et al. 1995, Doyle 2001, Friis et al. 2006). However, the Early Cretaceous record of monocots remains controversial. In 1973 one of us (Doyle 1973) reviewed possible monocot fossils in the context of the emerging record of early angiosperm pollen and leaves (Doyle 1969, Muller 1970, Doyle et al. 1975, Wolfe et al. 1975, Doyle and Hickey 1976, Hickey and Doyle 1977) and concluded that several were more likely monocots than "gymnosperms" or "magnoliid dicots." These included monosulcate pollen grains with "graded" reticulate sculpture, varying from coarse to fine on different parts of the grain, assigned by Doyle (1973) to the morphogenus *Retimonocolpites* Pierce, 1961 but later transferred to *Liliacidites* Couper, 1953 by Doyle and Hickey (1976) and Doyle and Robbins (1977), and a shoot bearing leaves with apically converging venation, described by Fontaine (1889) as *Acaciaephyllum*. Subsequently, Walker and Walker (1984) proposed that several additional exine characters could be used as evidence for monocot affinities, such as psilate muri, intermixed dimorphic lumina, and "frilled" muri. Based on these criteria, they argued that additional Early Cretaceous monosulcate pollen types represented monocots, including some without graded sculpture. However, all these reports were rejected by Gandolfo et al. (2000) and Crepet et al. (2004), who asserted that they were based on faulty systematic criteria for separation from non-angiospermous and "magnoliid" groups, and that the oldest reliable records of monocots were Late Cretaceous (Turonian) flowers assigned to Triuridaceae (Gandolfo et al. 1998, 2002). This critique has been accepted by some authors (e.g., Rudall and Buzgo 2002) but not by others (e.g., Friis et al. 2006).

Mesofossil studies have given conflicting evidence on this problem. Typical monocot flowers, with two whorls of

three tepals, two whorls of three stamens, and three carpels, which phylogenetic analyses have confirmed are probably ancestral in the group (Ronse De Craene et al. 2003, Zanis et al. 2003, Endress and Doyle 2009), have so far not been reported from rich assemblages of Early Cretaceous (Aptian and Albian) mesofossils (Crane et al. 1995, Friis et al. 2006). The closest approaches are two incompletely described types from Portugal (Friis et al. 2006), but one of these has three tepals and nine stamens and the other varies in numbers of parts. Furthermore, as noted by Gandolfo et al. (2000), mesofossil studies have refuted the monocot affinity of one pollen group that was assigned to monocots by Doyle (1973) and Walker and Walker (1984), namely monosulcate and trichotomosulcate grains that have graded sculpture but differ from typical *Liliacidites* in that the sculpture is finer at the proximal and distal poles rather than the ends of the grain (*Retimonocolpites* spp. D and E of Doyle 1973, *Liliacidites* sp. 2 of Walker and Walker 1984). Such grains were segregated as the new genus *Similipollis* by Góczán and Juhász (1984) and questioned as monocots by Doyle and Hotton (1991). Friis et al. (1997) associated *Similipollis* pollen with carpels and seeds from Portugal and the Potomac Group, named *Anacostia*, that have no evident monocot characters. Gandolfo et al. (2000) noted that another pollen type that Walker and Walker (1984) interpreted as monocotyledonous, identified as "*Liliacidites*" *minutus*, corresponds to pollen found in situ in *Virginianthus*, a flower that Friis et al. (1994) assigned to Calycanthaceae (Laurales).

Other new finds have been proposed as records of monocots, but some of these have been questioned. Friis et al. (2000) argued that stamens, a fragmentary male axis, and carpels associated with one of the most common Early Cretaceous angiosperm pollen types, variously identified as *Peromonolites*, *Liliacidites*, *Retimonocolpites*, and *Brenneripollis* (Brenner 1963, Singh 1971, Doyle et al. 1975, Walker and Walker 1984, Juhász and Góczán 1985) but assigned to the new genus *Pennipollis* by Friis et al. (2000), with an unusually coarse reticulum that tends to detach from the nexine, might represent monocots. This was based particularly on similarities to some members of the near-basal order Alismatales, such as extrorse anthers, the presence of granules rather than columellae below the reticulum, as in some Araceae (e.g., *Cyrtosperma*: Van Campo and Lugardon 1973, *Holochlamys* and *Spathiphyllum*: Hesse et al. 2000), and spikes of male flowers consisting of one stamen, as in other Araceae. Subsequently, Friis et al. (2004) described masses (anther contents) of inaperturate pollen with distinctive striate sculpture and a granular infratectal layer, named *Mayoa*, that they showed closely resembled pollen of *Holochlamys* and *Spathiphyllum* in the Araceae (Pothoideae, Monstereae). In a review of fossil Araceae, Hesse and Zetter (2007) accepted *Mayoa* as a record of Araceae. However, they questioned the araceous affinity of the *Pennipollis* plant, which they argued was more likely related to Chloranthaceae, one of the most prominent angiosperm groups in the Early Cretaceous fossil record (Doyle 1969, Muller 1981, Walker and Walker 1984, Crane et al. 1995, Eklund et al. 2004), as suggested by Doyle and Hotton (1991).

Molecular dating analyses by Bremer (2000) have introduced additional conflicts by indicating that ca. 14 major monocot lines extended back into the Early Cretaceous. However, it should be noted that similar analyses have given dates that conflict with better understood aspects of the Cretaceous fossil record. For example, Bremer et al. (2004) inferred that the eudicot clade Asteridae also began to diversify ca. 128 Mya in the mid-Early Cretaceous, slightly before any record of tricolpate pollen, which is ancestral for eudicots as a whole, and well before any clear record of the "core eudicot" clade (*Pentapetalae* of Cantino et al. 2007) that contains Asteridae. The first paleobotanical indications of *Pentapetalae* are more derived tricolporate pollen grains and pentamerous flowers near the Albian-Cenomanian boundary (Basinger and Dilcher 1984, Friis et al. 2006). Apparent conflicts between low molecular divergence among more basal eudicot lines and the Albian appearance of fossils apparently related to basal eudicot taxa such as *Platanus*, *Nelumbo*, and Buxaceae (Friis et al. 1988, Crane et al. 1993, Drinnan et al. 1991, Upchurch et al. 1994) have led to suggestions that evolution near the base of eudicots (and perhaps elsewhere) involved rapid changes in rates of molecular evolution that are inconsistent with existing molecular dating methods, including those that do not assume a molecular clock (Sanderson and Doyle 2001, Anderson et al. 2005).

In this paper, we reexamine reports of Early Cretaceous monocots in the light of recently accumulating data and improved methods. Since many previous discussions can be questioned because they did not use explicit phylogenetic methods (cf. Crepet et al. 2004), we have treated these fossils in a phylogenetic framework, using data sets of Doyle (2008) and Endress and Doyle (2009). Gandolfo et al. (2000) included *Liliacidites* and *Acaciaephyllum* in a cladistic analysis, which concluded that neither fossil was related to monocots. However, this analysis was not a valid test of the monocot hypothesis, because it used a data set (Donoghue and Doyle 1989) that treated monocots as a single taxon and did not include any apomorphies of monocots alone that might serve to link the fossils with monocots.

Material and Methods

Ages of fossils. Previously proposed ages for the fossils discussed here need some revision in light of recent palynological correlations with independently dated coastal sequences in Portugal (Heimhofer et al. 2005, 2007, Hochuli et al. 2006). The correlations of Heimhofer et al. (2005, 2007) indicate that the Buarcos, Vale de Agua, and Famalicão mesofossil localities, which contain *Anacostia* and the *Pennipollis* plant and were previously dated as Barremian-Aptian, are more likely early Albian. This is consistent with the low but appreciable number of floral types with tricolpate pollen in these floras (Von Balthazar et al. 2005). However, Friis et al. (2004, 2006) have argued that localities at Torres Vedras (the source of *Mayoa*) and Cateficá lie below a break in the sequence and may be significantly older (Barremian-Aptian).

In the Potomac Group, the correlations of Hochuli et al. (2006) indicate that the upper part of Zone I of Brenner (1963) is early Albian, a possibility recognized by Doyle

and Hickey (1976) and Doyle and Robbins (1977), rather than Aptian, as proposed by Brenner (1963) and Doyle (1992). This date is consistent with the occurrence in this interval of the first rare tricolpates and reticulate monosulcate pollen of the "*Clavatipollenites*" *rotundus* type (Kemp 1968; = *Liliacidites dividuus* of Brenner 1963, *Retimonocolpites* cf. *dividuus* of Doyle and Hickey 1976, aff. *Retimonocolpites dividuus* of Doyle and Robbins 1977), which appear in the early Albian of England (Kemp 1968), and the appearance of one of Brenner's (1963) most common Zone II index spores, *Apiculatisporis babsae*, at the base of the middle Albian in England (Kemp 1970). As argued by Hochuli et al. (2006), this interval is probably slightly older than the Portuguese early Albian localities, which may correlate with a missing interval in the Potomac sequence (or possibly the poorly known Subzone II-A of Brenner 1963). These conclusions are strengthened by the presence at Vale de Agua (Portugal) of flowers containing striate tricolpate pollen (Pedersen et al. 2007), a morphotype so far never found in upper Zone I.

These correlations do not affect previous views that the lower part of Zone I is Aptian, including the Trent's Reach locality with *Liliacidites* and the Dutch Gap locality with *Acaciaephyllum*. A Barremian age, suggested by Brenner (1963), appears to be excluded by the occurrence of *Pennipollis* (identified as *Retimonocolpites peroreticulatus*: Upchurch and Doyle 1981, Doyle 1992). It may be significant that no clear representatives of the *Liliacidites* pollen type were recognized by Hughes and collaborators during decades of work on the Hauterivian and Barremian of England (Hughes 1994). These correlations do not affect the previous dating of the lower Subzone II-B Bladensburg and Puddledock localities, the source of *Anacostia* and *Virginianthus*, as probably middle Albian (Doyle and Hickey 1976, Doyle and Robbins 1977, Doyle, unpublished observations).

Phylogenetic data sets. Our analyses of the phylogenetic position of fossils within angiosperms are based on a greatly expanded and revised version of a data set used in combined morphological and molecular analyses by Doyle and Endress (2000). Most of this data set, including all floral and pollen characters and those vegetative, fruit and seed, and embryological characters relevant to the position of *Ceratophyllum* and the Early Cretaceous fossil *Archaefructus*, was presented in Endress and Doyle (2009), with documentation of new characters and changes in the scoring of taxa. For the present analyses we used a further reduced matrix (Table 1, Appendix) consisting largely of characters that could be scored in *Liliacidites*, *Anacostia*, *Virginianthus*, and the *Pennipollis* plant, all of which concern floral, pollen, fruit, or seed morphology. This required the addition of four characters of seed anatomy that were omitted in Endress and Doyle (2009) because they were not informative with the taxon sampling in that study: structure of the mesotesta (60), presence or absence of a sarcotesta (61), endotesta structure (62), and tegmen structure (63). Data on these characters are primarily from Takhtajan (1985, 1988), with supplementary information on particular taxa from references cited in Endress and Doyle (2009). Although we deleted most micromorphological characters that cannot be determined in the four fossils considered here (e.g., types of stigmatic papillae, hairs, and nectaries), we retained other such characters that are known in other Early Cretaceous fossils or are of broader interest, such as perianth merism (11, treated as unknown in taxa with spiral perianth phyllotaxis) and carpel form (47, which is difficult to establish without anatomical or developmental information).

Pollen characters used in the data set are documented in Doyle (2005), with sources for the added monocot taxa listed in Endress and Doyle (2009). The most important change from Doyle (2005) is the addition of a character (39) that distinguishes uniform reticulate sculpture (state 0) from two graded types: one (state 1) with finer sculpture toward the ends of the grain, as in *Liliacidites*, and one (state 2) with finer sculpture toward the proximal and distal poles, as in *Similipollis* and some eudicots, represented in this data set by Trochodendraceae (*Tetracentron* and *Trochodendron*). We informally refer to states 1 and 2 as "liliaceous" and "rouseoid" (after the tricolpate fossil genus *Rousea*, for which this pattern is diagnostic: Srivastava 1969). Since presence or absence of perforations in the tectum was already expressed in another character (38), taxa with a continuous tectum were scored as unknown (for inapplicable). To evaluate potential problems with this procedure, we also analyzed the data set with tectal perforations and types of reticulate sculpture combined as one character, with continuous or microperforate tectum treated as a fourth state. The one change that we have made since Endress and Doyle (2009) is to rescore *Cabomba* and *Brasenia* as having endexine, based on Taylor and Osborn (2006) and Taylor et al. (2008).

To evaluate the hypothesis that *Acaciaephyllum* is a monocot rather than a non-angiospermous seed plant, we used a modified version of the seed plant data set of Doyle (2008), reduced to the seven characters that could be scored in *Acaciaephyllum* (Table 2, Appendix). The Doyle (2008) data set was itself based on Doyle (2006), with the addition of Hydatellaceae (a group of minute aquatics previously considered monocots but recently shown to be the sister group of Nymphaeales: Saarela et al. 2007) and modifications in the scoring of Gnetales, based particularly on evidence by Mundry and Stützel (2004) that the male "flowers" of *Ephedra* and *Welwitschia* are compound strobili with simple microsporophylls. To this data set we added *Acaciaephyllum* and an exemplar of monocots, scored the same for all characters except distichous phyllotaxis (Doyle 2008, character 27), which is highly variable within monocots and was scored as uncertain (0/1).

Addition of these taxa necessitated addition and redefinition of characters. In the leaf organization character (Doyle 2008, character 31), we combined the palmately veined state, found only in angiosperms, with the simple pinnate state. This was based on the assumption that simple pinnate and palmate leaves of angiosperms are more comparable to each other than they are to the pinnately compound, simple dichotomously veined, and simple one-veined leaves of other seed plants, in having both a simple blade and a median vein (midvein) with lateral veins on either side. Within angiosperms, we expressed the distinction between pinnate and palmate venation with a new character for secondary

(including lateral primary) venation, with pinnate redefined as uniformly pinnate, and added a third state for the monocot pattern, which is similar in having a median vein but different in having lower-angle, apically fused secondary veins. Outside angiosperms, this character was scored as unknown, except in *Gnetum*. In theory this procedure could introduce artifacts, because, assuming that uniformly pinnate venation was ancestral in angiosperms (Doyle and Endress 2000), it implies that all the lines between angiosperms and *Gnetum* had this state, as if in latent form. However, this may not be a problem in practice, since origin of apical vein fusion of the monocot type would represent a morphological step from any of the venation types found in non-angiospermous taxa, including *Welwitschia*.

We did not add another character shared by *Acaciaephyllum* and most monocots, presence of a sheathing leaf base, partly because it is less conclusively demonstrated in *Acaciaephyllum* than the venation characters, partly because it is uncertain whether or not it is comparable with the sheath formed by lateral fusion of the leaf bases in taxa with opposite phyllotaxis, such as Chloranthaceae and *Ephedra*. Similarly, we did not introduce a character for chevron-like cross-veins, which occurs in both Gnetales and monocots (although less strongly expressed in the latter) and would not help resolve whether *Acaciaephyllum* is related to one group or the other. The presence of higher-order cross-veins in general is specified by characters 6, reticulate laminar venation, and 7, two or more orders of laminar venation. The blade shape character of Doyle (2008, character 34), which distinguished elliptical or obovate from ovate or cordate and was scored only in angiosperms, was not included, because the more linear leaves of *Acaciaephyllum* and monocots are not readily assignable to either type and may be too closely correlated with the secondary venation character to merit recognition as a third state.

Analyses involving various modifications of the two data sets are described in the Results and Discussion.

Scoring of fossils. Our scoring of *Liliacidites* is based on two cohering Zone I (Aptian) grains, *Liliacidites* sp. A of Doyle and Hickey (1976), Doyle and Robbins (1977), and Hickey and Doyle (1977), identified as *Retimonocolpites* sp. C by Doyle (1973), from Trent's Reach, Virginia (Pl. 1, figs A, B); and two more widespread Zone II (Albian) pollen types: *Liliacidites* sp. F of Doyle and Robbins (1977), = *Retimonocolpites* sp. A of Doyle (1973) and *Liliacidites* sp. 1 of Walker and Walker (1984), with relatively fine sculpture (Pl. 1, figs C-F); and *Liliacidites* sp. D of Doyle and Hickey (1976), Doyle and Robbins (1977), and Hickey and Doyle (1977), which is close to *Retimonocolpites* sp. B of Doyle (1973), with coarser sculpture (Pl. 1, fig. G). All of these would be scored identically for the characters available. Scoring of nexine characters (44, lack of endexine; 45, thin nexine) is based on the TEM section of *Liliacidites* sp. 1 in Walker and Walker (1984, fig. 91; Pl. 1, fig. F). Sulcus structure is scored as unknown because the sulcus is deeply infolded in known specimens, and in the TEM section of Walker and Walker (1984) it is difficult to determine where the regular exine ends and the sulcus membrane begins.

Anacostia as treated here is a consensus of the four species described by Friis et al. (1997) based on isolated carpels (fruits) with enclosed seeds and adhering pollen from the Albian of Maryland (*A. marylandensis*), Virginia (*A. virginiensis*), and the Buarcos, Famalicão, and Vale de Agua localities in Portugal (*A. portugallica*, *A. teixeirae*). A floral axis with numerous immature spirally arranged carpels (Buarcos) was provisionally associated with *Anacostia* by Friis et al. (1997) and is used here to score the genus as having a pedicel (3), no hypanthium (6), an elongate receptacle (7), and more than one carpel (46). According to Friis et al. (1997), pollen diameter ranges from 12 to 18 μm, in our small state (2). However, similar dispersed pollen is usually considerably larger than 20 μm (Doyle 1973, Doyle and Robbins 1977, Walker and Walker 1984; Pl. 1, figs H, I), in our medium-sized state, suggesting that pollen may shrink in charcoalified fossils of this type, and we therefore scored pollen size (32) as uncertain (1/2). The pollen aperture varies from monosulcate to trichotomosulcate on the same specimen, but we have not represented this feature in our analysis, because none of the extant taxa are characterized by trichotomosulcate pollen and the character would be phylogenetically uninformative. The nexine appears to be thick in TEM sections of pollen of *A. marylandensis* (Friis et al. 1997, fig. 3), but this may be inaccurate because of obliqueness of the sections. Furthermore, a similar grain sectioned by Walker and Walker (1984, figs. 92-97) has a thinner nexine. For these reasons we have scored nexine thickness (45) as uncertain (1/2).

Virginianthus is based on a single flower (*V. calycanthoides*) described by Friis et al. (1994) from the Albian of Puddledock, Virginia. Friis et al. (1994) were tentative in interpreting the floral phyllotaxis as spiral, but a spiral arrangement is supported by the fact that their fig. 5A shows parastichy sets of different steepness and no orthostichies (cf. Staedler et al. 2007). The number of tepal series (character 12) is uncertain (two or more than two: 1/2), but there are three or four series of stamens (character 20). Friis et al. (1994) described pollen diameter as 18 μm, but because of the possibility of shrinkage we scored pollen size (32) as uncertain (1/2), as for *Anacostia*. Ovule number is not established but appears to be at least two, so we scored the character (51) as either two or more than two (1/2).

The *Pennipollis* plant is represented by isolated carpels (*Pennicarpus*), stamens (*Pennistemon*), associated pollen (*Pennipollis peroreticulatus*), and a fragment of a multistaminate axis described by Friis et al. (2000) from Vale de Agua and Buarcos. We assume that the male axis is a spike of ebracteate flowers consisting of one stamen, as favored by Friis et al. (2000), rather than a multistaminate flower. Both the associated pollen and similar dispersed grains (Doyle et al. 1975, Walker and Walker 1984) average less than 20 μm in diameter. Friis et al. (2000) tentatively interpreted the carpels as having a sessile stigma, but to be cautious we have scored the style character (48) as unknown.

Friis et al. (2000) described the stamens in the male spike as extrorse, but this was relative to the presumed inflorescence axis, whereas extrorse vs. introrse orientation is normally defined relative to the axis of the flower. With such radically reduced flowers, where the floral axis cannot be recognized, it is difficult to determine whether the single stamen was on the abaxial (anterior) or adaxial (posterior)

side of the flower relative to the inflorescence axis. In the case of the *Pennipollis* plant, an abaxial position (away from the inflorescence axis) would imply that the anther was extrorse, whereas an adaxial position would mean it was introrse. In the equally reduced male flowers of *Hedyosmum* and *Ascarina* (Chloranthaceae), the xylem in the vascular bundle of the stamen is oriented toward the inflorescence axis, indicating that the stamen is abaxial (and the anther latrorse to slightly introrse), as in the bisexual flowers of *Sarcandra* and *Chloranthus* in the same family (Endress 1987). Based on the positions of other floral organs, the stamen is also abaxial in the unistaminate flowers of Lacistemataceae and *Hippuris* (Plantaginaceae) (Endress 1999). However, it would be unwarranted to assume that single fertile parts can occur only on the abaxial side of a reduced flower. For example, in the female flowers of *Cercidiphyllum*, which consist of one carpel, the ventral suture faces away from the center of the inflorescence, indicating that the carpel is adaxial (posterior) relative to the inflorescence axis (Endress 1986, Yan et al. 2007).

Because Friis et al. (2000) did not observe a raphe, they interpreted ovule curvature as possibly orthotropous but cautioned that an anatropous curvature cannot be ruled out. However, the overall appearance of the seed suggests an orthotropous ovule with the chalaza (marked by a small dark spot) displaced toward one side of the base, as in *Amborella* (Endress and Igersheim 2000, Tobe et al. 2000) and Chloranthaceae (Endress 1987, Yamada et al. 2001). We initially interpreted a dark line running from the chalaza toward the micropyle (fig. 6H of Friis et al. 2000) as a raphal vascular bundle, implying that the ovule was anatropous, but it appears instead to be one of several longitudinal ridges in the seed coat (E. M. Friis, pers. comm., 2008), and we have therefore scored ovule curvature (54) as orthotropous. Friis et al. (2000) did not characterize the ovule direction. According to E. M. Friis (pers. comm., 2006), although the orientation of the fruit is difficult to establish, the micropylar end of the seed is directed toward what appears to be the stigmatic end of the fruit, implying that the ovule was basal and ascendent. However, we hesitate to accept this interpretation because of the asymmetry of the base of the ovule. To our knowledge, such asymmetry (sometimes questionably described as hemitropous or hemianatropous) is correlated with apical and pendent ovule attachment in a narrow locule, as in *Amborella* and Chloranthaceae, whereas taxa with basal and ascendent ovules (such as Piperaceae and some Araceae) have a symmetric ovule base (P. K. Endress, personal observations).

Because of these uncertainties, we scored stamen orientation (29) in the *Pennipollis* plant as either introrse or extrorse (0/2) and ovule direction (53) as unknown (?). However, to test the implications of the interpretations of Friis et al. (2000, E. M. Friis, pers. comm., 2006), we also analyzed the data set with stamen orientation scored as extrorse (2) and ovule direction as ascendent (2).

Friis et al. (2000) referred to *Pennipollis* as ranging from Barremian to Cenomanian or Turonian in the dispersed pollen record, but to our knowledge the oldest adequately dated records are early Aptian, confirming the use of *Pennipollis* as a guide fossil for Aptian and younger sediments (Penny 1988, Doyle 1992). Hughes et al. (1979) reported probable relatives of *Pennipollis* (as Retisulc-*dubdent*) with vestigial columellae as late Barremian, but these are from an interval at the top of the Wealden (Weald Clay = Vectis Formation) that is now dated as earliest Aptian based on magnetostratigraphy (Kerth and Hailwood 1988, Allen and Wimbledon 1991, Hughes 1994), and typical forms with no columellae appear to be slightly younger (still early Aptian).

Our interpretation of *Acaciaephyllum* (discussed in detail below) is based on observations of Doyle (1973), Doyle and Hickey (1976), and Hickey and Doyle (1977) on USNM specimen 3256, a stem with several attached leaves assigned by Fontaine (1889) to *A. spatulatum* (Pl. 1, figs J, K), and reexamination of the original photos of Doyle (1973).

Analyses. As in Endress and Doyle (2009), most analyses of the relationships of fossils were performed with the arrangement of Recent taxa held constant using two backbone constraint trees. One tree (D&E) is based primarily on the combined analysis of morphology, 18S nrDNA, *rbcL*, and *atpB* by Doyle and Endress (2000), but with changes in relationships and addition of taxa at positions based on more recent analyses, as explained in Endress and Doyle (2009). An important addition was *Ceratophyllum*, which was assumed to be the sister group of Chloranthaceae based on morphological data and some molecular analyses (Antonov et al. 2000, Duvall et al. 2006, Qiu et al. 2006). The other backbone tree (J/M) incorporates different relationships among major clades above the ANITA grade (*Mesangiospermae* of Cantino et al. 2007) found in analyses of nearly complete chloroplast genomes (Jansen et al. 2007, Moore et al. 2007), but with the same relationships within clades as in the D&E tree. Specifically, Chloranthaceae are sister to Magnoliidae, *Ceratophyllum* is sister to eudicots, and the two latter clades are linked with monocots. This procedure assumes that the addition of fossils would not substantially affect inferred relationships in a hypothetical analysis using combined morphological and molecular data. This assumption seems reasonable in light of the small proportion of characters preserved in fossils and their general congruence in fossil and extant taxa, but it should be tested in future studies.

Positions of fossils were evaluated by adding them individually to the extant data set and performing parsimony analyses with PAUP (Swofford 1990), with one of the two backbone constraint trees, random addition of taxa, and TBR branch swapping. The strength of the relationships obtained and the relative parsimony of alternative arrangements were evaluated by searching for trees one, two, three, and sometimes more steps longer than the most parsimonious trees and by moving taxa manually with MacClade (Maddison and Maddison 2003).

Analyses of the position of *Acaciaephyllum* used a backbone constraint tree corresponding to one of the most parsimonious trees found in the analysis of Doyle (2008) when the arrangement of living seed plant taxa was fixed to a tree based on molecular data, with monocots added as the sister group of the magnoliid clade (represented by Winteraceae, Asaroideae, and Saururaceae).

Character evolution and characters supporting the relationships obtained were evaluated using MacClade (Maddison and Maddison 2003). When characters are described as unequivocal synapomorphies of particular clades, this means that the position of the character state change is unequivocal, not necessarily that it occurs only once on the entire tree.

Results and Discussion

Liliacidites. In this discussion we restrict the name *Liliacidites* to boat-shaped reticulate monosulcate pollen with finer sculpture at the ends of the grain ("liliaceous" grading). These features are well developed in the type species *Liliacidites kaitangataensis* Couper (1953) from the Tertiary of New Zealand. This excludes a large number of other fossil pollen types with different sculpture that various authors have assigned to *Liliacidites*. Gandolfo et al. (2000) cited identifications of the latter sort as evidence against the monocot affinity of *Liliacidites*. Although this is a good reason not to use literature identifications of *Liliacidites* uncritically as evidence on the past distribution of monocots, it has no bearing on the affinities of *Liliacidites* in the restricted sense used here.

Since Doyle (1973), extensive surveys of pollen in basically monosulcate angiosperms other than monocots ("magnoliids" in the old paraphyletic sense) have only confirmed the impression that pollen of this type is restricted to monocots today (Walker 1976a, 1976b, Walker and Walker 1984, Sampson 2000, 2007: for a review of other recent studies, see Doyle 2005). Relatively few of these non-monocotyledonous taxa have reticulate sculpture: Austrobaileyales (Endress and Honegger 1980, Sampson and Endress 1984, Zavada 1984, Liu and Yang 1989, Gabarayeva and Grigorjeva 2003, Sampson 2007), Chloranthaceae (Walker 1976a, 1976b, Walker and Walker 1984, Eklund et al. 2004), *Saruma* (Aristolochiaceae) in the Piperales (Dickison 1992), Winteraceae and some members of the sister family Canellaceae in the Canellales (Wilson 1964, Praglowski 1979), Atherospermataceae in the Laurales (Sampson and Foreman 1988, Sampson 1996), and Myristicaceae (Walker and Walker 1979, 1980, 1981, 1983, Sauquet and Le Thomas 2003) and many Annonaceae (Walker 1971, Le Thomas 1980-1981) in the Magnoliales. These surveys show that none of these taxa have the classic liliaceous type of grading toward the ends of the grain; instead, the reticulum is usually uniform, except for occasional minor fining toward the sulcus margins. Most reticulate monosulcate grains in these groups also differ from *Liliacidites* and similar extant monocot pollen in being round rather than boat-shaped. Outside monocots, boat-shaped monosulcate angiosperm pollen is restricted to Nymphaeales and Magnoliales, and most such grains have a continuous or microperforate tectum, except for derived members of Annonaceae, namely the *Malmea* tribe of Walker (1971) or malmeoids plus *Annickia* of Doyle and Le Thomas (1996) and Doyle et al. (2000), in which the reticulum is uniform rather than graded.

Conversely, surveys of monocot pollen reaffirm the widespread occurrence of liliaceous grading. In Alismatales, it occurs in several near-basal lines, namely *Butomus* (Zavada 1983, Chanda et al. 1988), the near-basal genera *Lysichiton* and *Pothos* in the Araceae (Grayum 1992), and probably Tofieldiaceae, although this is uncertain because the pollen is disulculate and the areas of finer sculpture between the ends of the sulculi are smaller (Takahashi and Kawano 1989). In core monocots (*Petrosaviidae* of Cantino et al. 2007) it occurs in numerous Liliales and Asparagales, as well as Bromeliaceae in the Poales (Zavada 1983, Walker and Walker 1984). It is not clear whether such sculpture is ancestral or derived within monocots, because other monocots have a continuous or microperforate tectum, including the basal genus *Acorus* and taxa such as *Gymnostachys* and *Orontium* near the base of the Araceae (Grayum 1992), in which we scored the grading character as unknown (inapplicable). With the taxon sampling in Endress and Doyle (2009; Text-fig. 1), *Liliacidites*-type grading may have arisen either on the line leading to monocots or after the divergence of *Acorus* (with a continuous tectum).

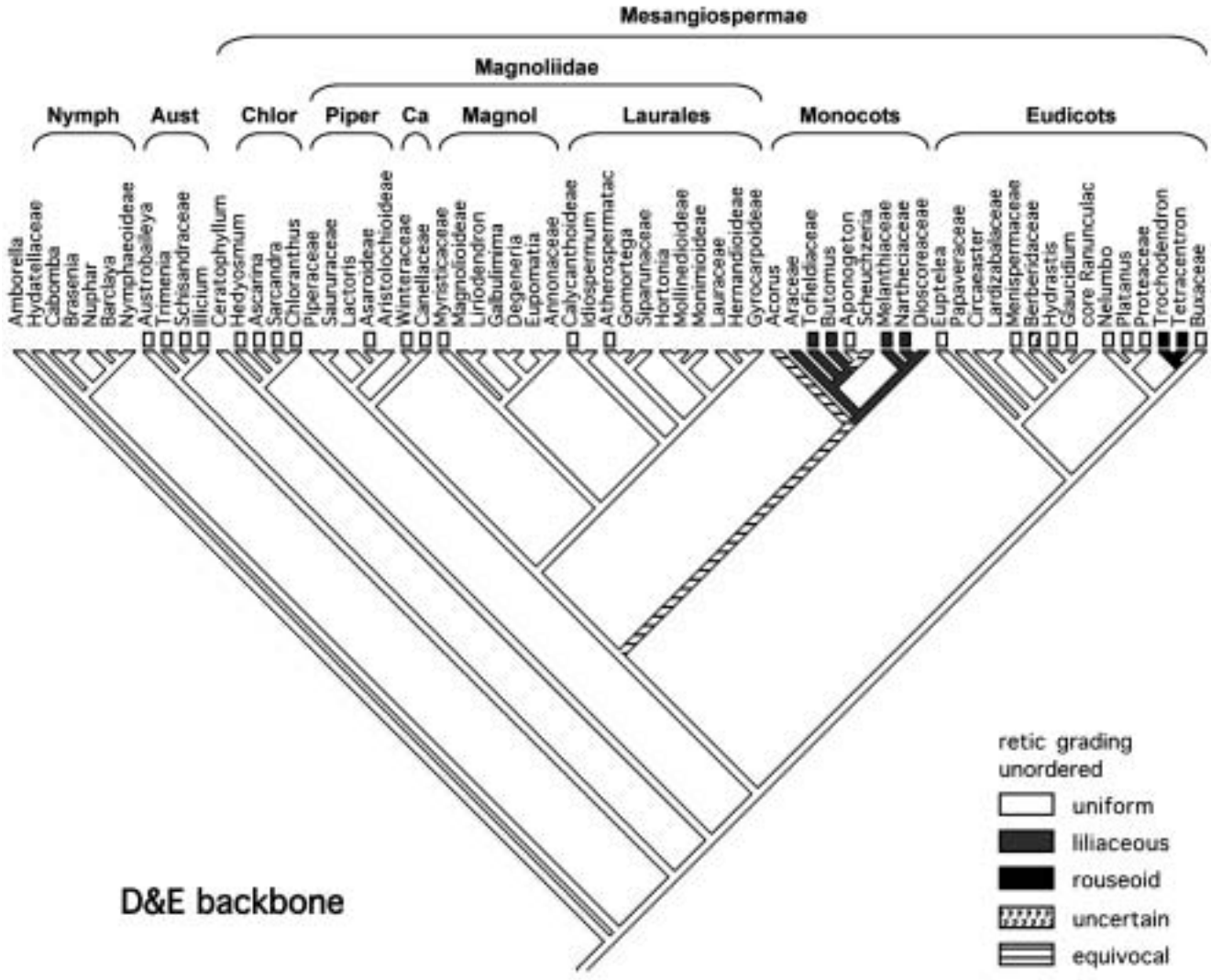
This assessment is confirmed when *Liliacidites* is added to the phylogenetic data set of Endress and Doyle (2009; Text-fig. 2). With the D&E backbone tree (Text-fig. 2A), *Liliacidites* is uniquely associated with monocots, either as the sister group of the whole clade or nested within it. The two unequivocal synapomorphies linking *Liliacidites* with monocots as a whole are boat-shaped pollen (33) and liliaceous grading of the reticulum (39). All positions within monocots are equally parsimonious. This includes positions sister to *Acorus* and Dioscoreaceae, which have a continuous tectum, and to *Aponogeton*, which has a uniform reticulum: the next most closely related lines have a graded reticulum that can still be homologous with that of *Liliacidites*. The most parsimonious positions not linked to monocots are two steps worse, on the line leading to the clade including monocots and Magnoliidae and on eight branches within Magnoliidae. One such position is nested within Magnoliales, immediately above the divergence of Myristicaceae, where *Liliacidites* is linked with the remaining Magnoliales by a shift to boat-shaped pollen but retains a perforate tectum (38), as in Myristicaceae.

With the J/M backbone tree (Text-fig. 2B), *Liliacidites* is nested within monocots, and positions sister to monocots as a whole and to *Acorus* are one step less parsimonious. This is a consequence of the fact that *Liliacidites* appears to lack an endexine (Walker and Walker 1984), like most monocots, but *Acorus* has a thin endexine (Rudall and Furness 1997). With the arrangement of other clades in the D&E tree (Text-fig. 2A), this does not affect the position of *Liliacidites*, because the state of the nexine stratification character (44) on the line leading to monocots is equivocal. However, with the J/M arrangement, it is most parsimonious to assume that pollen on the monocot stem lineage had an endexine. With this arrangement, an additional synapomorphy of *Liliacidites* and monocots as a whole is loss of sculpture on the aperture membrane (43, reversed in *Aponogeton* and Melanthiaceae); optimization of this character is ambiguous with the D&E backbone. As with the D&E backbone tree, the best positions for *Liliacidites* that are not linked to monocots are two steps less parsimonious, but there are only three such positions, all nested within Magnoliidae.

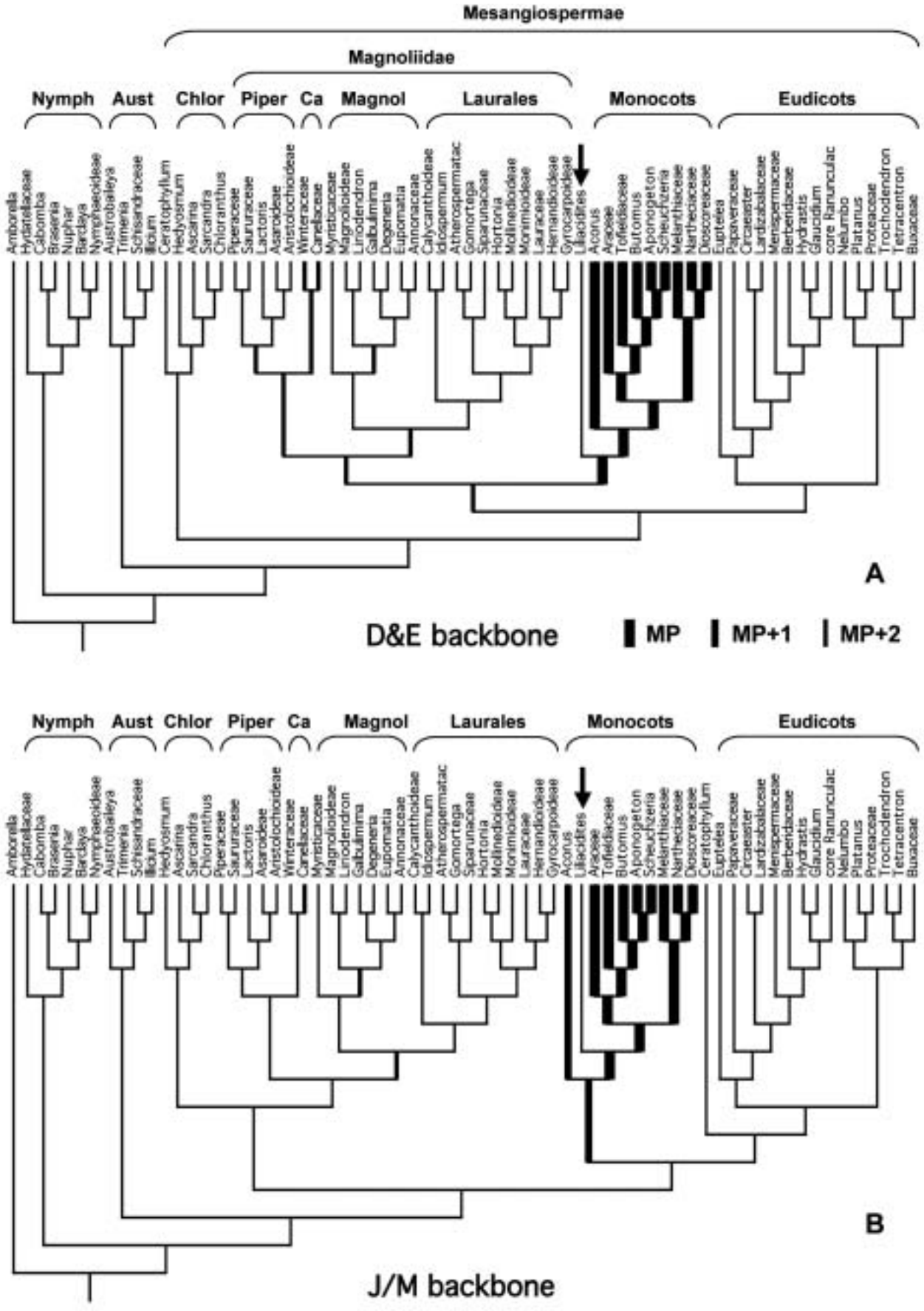
In these analyses, taxa with a continuous or microperforate tectum (character 38) were scored as unknown (inapplicable) for the sculpture grading character (39; see blanks below taxon names in Text-fig. 1). This procedure could conceivably introduce artifactual "long-distance" effects (Maddison 1994), since it assumes that the taxa scored as unknown have one or another state of the sculpture character, based on the neighboring groups. An alternative approach would be to combine the two characters and treat continuous tectum, uniform reticulum, and the two types of graded reticulum as four unordered states. When the two characters are combined in this manner, with taxa with a reduced tectum (e.g., Lauraceae) scored as unknown, the results are slightly different: *Liliacidites* is nested within monocots with both backbone trees, and positions sister to monocots as a whole and to *Acorus* are one step worse, as with the J/M backbone and the original character definitions (Text-fig. 2B). However, once again all trees in which *Liliacidites* is not associated with monocots are at least two steps longer.

These results suggest that the *Liliacidites* pollen group as circumscribed here is no less distinctively monocotyledonous than the presumed araceous pollen *Mayoa* (Friis et al. 2004), discussed below, which has been widely accepted as an Early Cretaceous record of monocots (Stockey 2006, Hesse and Zetter 2007, Crepet 2008, Stevens 2008). It is of course possible that the *Liliacidites* pollen type originated convergently in some non-monocotyledonous group, but until it is found in situ this hypothesis would be unwarranted.

In contrast, better information from associated plant parts and phylogenetic analyses indicate that two other pollen types once referred to *Liliacidites* are not monocots, as argued by Gandolfo et al. (2000) and Crepet et al. (2004).



Text-fig. 1. D&E tree of Endress and Doyle (2009), from the combined morphological and molecular analysis of Doyle and Endress (2000), with modifications based on more recent data, showing the inferred evolution of the reticulum grading character (39). Boxes under names of taxa indicate their character state; shading of branches indicates their reconstructed state based on parsimony optimization with MacClade (Maddison and Maddison 2003). Nymph = Nymphaeales, Aust = Austrobaileyales, Chlor = Chloranthaceae, Piper = Piperales, Ca = Canellales, Magnol = Magnoliales.

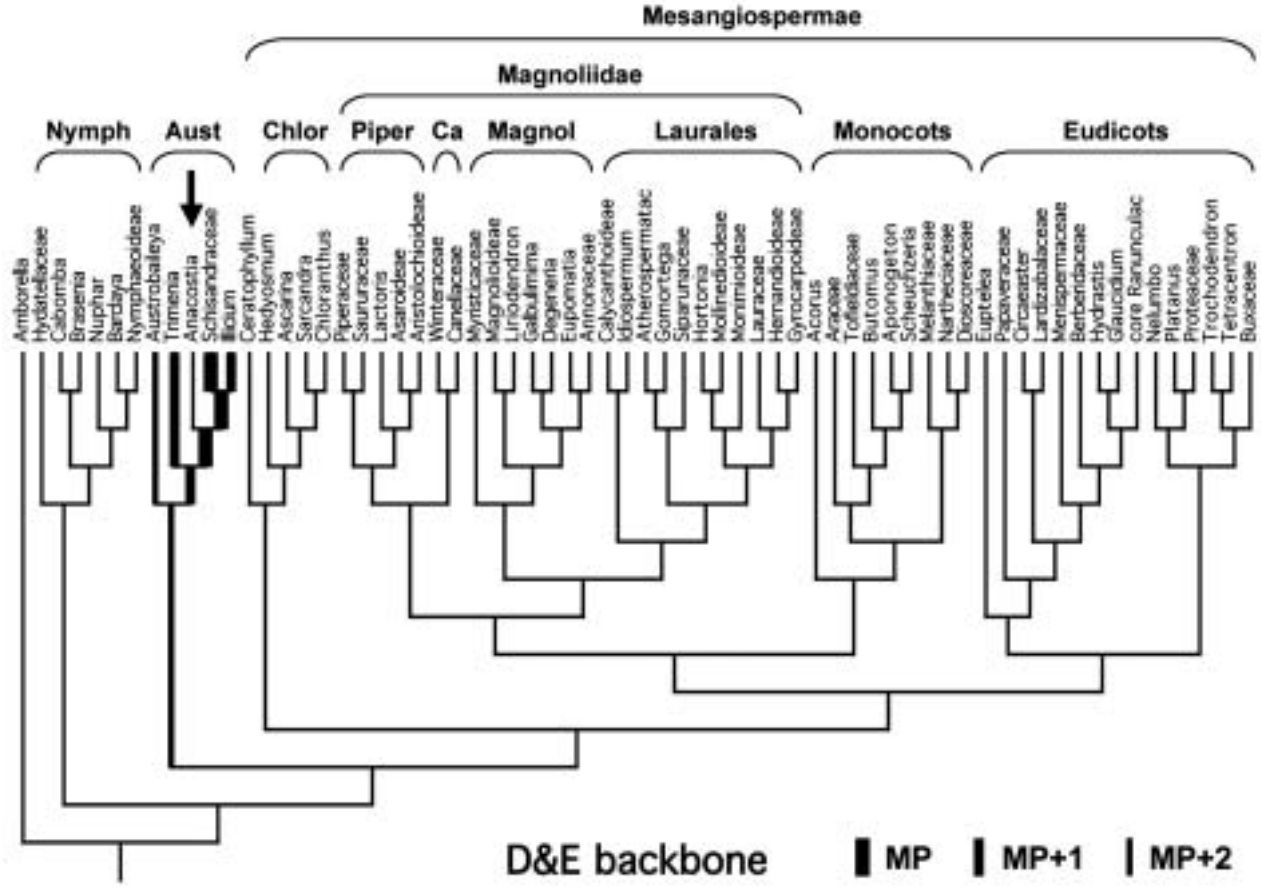


Text-fig. 2. Representative most parsimonious trees obtained after addition of *Liliacidites* to (A) the D&E tree (Text-fig. 1) and (B) the J/M tree, with relationships among major clades based on the plastid genome analyses of Jansen et al. (2007) and Moore et al. (2007). Thicker lines indicate all most parsimonious (MP), one step less parsimonious (MP+1), and two step less parsimonious (MP+2) positions for *Liliacidites*. Abbreviations as in Text-fig. 1.

***Similipollis* and *Anacostia*.** Doubts concerning the monocot affinities of *Similipollis* pollen, segregated from *Liliacidites* by Góczán and Juhász (1984), were raised by Doyle and Hotton (1991), based on the fact that its pattern of sculpture gradation, with finer sculpture toward the proximal and distal poles, had not been reported in monocots. Subsequently Harley (1997) recognized similar sculpture in some palms, with pronounced fining of the sculpture at the proximal pole in *Chamaedorea* and weaker differentiation in *Pseudophoenix* (Dransfield et al. 2008). Molecular phylogenetic analyses indicate that both genera are deeply nested within palms, in the arecoid and ceroxyloid clades respectively (Hahn 2002, Asmussen et al. 2006). Because the inferred relationships imply that this condition is derived within palms, it is not evidence for a monocot affinity unless the fossil in question is also nested within palms. This would be surprising in light of the fact that palm macrofossils and other distinctively palm-like pollen types are not known until well into the Late Cretaceous (Coniacian, possibly Turonian: Harley 2006) but common in the record from then onward.

Stronger evidence against a monocot interpretation came from the association of *Similipollis* pollen with Albian flowers, carpels, and seeds described by Friis et al. (1997) as *Anacostia*. *Anacostia* has no diagnostic features of either palms or monocots as a whole. Instead, Friis et al. (1997) noted that its seeds resemble those of Winteraceae and Canellaceae (now grouped as Canellales: APG II 2003) and *Illicium* and Schisandraceae (now placed in Austrobaileyales, in the basal ANITA grade) in having a palisade exotesta (a layer of thick-walled cells derived from the outer epidermis of the outer integument). In addition, the exotesta is underlain by a layer of sclerotic cells with digitate anticlinal walls, which corresponds closely to the sclerotic mesotesta (derived from the mesophyll of the outer integument) of *Illicium* (Oh et al. 2003) and other Austrobaileyales (Corner 1976, Takhtajan 1988), and there is a single basal ovule, as in *Illicium*.

These arguments are confirmed by our analyses, which nest *Anacostia* in the Austrobaileyales (Text-fig. 3), supported by sclerotic mesotesta (60), palisade exotesta (59), and basal (ascendent) ovule position (53), which appear to have arisen stepwise in that sequence in Austrobaileyales. Results using the two backbone trees are identical. *Anacostia* has two equally parsimonious positions: sister to both *Illicium* and Schisandraceae, based on the combination of ascendent ovule direction (53) and lack of the "syntricolpate" or hexacolpate pollen (34) of the two modern taxa; or sister to Schisandraceae, based on its elongate floral receptacle (7). All positions up to two steps less parsimonious are also nested in or sister to Austrobaileyales. Because *Similipollis* pollen varies between monosulcate and trichotomosulcate, it is interesting in suggesting that the peculiar "syntricolpate" aperture condition of *Illicium* and Schisandraceae was derived from trichotomosulcate (Liu and Yang 1989, Doyle et al. 1990), but it evidently has nothing to do with monocots.



Text-fig. 3. One of two most parsimonious trees obtained after addition of *Anacostia* (with *Similipollis* pollen) to the D&E tree. Relative parsimony of alternative positions of *Anacostia* is indicated as in Text-fig. 2; abbreviations as in Text-fig. 1.

"*Liliacidites*" *minutus* and *Virginianthus*. Another case of in situ pollen that was cited by Gandolfo et al. (2000) as evidence against the monocot affinity of *Liliacidites* concerns the Early Cretaceous (Albian) fossil flower *Virginianthus* (Friis et al. 1994), which has reticulate monosulcate pollen similar to dispersed grains that Walker and Walker (1984) called "*Liliacidites*" *minutus*. *Virginianthus* differs profoundly from the flowers of monocots in having numerous spiral tepals, laminar stamens, and inner staminodes at the edge of a deep floral cup (hypanthium) and free carpels within it, characters that Friis et al. (1997) used to assign it to Calycanthaceae in the magnoliid order Laurales. The case of *Virginianthus* is irrelevant to the affinities of *Liliacidites* as defined here, because "*Liliacidites*" *minutus* is round and shows no significant grading toward the ends, or even toward the sulcus margins. However, it is significant in casting doubt on other characters that Walker and Walker (1984) proposed as criteria for monocot affinities of this and other dispersed pollen types, particularly smooth muri and dimorphic lumina.

Our analyses associate *Virginianthus* with Laurales, but not necessarily with Calycanthaceae. With the D&E backbone (Text-fig. 4A), it has two most parsimonious positions: one as the sister group of Calycanthaceae (including the Australian genus *Idiospermum*), supported by an extended anther connective (26); the other sister to the remaining Laurales, supported by embedded pollen sacs (28). The contrast with the protruding pollen sacs of extant Calycanthaceae was noted by Friis et al. (1994). Presence of a hypanthium (6) links *Virginianthus* with Laurales as a whole, while spiral stamen phyllotaxis (18) and more than two series of stamens (20) associate it with Laurales plus Magnoliales. If *Virginianthus* is related to Calycanthaceae, the fact that its pollen is monosulcate, whereas pollen of Calycanthaceae is disulculate (34), implies that it is a stem relative of the family rather than nested within it. A sister-group relationship to Laurales as a whole is one step less parsimonious, as is a position sister to Chloranthaceae and *Ceratophyllum*; *Virginianthus* resembles the latter two taxa in having embedded pollen sacs (28) and Chloranthaceae in having a thick nexine (45; *Ceratophyllum* was scored as unknown for this character because its exine is so highly reduced). Two positions nested within Magnoliales, supported by extended anther connective (26), embedded pollen sacs (28), and H-valvate anther dehiscence (30), noted as a similarity to some Magnoliales by Friis et al. (1994), are two steps less parsimonious. H-valvate anther dehiscence occurs in one living member of the Calycanthaceae, *Sinocalycanthus* (Staedler et al. 2007), but this genus is nested within Calycanthoideae, and its dehiscence is therefore unlikely to be homologous with that in *Virginianthus*.

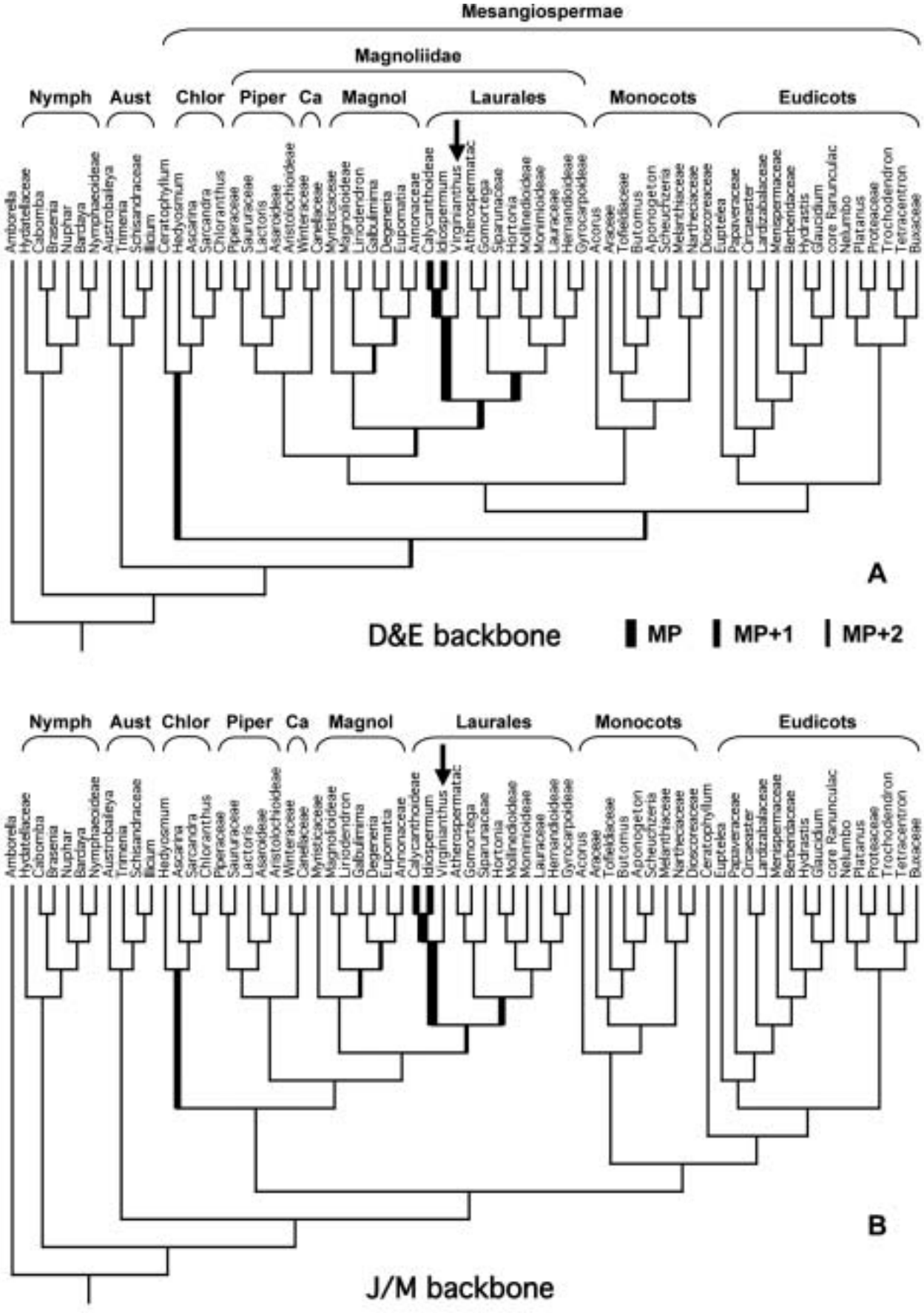
With the J/M backbone tree (Text-fig. 4B), there is only one most parsimonious position of *Virginianthus*, as the sister group of Calycanthaceae. This position is supported by extended anther connective (26) and two ovules per carpel (51). Optimization of the latter character is equivocal with the D&E backbone, but with the J/M backbone one ovule is ancestral in this part of the tree and two ovules are derived (Endress and Doyle 2009). Calycanthaceae differ from other Laurales in having two ovules (only one of which develops) rather than one (Staedler et al. 2009); ovule number in *Virginianthus* is uncertain but appears to be either two or more (Friis et al. 1997).

***Mayoa*.** The Early Cretaceous striate inaperturate pollen of *Mayoa* (Friis et al. 2004) resembles the related araceous genera *Holochlamys* and *Spathiphyllum* (Monsteroideae; Hesse et al. 2000) in close detail, particularly the unique pattern of tectal striations and the granular infratectum, both presumably derived in the context of angiosperms in general. Like Stockey (2006), Hesse and Zetter (2007), and Crepet (2008), we see no reason to question its most likely relationship with Araceae, although as is always the case with dispersed pollen grains the small number of available characters is reason for caution in ruling out convergence in some extinct line. Because of the close correspondence and the lack of similar clearly derived features in any other known extant group, a formal cladistic analysis would be superfluous, but of course confirmation of a relationship to Araceae by association with floral organs would be desirable.

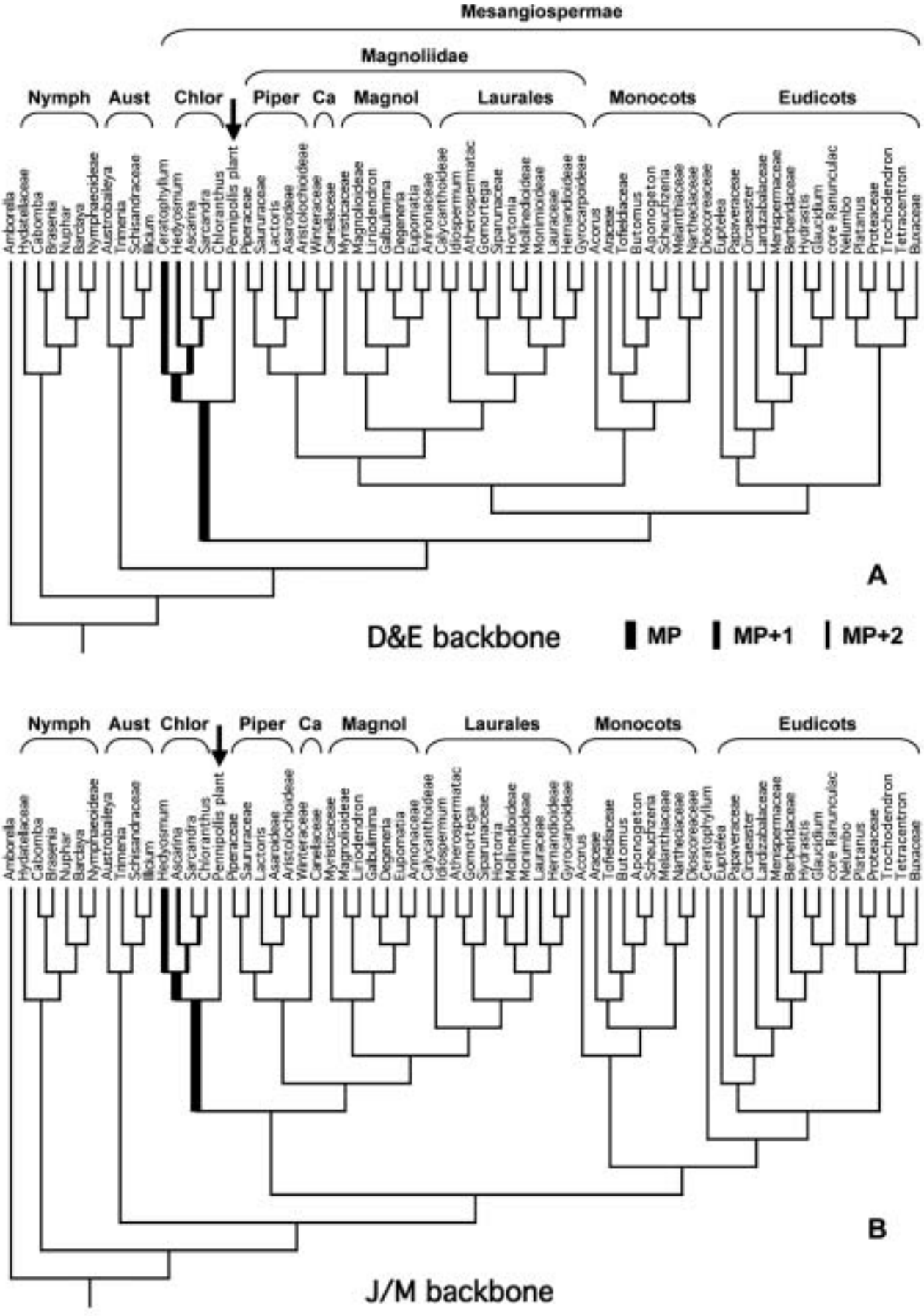
The *Pennipollis* plant. In contrast, our analyses do not support the comparison of *Pennipollis* and associated floral structures with Araceae and other Alismatales (Friis et al. 2000), based primarily on the extrorse anthers, coarse reticulum, supratectal spinules, granular infratectum, and unistaminate male flowers, in agreement with Wilde et al. (2005) and Hesse and Zetter (2007). Instead, our results link the *Pennipollis* plant with Chloranthaceae, the alternative suggested by Doyle and Hotton (1991), Wilde et al. (2005), and Hesse and Zetter (2007). With the D&E backbone (Text-fig. 5A), the *Pennipollis* plant is the sister group of *Ceratophyllum* and Chloranthaceae, which form a clade. It is linked with this clade by loss of bracts subtending the male flowers (4), single stamen (17), thick nexine (45), and orthotropous ovule (54), but it is more basal because of its protruding rather than embedded pollen sacs (28). Its next most parsimonious positions are sister to *Ceratophyllum* and to Chloranthaceae. Positions nested within Chloranthaceae are two or more steps worse. Its two most parsimonious positions that are not associated with the Chloranthaceae-*Ceratophyllum* line are four steps worse.

With the J/M backbone (Text-fig. 5B), where *Ceratophyllum* is linked with eudicots rather than Chloranthaceae, the *Pennipollis* plant is the sister group of Chloranthaceae, based on unisexual flowers (5), one stamen, supratectal spinules (41), thick nexine, and orthotropous ovule. A relationship with *Hedyosmum* is one step less parsimonious, while other positions nested in Chloranthaceae are two or more steps worse. Its most parsimonious position not associated with Chloranthaceae, which is three steps less parsimonious, is linked with *Ceratophyllum*, based on loss of floral subtending bracts, unisexual flowers, single stamen, and orthotropous ovule (all characters inferred to be convergences with Chloranthaceae).

In arguing for a chloranthaceous affinity of the *Pennipollis* plant, Hesse and Zetter (2007) cited similarities between *Pennipollis* and *Ascarina* pollen, which is also monosulcate and has a reticulum with supratectal spinules. However, these similarities do not support any special relationship of the fossil with *Ascarina*, because they are all pollen features that appear to be plesiomorphic for Chloranthaceae as a whole (Eklund et al. 2004).



Text-fig. 4. Most parsimonious trees obtained after addition of *Virginianthus* (with "*Liliacidites*" *minutus* pollen) to the (A) D&E and (B) J/M trees. Relative parsimony of alternative positions of *Virginianthus* is indicated as in Text-fig. 2; abbreviations as in Text-fig. 1.



Text-fig. 5. Most parsimonious trees obtained after addition of the *Pennipollis* plant to the (A) D&E and (B) J/M trees. Relative parsimony of alternative positions of the *Pennipollis* plant is indicated as in Text-fig. 2; abbreviations as in Text-fig. 1.

The most parsimonious position of the *Pennipollis* plant in Alismatales, with *Aponogeton*, is seven (J/M) or eight (D&E) steps less parsimonious. The fossil does share several potential synapomorphies with *Aponogeton* (loss of floral subtending bracts, granular infratectum, and supratectal spinules), but *Aponogeton* differs in having a thin nexine (Thanikaimoni 1985), like most monocots, and less reduced, multiparted flowers. Conversely, some other Alimatales have similarly simplified flowers, but they have more reduced pollen with no exine (e.g., Cymodoceaceae, Zosteraceae: Pettitt and Jermy 1975, Furness 2007).

A sister group relationship of the *Pennipollis* plant with Araceae is nine (J/M) or ten (D&E) steps less parsimonious. We have not tested a position of the fossil within Araceae, which would require extensive taxon sampling in that family. However, we suspect that an appropriate analysis would give similar results, because the pollen and floral similarities between the *Pennipollis* plant and Araceae occur in different living taxa. The taxa with the most similar pollen belong to the grade made up of all subfamilies other than the large clade Aroideae, all of which (except Lemnoideae and a few isolated species) have bisexual, multiparted flowers with a perianth and several stamens. Taxa with male flowers reduced to one stamen belong either to Lemnoideae, which have one or two male flowers per spadix and spinulose monoporate pollen (Hesse 2006a), or to Aroideae, in which the pollen is inaperturate and has a highly reduced exine consisting of only a spongy endexine (Mayo et al. 1997, Hesse 2006b). According to Mayo et al. (1997), unistaminate Aroideae belong to two major clades of Cabrera et al. (2008): Schismatoglottideae plus Cryptocoryneae (except *Schismatoglottis*) and the clade including Thomsonieae through Areae (several scattered lines including Zomicarpeae, *Arisarum*, *Colletogyne*, *Pinellia*, and *Typhonium*).

As noted by Friis et al. (2000), the closest approaches to *Pennipollis* pollen occur in *Anthurium* (Pothoideae) and *Cyrtosperma* (Lasioideae). *Anthurium* has a reticulate tectum that sometimes approaches that of *Pennipollis* in bearing supratectal spinules (e.g., *A. redolens*, *A. gracile*: Grayum 1992), although it has short columellae (Hesse et al. 1999). *Anthurium* pollen also differs from *Pennipollis* in being di- to polyporate rather than sulcate (Grayum 1992), but this is presumably an autapomorphy and would not preclude a relationship with the *Pennipollis* plant. The reticulate monosulcate pollen of *Cyrtosperma* lacks supratectal spinules, but it resembles *Pennipollis* and differs from most other monocots in having a granular infratectum and a thick nexine (Van Campo and Lugardon 1973, Hesse 2002), the latter also seen in the lasioid genus *Anaphyllopsis* (Hesse 2002). Unless the molecular relationships are drastically incorrect, assuming that the *Pennipollis* plant was related to either group would add steps by implying that its unisexual flowers, lack of perianth, and single stamen were convergences with derived Aroideae. Conversely, assuming that the *Pennipollis* plant was related to any of the unistaminate Aroideae would imply that its sulcus, well-developed exine, and reticulate ectexine were convergences with more basal taxa. To maintain that both its pollen and floral features were homologous with similar features in Araceae would require even more unparsimonious scenarios, such as retention of reticulate monosulcate pollen to a position within Aroideae and parallel losses of the sulcus and the ectexine in all more basal aroid lines.

Our results imply that the granular infratectal structure of *Pennipollis* is an autapomorphy derived from columellar structure. This is consistent with observations that the oldest (early Aptian) dispersed pollen of the *Pennipollis* group (Retisulc-*dubdent***)** had short remnants of columellae (Hughes et al. 1979, Penny 1988, Hughes 1994) – an interesting convergence with the situation in some Araceae and other monocots.

These results are somewhat uncertain because of problems concerning stamen, carpel, and ovule characters in the *Pennipollis* plant. As discussed in Materials and Methods, we scored stamen orientation (29) as either introrse or extrorse, ovule curvature (54) as orthotropous, and ovule direction (53) as unknown, but Friis et al. (2000) described the stamens as extrorse, and E. M. Friis (pers. comm., 2006) favored a basal, ascendent ovule position, based on her interpretation of the orientation of the carpel. To test whether our treatment of these characters affected the results, we analyzed the data set with stamen orientation scored as extrorse and ovule direction as ascendent. With both backbone trees, the most parsimonious positions of the fossil and all other placements up to two steps less parsimonious are identical to those found when stamen orientation was scored as uncertain and ovule direction as unknown (Textfig. 5). However, trees with the *Pennipollis* plant linked with *Aponogeton*, which has extrorse anthers and ascendent ovules, are one step less unparsimonious than they were with our preferred scorings of the fossil (e.g., seven steps less parsimonious with the D&E backbone, rather than eight), and the same is true of a sister-group relationship with Araceae.

A basal ovule in the *Pennipollis* plant would be more consistent with a position in Alismatales than with Chloranthaceae, but extrorse anthers would be equally consistent with either position. If the *Pennipollis* plant is assumed to have extrorse anthers and is linked with Chloranthaceae (with or without *Ceratophyllum*), its extrorse condition is a retention of the basic state in mesangiosperms, which shifts to latrorse in Chloranthaceae. A position of *Ceratophyllum* between the *Pennipollis* plant and Chloranthaceae would be consistent with the fact that the stamens of *Ceratophyllum* are extrorse relative to the inflorescence axis (Endress 1994), as in the *Pennipollis* plant and in contrast to Chloranthaceae, but their orientation relative to the floral axis of *Ceratophyllum* is unknown.

Although the *Pennipollis* plant is fragmentary and many aspects of its morphology are uncertain, the characters that are available, when considered in combination and in the context of current evidence on their phylogenetic distribution in Recent plants, do not support a monocot affinity. Existing data suggest rather that it was an extinct, autapomorphic member of the chloranthaceous line.

Other potential monocot flowers. Two flowers cited as possible monocots by Friis et al. (2006) are more promising, but not enough information is available for a phylogenetic analysis. One, which is epigynous, usually has six tepals and six stamens, but numbers of parts vary from five to seven. The other has three tepals, nine stamens, and three carpels, features that would be consistent with a relation-

ship to Piperales (cf. *Lactoris* and Aristolochiaceae). The lack of definite floral remains of monocots does not necessarily conflict with the pollen record, since the mesofossil floras that have been studied most intensively are Aptian and early Albian in age. During this interval pollen of the *Liliacidites* type is rare and sporadic; it does not become common until the middle and late Albian (Doyle and Robbins 1977).

***Acaciaephyllum*.** The best candidate for a record of vegetative parts of Early Cretaceous monocots is still *Acaciaephyllum*, from Fontaine's (1889) Fish Hut above Dutch Gap Canal locality in the Potomac Group of Virginia (lower Zone I, probably Aptian; Doyle 1973, Doyle and Hickey 1976, Hickey and Doyle 1977, Upchurch and Doyle 1981). Our interpretation is based on the most complete specimen (USNM 3256; Pl. 1, figs J, K), which consists of a curved and flattened stem that bears several narrow, oblanceolate leaves with decurrent, apparently sheathing bases. A confusing factor is the fact that Fontaine included several fragmentary specimens in *Acaciaephyllum* that show no obvious relationship to either monocots or the best specimen. Some of these specimens have a finely tuberculate surface similar to that of leaves of Mesozoic "seed ferns" variously assigned to *Thinnfeldia* and *Pachypteris*, which led Berry (1911) to include all specimens of *Acaciaephyllum* in *Thinnfeldia granulata* Fontaine. Some other leaves apparently represent the same species as the leafy shoot considered here, but in order to avoid further confusion, all our discussion refers to this best specimen.

Doyle (1973) proposed criteria for distinguishing leaves of monocots from those of non-angiospermous taxa, particularly linear leaves with "parallel" venation of the type found in cordaites, some conifers, and Mesozoic fossils of uncertain affinities such as *Pelourdea* and *Desmiophyllum* (e.g., Ash 1987, Van Konijnenburg-van Cittert 1992). These criteria included more than one order of longitudinal venation, presence of finer cross-veins connecting the major longitudinal veins, and convergence and fusion of the longitudinal veins toward the apex. This formulation now seems somewhat naïve, particularly because Doyle (1973) noted only parenthetically that *Welwitschia*, in the Gnetales, might represent an exception. In fact, *Welwitschia* resembles *Acaciaephyllum* in having roughly parallel major veins and finer cross-veins that form upward-directed chevrons (Rodin 1953, 1958, Martens 1971, Crane and Upchurch 1987; Pl. 2, figs A, E), more easily seen in the cotyledons than in the larger and thicker mature leaves. In 1973 the only recognized Early Cretaceous record of Gnetales consisted of striate (plicate) "ephedroid" pollen, but since then a growing number of macrofossils have been reported (Krassilov 1986, Crane and Upchurch 1987, Crane 1988, 1996, Rydin et al. 2003, 2004, 2006, Dilcher et al. 2005). Most notable is *Drewria* (Crane and Upchurch 1987), from the upper Zone I Drewrys Bluff locality in Virginia (early Albian?), which has opposite leaves with four (or possibly six) longitudinal veins connected by apically directed chevron-like cross-veins, a pattern that Crane and Upchurch (1987) compared with the venation in *Welwitschia* cotyledons. These similarities were cited by Gandolfo et al. (2000) as evidence that *Acaciaephyllum* might be a gnetophyte rather than a monocot. Similar venation occurs in cotyledons of *Welwitschia*-like seedlings from the late Aptian of Brazil (*Cratonia*: Rydin et al. 2003, *Welwitschiella*: Dilcher et al. 2005). However, chevron-like cross-veins are not evidence against a monocot relationship, since they also occur in some monocots, such as *Lilium* (Pl. 2, figs B, C, F) and *Chamaelirium* (Melanthiaceae, Liliales; Doyle 1973, fig. 3a). It may be significant that such chevrons make up most of the finer venation in *Welwitschia* and similar fossil forms but represent only part of the spectrum of variation in vein behavior in *Acaciaephyllum*, *Lilium*, and *Chamaelirium*.

Although the similarities in the fine venation of *Acaciaephyllum* and Gnetales weaken some of the supposed evidence for the monocot hypothesis, other characters conflict with the view that *Acaciaephyllum* was a gnetophyte. Most obvious, as noted by Crane and Upchurch (1987) and Doyle (2001), is the fact that all living and known fossil Gnetales have opposite or more rarely whorled phyllotaxis, including the Late Triassic genus *Dechellyia* (Ash 1972), a possible stem relative of Gnetales (Crane 1996, Doyle 1996). In contrast, *Acaciaephyllum* has alternate, apparently spiral phyllotaxis.

A second difference between leaves of *Acaciaephyllum* and Gnetales concerns the behavior of the venation toward the apex. In most leaves in the specimen of *Acaciaephyllum* (Pl. 1, figs J, K), the exact course of the major veins is uncertain, but on one side of one leaf (Pl. 1, fig. K, arrows) it is clear that the outermost vein first joins the next vein toward the inside, the resulting vein then joins the innermost secondary vein, and then this vein joins the midvein at the very apex. This successive apical fusion of major veins, which results in complete vein closure at the apex, is readily visible in many monocotyledons, such as *Lilium* (Pl. 2, fig. F, arrows), and was considered a basic feature of monocot leaves by Kaplan (1973). In contrast, as noted by Crane and Upchurch (1987), the major veins of *Welwitschia* and *Drewria* converge somewhat but become thinner, less straight, and hard to distinguish from the higher-order cross-veins (Pl. 2, figs A, E). Some veins in the apical region of *Welwitschia* end blindly at the margin (Pl. 2, figs A, E), in contrast to monocots. In cotyledons of *Cratonia*, Rydin et al. (2003) described the parallel veins as fusing successively with a higher-order marginal vein, which they contrasted with the situation in monocots; in *Welwitschiella*, Dilcher et al. (2005) reported that some major veins may join toward the apex but others end at the margin.

The situation in other living Gnetales is harder to compare. In the much simpler scale-like leaves of *Ephedra*, there are two or three veins that converge without meeting, although sometimes they are connected by transfusion tracheids (Foster 1972). The secondary veins of the angiosperm-like leaves of *Gnetum* form typical closed brochidodromous loops (Rodin 1966).

A third and perhaps more significant difference between *Acaciaephyllum* and parallel-veined Gnetales concerns presence or absence of a midvein and patterns of venational symmetry within the lamina. As illustrated by Rodin (1953, 1958), Martens (1971), Crane and Upchurch (1987), Rydin et al. (2003), Dilcher et al. (2005), and our figures (Pl. 2, figs A, E), the leaves and/or cotyledons of *Drewria*, *Welwitschia*, *Cratonia*, and *Welwitschiella* have a basically

dichotomous venation pattern, in which an even number of major veins are arranged symmetrically to either side of the midline of the blade. No median vein is present, and instead the longitudinal line of symmetry within the lamina is located in an area between major veins. The much smaller leaves of *Ephedra* are usually similar in having two veins; they sometimes have a third, median vein, but this does not always connect to the stele (Foster 1972). In contrast, as emphasized by Crane and Upchurch (1987), *Acaciaephyllum* has a definite median vein from which secondary veins depart at low angles on either side. In other words, its venation is basically pinnate rather than dichotomous. As illustrated and discussed by Arber (1925) and confirmed by our observations, this pattern is prevalent in monocot leaves of similar shape (e.g., *Lilium*: Pl. 2, figs B, C; *Chamaelirium*: Doyle 1973, fig. 3a). In some cases (e.g., *Veratrum*), a midvein is difficult to distinguish toward the leaf apex, but it is clearly present toward the base of the blade. In other monocots a single midvein is not readily identifiable, but several veins are crowded toward the midline of the leaf (cf. Kaplan 1973).

As noted by Gandolfo et al. (2000), some monocot leaves lack a recognizable midvein. Many (though not all) unifacial, equitant leaves are particularly obvious examples (Arber 1925), and Hagemann (1970, fig. 8b) illustrated the presence of apical vein fusion and absence of a midvein in the grass *Dactylis*. However**,** a distinct midvein is present in a variety of basal monocot taxa, including *Acorus* (which is unifacial: Kaplan 1970) and such Alismatales as Tofieldiacae, Alismataceae, *Butomus*, and Araceae (e.g., *Orontium*, *Lysichiton*, and *Symplocarpus*: Bogner et al. 2007, figs. 17-20, 25). Further, in monocots that have bifacial leaves with only one thickness of longitudinal veins, such as Pandanaceae (Pl. 2, fig. D) and certain grasses, there is usually a midrib and/or a longitudinal vein that defines the midline of the blade. Monocot leaves, therefore, have a constructional pattern that differs from the system seen in parallel-veined Gnetales, as well as in cordaites, ginkgophytes, and multiveined conifers, which differ further in having only one order of venation.

The contrast with *Gnetum* is less clearcut – as Gandolfo et al. (2000) noted, *Gnetum* differs from other Gnetales in having a median vein. This consists of several parallel bundles that diverge and dichotomize to form secondary veins, a pattern that Rodin (1967) interpreted as derived from a dichotomous system, but there is usually an odd number of bundles in the midvein, with a median vein from which secondaries diverge on either side near the apex.

Gandolfo et al. (2000) also argued that existing data were not sufficient to distinguish *Acaciaephyllum* (and many extant monocots) from palmately veined dicotyledonous angiosperms, such as Piperales. However, *Acaciaephyllum* differs from Piperales in that its secondary veins depart from the midvein at much lower angles and fuse successively toward the apex, rather than forming brochidodromous loops or thinning and losing their identity in a reticulum.

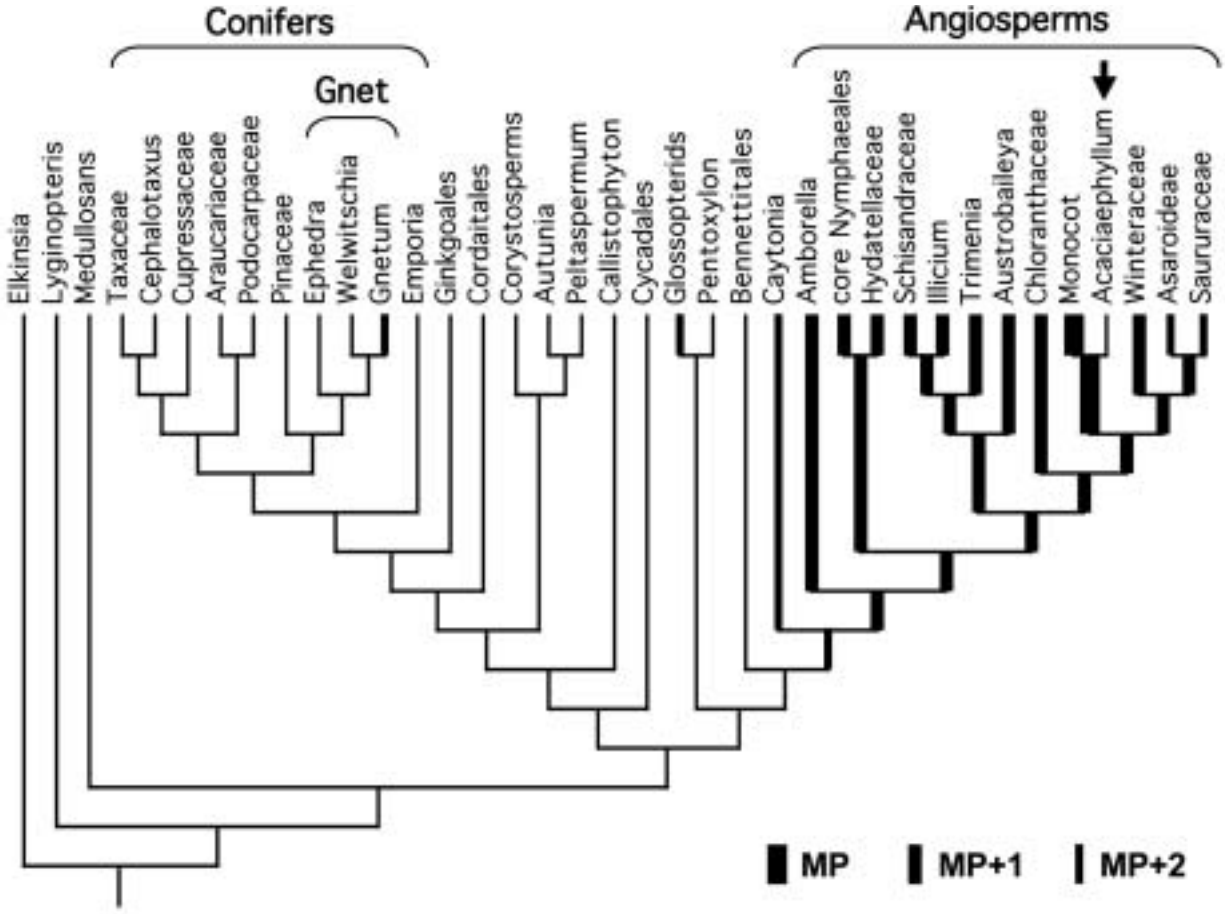
Despite the small number of characters involved, a formal phylogenetic analysis of the position of *Acaciaephyllum* may bring the issues into clearer focus. As described in Material and Methods, our analysis was based on the seed plant data set of Doyle (2008), with the addition of *Acaciaephyllum* and an exemplar of monocots (not included in Doyle 2008) and with changes in character definition designed to express the insights just discussed on venational similarities and differences among taxa. Because the combined morphological and molecular analysis of Doyle and Endress (2000) indicated that molecular data overrule conflicting morphological evidence on most relationships within angiosperms, we used a constraint tree that assumed relationships among Recent taxa derived from molecular data, as in Doyle (2008), with monocots specified as the sister group of the three magnoliids in the data set (Winteraceae, Saururaceae, and Aristolochiaceae-Asaroideae), and with fossil seed plant taxa arranged as in one of the most parsimonious trees found in the similar constrained analysis of Doyle (2008).

In this analysis, the most parsimonious position of *Acaciaephyllum* is linked with monocots (Text-fig. 6), supported by low-angle, apically fused secondary venation (character 4). All other positions in or sister to angiosperms, except nested in Piperales, are one step less parsimonious, because they require an extra step (convergence or origin plus reversal) in the secondary venation character. Linking *Acaciaephyllum* with either Asaroideae or Saururaceae (Piperales) adds two steps, because it requires separate origins of distichous phyllotaxis (1) in these taxa, or an origin plus a reversal. A position in Gnetales linked with *Welwitschia*, which has the superficially most similar leaves, is three steps less parsimonious, because of extra steps in phyllotaxis (reversal from opposite to alternate), leaf organization (3; simple pinnate organization must originate independently in *Acaciaephyllum* and *Gnetum* or be reversed in *Welwitschia*), and apically fused secondary venation (in this case a convergence with monocots). A position sister to *Gnetum* is only two steps less parsimonious, because *Gnetum* is more like *Acaciaephyllum* in having simple pinnate leaf organization. Three other positions among non-angiospermous seed plants have the same parsimony score: sister to glossopterids, *Caytonia*, and *Caytonia* plus angiosperms, all of which have reticulate rather than open laminar venation (6).

As noted in the discussion of the D&E and J/M constraint trees, the relative positions of monocots, Chloranthaceae, and Magnoliidae vary among molecular analyses. However, this uncertainty does not affect the present results, since a constrained analysis with the positions of monocots and Chloranthaceae reversed gave the same most parsimonious and one- and two-step less parsimonious relationships of *Acaciaephyllum*.

Another potential source of error, as noted in Materials and Methods, is scoring the secondary venation character (4) used in angiosperms and *Gnetum* as unknown (inapplicable) in other taxa. To test whether this treatment led to artifactual results, we rescored all taxa previously scored as unknown as having a fourth "other" state. This analysis too gave identical results concerning the position of *Acaciaephyllum*.

These results are far from compelling, given the small number of characters involved, but they show that interpreting *Acaciaephyllum* as a monocot agrees with all characters considered, whereas nesting it in Gnetales is less parsimonious in requiring a reversal from opposite to alternate phyllotaxis and independent origins of monocot-type secondary



Text-fig. 6. Most parsimonious tree obtained after addition of *Acaciaephyllum* to the data set of Doyle (2008), with modifications discussed in the text, and with relationships of other taxa fixed with a backbone constraint tree based on results of Doyle (2008). Relative parsimony of alternative positions of *Acaciaephyllum* is indicated as in Text-fig. 2. Gnet = Gnetales.

venation. Similarly, assuming that *Acaciaephyllum* represented a non-monocotyledonous line of angiosperms that converged with monocots in its major venation would add at least one step, implying that such a scenario cannot be ruled out but is currently unsupported. Of such scenarios, the most plausible may be that *Acaciaephyllum* belonged to a group with palmate acrodromous venation, as seen in some Piperales, and underwent reduction in the angle of secondary vein divergence to a lower-angle "parallel" pattern. However, a position nested within Piperales themselves would require an additional step in phyllotaxis. Clearly, more information on other characters of *Acaciaephyllum*, for example stomatal structure, is needed to establish its position, but the existing data suggest that its rejection as a monocot by Gandolfo et al. (2000) was premature.

If *Acaciaephyllum* is a monocot, more investigations on the distribution of leaf architectural characters in Recent monocots are needed to determine its most likely position within the group. Judging from our cursory observations, the possibility of a relationship to Liliales may deserve special consideration. Better understanding of the relations between venation and development of the blade from the upper and lower zones of the leaf primordium (Hagemann 1970, Kaplan 1973, Bharathan 1996, Rudall and Buzgo 2002, Doyle 2007) is also desirable.

Other vegetative macrofossil remains. Two other proposed Potomac monocots were considered doubtful by Doyle (1973) and still appear so. The leaf *Alismaphyllum victor-masoni* from the middle Albian Mount Vernon locality (Ward 1895, Berry 1911, Doyle and Hickey 1976) has a sagittate base and campylodromous primary venation suggestive of *Sagittaria* and other aquatic Alismatales with emergent leaves, but preservation is insufficient to show fine venation and the behavior of the major veins toward the apex. Spatulate leaves called *Plantaginopsis* from the early Albian Baltimore locality (Fontaine in Ward 1905, Berry 1911) have parallel venation superficially resembling that of monocots. However, the leaves are anomalous for monocots in having serrate margins with broadly convex teeth, some of which are apparently supplied by branches of the major veins. Extant serrate-margined monocot leaves, such as those of Pandanaceae and many grasses, differ in having non-vascularized spinose teeth (Pl. 2, fig. D). Furthermore, there is no evidence that the major veins in *Plantaginopsis* converged and fused toward the apex, as occurs in extant monocots.

Trifurcatia flabellata, described by Mohr and Rydin (2002) from the late Aptian or early Albian of Brazil, has fan-shaped to orbicular leaves attached to trifurcating stems, flabellate major venation, and finer longitudinal and

transverse veins between the major veins. The fine venation is monocot-like, but the major venation is not, because the major veins do not converge and join toward the apex, but rather end in teeth along the apical margin. There is no identifiable midvein; as noted above, presence of a midvein may be evidence for a relationship to monocots rather than gymnospermous seed plants, but its absence is less significant. Mohr and Rydin (2002) described the veins as fusing apically because they join a fine fimbrial vein that runs just inside the margin in the teeth, but this is quite different from the successive fusion of major veins in typical monocot leaves.

Dispersed cuticles and fragmentary leaves. The leaves of monocots and other angiosperms can be distinguished by their epidermal anatomy, which makes them potentially identifiable as small fragments (Upchurch 1995). Leaves of monocots are characterized by longitudinally aligned epidermal cells and longitudinally aligned stomata that are organized into distinct rows. Rows of cells with stomata alternate with rows of cells without stomata. The typical monocot stomatal complex has an epidermal cell lateral to each guard cell and an epidermal cell at each stomatal pole, such that each pair of guard cells is contacted by a total of four cells. The pattern of specialization in these cells varies such that the stomatal complex can have zero, two, four, or more subsidiary cells (e.g., Stebbins and Khush 1961, Dilcher 1974). When lateral subsidiary cells are present, they are derived from different rows of protodermal cells than the guard cells. Leaves of other angiosperms differ from those of monocots in having epidermal cells and guard cells that have no predominant orientation in regions between veins. Cells under major veins are longitudinally aligned on a local scale but have multiple orientations elsewhere on the leaf, reflecting differences in the pattern of venation. Other angiosperms also have a much more diverse array of subsidiary cell patterns than monocots and a variable number of cells that contact the guard cells. The longitudinal alignment of stomata and of other epidermal cells and the alternating rows of cells with and without stomata are probable monocot synapomorphies, based on their common occurrence in monocots, their presence in the basal monocot genus *Acorus* (Keating 2003), and their absence in other basal angiosperm lineages.

There are several partial exceptions to these generalizations, but these do not rule out the use of epidermal characters for recognition of monocots. Among other angiosperms, the most notable exception is the aligned diacytic stomata of Caryophyllaceae (e.g., Rohweder et al. 1971), but these have apical rather than lateral subsidiary cells and do not alternate with rows of cells that lack stomata. Among monocots, a partial exception is the presence of multiple stomatal orientations in taxa with broad leaves and variable vein orientations, such as Dioscoreaceae (Ayensu 1969) and certain Araceae (Keating 2003). Together, these exceptions mean that dispersed cuticles from monocot leaves with "reticulate" venation might be confused with those of other angiosperms, but dispersed cuticle from narrow dicotyledonous leaves with "parallel" venation should be distinguishable from that of monocots.

Most gymnospermous seed plants resemble monocots in having longitudinally aligned epidermal cells. However, monocots can be distinguished from gymnosperms by their possession of derived features of guard cell structure that are shared with other angiosperms. In angiosperms, the stomatal poles are level with the stomatal pore, rather than raised as in most gymnosperms (Harris 1932), and a prominent vestibule is produced by cuticular thickenings termed outer stomatal ledges. The only non-angiospermous group that could be confused with angiosperms is Caytoniales, which have angiosperm-like stomata with level guard cell poles and stomatal ledges (Barbacka & Bóka 2000); the presence of level guard cell poles is a synapomorphy of Caytoniales and angiosperms in some phylogenetic analyses (e.g. Doyle 1996, 2006, 2008, Hilton and Bateman 2006). However, stomata of Caytoniales differ from those of angiosperms in having a much smaller vestibule formed by the outer stomatal ledges and a much larger vestibule formed by the inner stomatal ledges. Within Gnetales, *Welwitschia* and *Gnetum* resemble many angiosperms in possessing paracytic stomata, but they have typically gymnospermous guard cell structure and lack prominent outer stomatal ledges.

Studies of angiosperm cuticles from Zone I of the Potomac Group revealed taxa with some monocot features (Upchurch 1984a, b), but critical examination of these remains and additional dispersed cuticles provides no fully definitive evidence for monocots. The most monocot-like cuticle illustrated in earlier studies is Dispersed Cuticle Type #5 from the Aptian Dutch Gap Canal locality (Upchurch 1984b, fig. 29), which has longitudinally aligned epidermal cells with striate papillae and infrequent longitudinally aligned stomata with a tendency for paracytic subsidiary cell arrangement. However, distinct rows of stomata are absent, and observation of additional cuticle fragments indicates that the illustrated specimen probably represents a large vein from the leaf of a basal angiosperm. One newly discovered fragment of dispersed angiosperm cuticle from Dutch Gap does have the dense, longitudinally oriented stomata characteristic of monocots, but the cuticle is too thin to preserve other features needed to corroborate a monocot affinity.

Convincing monocotyledonous leaf structure is present in fragmentary remains from the latest Albian to earliest Cenomanian Winton Formation of the Eromanga Basin, central Queensland, Australia (Pole 1999). Monocot 1 consists of strap-shaped leaf fragments with entire margins. No midvein is visible, but two or three thicknesses of longitudinal parallel veins are present. Cross-veins are all of the same thickness and consist of obliquely oriented veins that interconnect adjacent parallel veins. Although more complete specimens would be desirable, sufficient venation is preserved to show that Monocot 1 differs from parallel-veined Gnetales in having two or three thicknesses of longitudinal parallel veins, rather than one, and simple cross-veins that are obliquely oriented rather than chevron-shaped.

Epidermal anatomy in Monocot 1 is also distinctly monocotyledonous. The guard cells have poles that are level with the stomatal pore and outer stomatal ledges that form a large and prominent vestibule. Rows of cells with stomata alternate with rows of cells without stomata. The stomatal complexes are longitudinally aligned and are described as para-tetracytic. Each stomatal complex has a pair of lat-

eral subsidiary cells and a pair of polar epidermal cells. The lateral subsidiary cells differ from other epidermal cells in their size, shape, and orientation of the anticlinal walls. Polar cells can resemble ordinary epidermal cells or be significantly shorter. Pole (1999) compared the stomatal anatomy of Monocot 1 with that of Arecales, although he noted that it is more variable than stomatal anatomy in the extant taxa described by Tomlinson (1974). The comparisons with Arecales need to be reassessed in light of the current more restricted concept of this group. However, the high variability is consistent with Upchurch's (1984a) hypothesis that the ancestral pattern of subsidiary cell arrangement in angiosperms was characterized by high variability on a single leaf, and that subsequent evolution involved progressive reduction in variability of the stomatal complex through reduction in developmental variation.

Conclusions

These analyses indicate that several fossil taxa originally interpreted as monocots but subsequently questioned belong to other lines that underwent intriguing convergences with monocots in certain plant parts (*Similipollis* pollen associated with *Anacostia*; the *Pennipollis* plant; "*Liliacidites*" *minutus* pollen associated with *Virginianthus*). However, they confirm that other Early Cretaceous fossils, particularly typical *Liliacidites* pollen and *Acaciaephyllum*, are more likely to be monocots than members of any other plant group. This survey underlines the desirability of association of typical *Liliacidites* pollen with floral stuctures, better evidence on the morphology and epidermal anatomy of possible monocot macrofossils, and more extensive phylogenetic surveys of venational characters in living monocots.

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Appendix

Table 1. Data matrix of basal angiosperms for analyses of positions of the *Pennipollis* plant, *Anacostia*, *Virginianthus*, and *Liliacidites*, reduced and modified from Endress and Doyle (2009).

A = 0/1, B = 0/2, C = 0/4, D = 1/2, E = 0/1/2.

	1	2	3	4	5	6
	12345678901234567890123456789012345678901234567890123456					
Amborella	1000110000?2001000?2000100000001107020?0101110000000010010000000					
Cabomba	2000000001012?10010010?2010020000000020?1A0111001002100017010000010					
Brasenia	?00?000001012?0001021002010010000000020?0001110010011000170100000010					
Nuphar	2000000001021100012210000210010000001 0?0111110000221000000100000010					
Barclaya	200?0200012210000122?0000010000112??20?000???0100221?10000???00010					
Nymphaeoideae	2002020101221000012 2?0010010000012??10?000?1200002210000001000001 0					
Hydatellaceae	21021?0?1??????01??????201?0100200002 0?010?01100??0?0001?01??00010					
Austrobaileya	0000000000?2100000?2001100000001100021000011100100201000000110010 0					
Trimenia	10A0A00?00?2000000?D00020000D00112??2100101111000?0000000011000000					
Illicium	0000000100?2100000?D000101000001 13??2100001110110000 2001?111000000					
Schisandraceae	B000101000?2100000?E01010100B00113??2100001110000010100000110000 00					
Hedyosmum	2111120?0100A?001??????00E10100110012100101021010?000101?000000000					
Ascarina	20101?0?1??????0A??000?000101001100021001010210000?000100000??12000					
Sarcandra	20100?0?1??????01??????10110110111???2100001021000?000100000001 0000					
Chloranthus	20100?0?1??????0???????A000001011???21000011D1000?000100000001B000					
Liriodendron	0000001001021001 00?2000001102000000020?000021021101010017001020000					
Magnolioideae	000000100102D00100?200000A100A000000D0?000021021 00D01001?100120000					
Degeneria	0000000000?2101000?2001000102100000000?0000?01200?2010000100120100					
Galbulimima	00000010???????100?2001000102101100000?0000?002010001000100010 0?00					
Eupomatia	000001001??????100?2011A00100101 12??00?0000210?01?2010000002000100					
Annonaceae	1000000001021000010210A000102100000000?00002102A10D0D00A0A02000100					
Myristicaceae	20AB100?0100A?100A00?1??0100200110002100001 2D1101?0020000100042200					
Calycanthoideae	0000010000?2100000?2001000002001 12??2100000210211?102001?000030000					
Idiospermum	0000010000?210?000?2001000002001 12???0?000???A2010102001?0?????000					
Atherospermataceae	1000010000?2100000?2001A1A11E2011000210000A2101110002001?000030000					
Siparunaceae	210?11000??AA??00????0?A01110202 11??10?010?2101110002010100????000					
Hortonia	1000010000?2100000?D001211002001 11???0?010??0011100000001000030000					
Monimioideae	100011000??DA0000??2?0?211000101 11??10?001??0011100000001000030000					
Mollinedioideae	1000110001DD00?001DDA0?0010000AD11??1B?0AA??0000000000001000030000					
Gomortega	1000020000?2000000??0012111102011 1??10?010??00111?0001001000030000					
Lauraceae	1000020?0101000001020012111A020111??02?001??11111?000000A000030000					
Hernandioideae	2100020?01EDB000012100121111020011??02?001??11111?0000001000200D00					
Gyrocarpoideae	2100020?01200?A0012A00A211112201 11?????0?1???1111?0000001000230000					
Winteraceae	1000000001121010012 2A0010100201110102100001110200A2010000010000000					
Canellaceae	A0000000010D10100121010?0100200110002100000002020?1D010000010000000					
Saururaceae	201002001??????00101?0020110100210002 0?0001020210120110001 0??01000					
Piperaceae	201000001??????001AA?0020110A002100020?0101010?A?10?210000000 01000					
Lactoris	1000A0000100A?0001010000000020111010 10?0000102100201001?10??00000					
Asaroideae	00000200010AAA10010D1002000020011A002A000011102A02201001?10??02000					
Aristolochioideae	210002000100A?10010A1A0B0100200111??20?0A0?11020?2201001??A??C2000					
Euptelea	200000001??????001?0?0?2000011011 4??2100101111010001000 01?020040000					
Papaveraceae	D000000001 12A100011A100201002001 14??2A?0A011D021?1200001?21??A2000					
Lardizabalaceae	2000100001022100010 10A0201002001 14??20?0001110201 0B010000010000000					
Circaeaster	1000000000?0A?0000?000?2010100011 4??20?1001??A0010100111?00????000					
Menispermaceae	10A010000102A10001010A020100A00214??21000011102A101020001000000A00					
Berberidaceae	1000000?0102110001010 00B0100E20114??21B00011D10A0?20D0000B10000000					
Glaucidium	0000000001112000 0??2?0020100?00114??210010?1202010201001?110000000					
Hydrastis	000000000100A?000??2?0010100100114??2101001120211020B001?110000000					
core Ranunculaceae	1000000000?1210000?2000201001001 14??20?01011102110E0?001?110000000					
Nelumbo	0000000000?2100000??200020000D00014??2100001110000000000 1?000000000					
Platanus	D012100001B1000001EA000002A0110114??2100001120210010010 1?001000000					
Proteaceae	2000000?0111000001110002010000124??2A0000?0212 11?10010A1000000000					
Tetracentron	D010020001110000011100020110110 1 14??2121001120210220000 1?12??42000					
Trochodendron	10000200???????00A2200020110110 1 14??2121001120210220000 1?12??42000					
Buxaceae	10A010000111000001110002000000 1 14??210A001?10210210000A0A1??C0000					
Acorus	2012000001010000010100020100000200002 0?000110101 22?0100000000 1000					
Tofieldiaceae	2A0000000101000001 01A0020100000100002110000010211020100 1?1A??00000					
Butomus	2100000001011000010110020100200100002110000010211021200 1?12??00000					
Aponogeton	20120000010AB000010100020100200 1A0000100101010211020200 1??30200000					
Scheuchzeria	1000000001010000010100020000 20?111??21?000???0211010D001?131000000					
Araceae	2012000001A1000001A1000101002001000 02A?000011AA0A2A0BAA000000?0000					
Nartheciaceae	2000000001012000010100020100000100002110000010211220200 1?110000000					
Dioscoreaceae	D000020001012000010100020100000100002 0?0000010211DD0A001?A000C2000					
Melanthiaceae	2000000001012000010100020100200100002110001010211220200 1?110000000					
Ceratophyllum	201D1?0?1??????01??????00?10B00111??????????101??000111?00????000					
Pennipollis plant	2??D1A??????????1??????00000B00210000100101 02????0??1?000B????000					
Anacostia	??0??01?????????????????????????0D100021200011D0?0?00?200000110000 00					
Virginianthus	??0?010?00?D??0000?200100010210D10002100001020???0D?????????????0					
Liliacidites	?????????????????????????????????0100002110000 01?????????????????0					

Characters in Table 1. ED = number of character in Endress and Doyle (2009); DE = number of character in Doyle and Endress (2000).

1 (ED 22) Inflorescence (0) solitary flower, (1) botryoid, panicle, or thyrsoid, (2) raceme, spike, or thyrse.
2 (ED 23). Inflorescence partial units (0) single flowers, (1) cymes.
3 (ED 24). Pedicel (0) present in some or all flowers, (1) absent or highly reduced (flower sessile or subsessile).
4 (ED 25). Floral subtending bracts (0) present, (1) present in female, absent in male flowers, (2) absent in all flowers.
5 (ED 26). Sex of flowers (0) bisexual, (1) unisexual.
6 (ED 27). Floral base (0) hypanthium absent, superior ovary, (1) hypanthium present, superior ovary, (2) partially or completely inferior ovary.
7 (ED 28). Floral receptacle (female portion) (0) short, (1) elongate.
8 (ED 30). Floral apex (0) used up after production of carpels, (1) protruding in mature flower.
9 (ED 31). Perianth (0) present, (1) absent.
10 (ED 32). Perianth phyllotaxis (0) spiral, (1) whorled.
11 (ED 33). Perianth merism (0) trimerous, (1) dimerous, (2) polymerous. Spiral taxa scored as unknown.
12 (ED 34). Perianth whorls (series when phyllotaxis is spiral) (0) one, (1) two, (2) more than two. Taxa with no perianth scored as unknown.
13 (ED 35). Tepal differentiation (0) all more or less sepaloid; (1) outer sepaloid, inner distinctly petaloid; (2) all distinctly petaloid. Single sepaloid cycle scored as 0/1.
14 (ED 36). Petals (0) absent, (1) present.
15 (ED 38). Outermost perianth parts (0) free, (1) at least basally fused.
16 (ED 39). Calyptra derived from last one or two bracteate organs below the flower (0) absent, (1) present.
17 (ED 40). Stamen number (0) more than one, (1) one.
18 (ED 41). Androecium phyllotaxis (0) spiral, (1) whorled.
19 (ED 42). Androecium merism (0) trimerous, (1) dimerous, (2) polymerous. Spiral taxa scored as unknown.
20 (ED 43). Number of stamen whorls (series when phyllotaxis is spiral; includes inner staminodes) (0) one, (1) two, (2) more than two. Single stamens scored as unknown.
21 (ED 44). Stamen positions (0) single, (1) double (at least in outer whorl). Taxa with no perianth and/or single stamens scored as unknown.
22 (ED 45). Stamen fusion (0) free, (1) connate. Taxa with one stamen scored as unknown.
23 (ED 46). Inner staminodes (0) absent, (1) present. Taxa with one stamen or one whorl of stamens scored as unknown.
24 (ED 48). Stamen base (0) short (2/3 or less the length of anther), (1) long (>2/3 length of anther) and wide (>1/2 width of anther), (2) long (2/3 or more length of anther) and narrow (<1/2 width of anther).
25 (ED 49). Paired basal stamen glands (0) absent, (1) present.
26 (ED 50). Connective apex (0) extended, (1) truncated or smoothly rounded, (2) peltate.
27 (ED 51). Pollen sacs (0) protruding, (1) embedded.
28 (ED 52). Microsporangia (0) four, (1) two.
29 (ED 53). Orientation of dehiscence (0) distinctly introrse, (1) latrorse to slightly introrse, (2) extrorse.
30 (ED 54). Mode of dehiscence (0) longitudinal slit, (1) H-valvate, (2) valvate with upward-opening flaps.
31 (ED 59). Pollen unit (0) monads, (1) tetrads.
32 (ED 60). Pollen size (average) (0) large (> 50 µm), (1) medium (20-50 µm), (2) small (< 20 µm), ordered.
33 (ED 61). Pollen shape (0) boat-shaped, (1) globose, (2) triangular, angulaperturate.
34 (ED 62). Aperture type (0) polar (including sulcate, ulcerate, and disulcate), (1) inaperturate, (2) sulculate, (3) (syn)tricolpate with colpi arranged according to Garside's law, with or without alternating colpi, (4) tricolpate.
35 (ED 63). Distal aperture shape (0) elongate, (1) round.
36 (ED 64). Distal aperture branching (0) unbranched, (1) with several branches.
37 (ED 65). Infratectum (0) granular, (1) intermediate, (2) columellar, ordered.
38 (ED 66). Tectum (0) continuous or microperforate, (1) perforate (foveolate) to semitectate (reticulate), (2) reduced.
39 (ED 67). Grading of reticulum (0) uniform, (1) finer at ends of sulcus (liliaceous), (2) finer at poles (rouseoid). Scored only in taxa with state (1) in character 38. *Scheuchzeria* scored as unknown because it is inaperturate.
40 (ED 68). Striate muri (0) absent, (1) present.
41 (ED 69). Supratectal spinules (0) absent, (1) present.
42 (ED 70). Prominent spines (0) absent, (1) present.
43 (ED 71). Aperture membrane (0) smooth, (1) sculptured.
44 (ED 72). Extra-apertural nexine stratification (0) foot layer, not consistently foliated, no distinctly staining endexine or only problematic traces, (1) foot layer and distinctly staining endexine, or endexine only, (2) all or in part foliated, not distinctly staining.
45 (ED 73). Nexine thickness (0) absent or discontinuous traces, (1) thin but continuous, (2) thick (1/3 or more of exine), ordered.
46 (ED 74). Carpel number (0) more than one, (1) one.
47 (ED 75). Carpel form (0) ascidiate up to stigma, (1) intermediate (both plicate and ascidiate zones present below the stigma) with ovule(s) on the ascidiate zone, (2) completely plicate, or intermediate with some or all ovule(s) on the plicate zone.
48 (ED 79). Style (0) absent (stigma sessile or capitate), (1) present (elongated, distinctly constricted apical portion of carpel).
49 (ED 80). Stigma (0) extended (half or more of the style-stigma zone), (1) restricted (above slit or around its upper part).
50 (ED 84). Carpel fusion (0) apocarpous, (1) parasyncarpous, (2) eusyncarpous (at least basally). Taxa with one carpel scored as unknown.
51 (ED 90). Number of ovules per carpel (0) one, (1) two or varying between one and two, (2) more than two.
52 (ED 91). Placentation (0) ventral, (1) laminar-diffuse or "dorsal."
53 (ED 92). Ovule direction (0) pendent, (1) horizontal, (2) ascendent.
54 (ED 93). Ovule curvature (0) anatropous, (1) orthotropous (including hemitropous).
55 (ED 94). Integuments (0) two, (1) one.
56 (ED 97). Fruit wall (0) wholly or partly fleshy, (1) dry.
57 (ED 98). Lignified endocarp (0) absent, (1) present. Taxa with dry fruit wall (56) scored as unknown.
58 (ED 99). Fruit dehiscence (0) indehiscent or dehiscing irregularly, dorsally only, or laterally, (1) dehiscent ventrally or both ventrally and dorsally, (2) horizontally dehiscent with vertical extensions.
59 (ED 101). Exotesta (0) unspecialized, (1) palisade or shorter sclerotic cells, (2) tabular, (3) longitudinally elongated, more or less lignified cells. State (3) added for *Aponogeton* and *Scheuchzeria* (Takhtajan 1985). Tofieldiaceae changed from (2) to (0/2); Proteaceae from (0/1) to (0).
60 (DE 97, in part). Mesotesta lignification (0) unlignified, (1) with sclerotic layer, (2) with fibrous layer.
61 (DE 97, in part). Mesotesta fleshiness (0) not juicy or spongy, (1) wholly or partly modified into a juicy sarcotesta, (2) spongy.
62 (DE 98). Endotesta (0) unspecialized, (1) single layer of thin-walled cells with fibrous endoreticulum, (2) multiple layer of thin-walled cells with fibrous endoreticulum, (3) tracheidal, (4) palisade of thick-walled cells.
63 (DE 99). Tegmen (0) unspecialized, (1) both ecto- and endotegmen thick-walled, (2) exotegmen fibrous to sclerotic.
64 (ED 102). Ruminations (0) absent, (1) testal, (2) tegminal and/or chalazal.
65 (ED 103). Operculum (0) absent, (1) present.

Table 2. Data matrix of seed plants for analysis of the position of *Acaciaephyllum*, reduced and modified from Doyle (2008).

	1	2	3	4	5	6	7
Elkinsia	0	0	0	?	?	0	0
Lyginopteris	0	0	0	?	?	0	0
Medullosans	0/1	0	0	?	?	0	0
Callistophyton	0	0	0	?	?	0	0
Cordaitales	0	0	2	?	?	0	0
Emporia	0	0	3	?	?	?	0
Pinaceae	0	0	3	?	?	?	0
Podocarpaceae	0	0	3	?	?	?	0
Araucariaceae	0/1	0	2/3	?	?	0	0
Cupressaceae	0	0	3	?	?	?	0
Cephalotaxus	0	0	3	?	?	?	0
Taxaceae	0	0	3	?	?	?	0
Ginkgoales	0	0	2	?	?	0	0
Corystosperms	0	0	0	?	?	0	0
Autunia	?	?	0	?	?	0	0
Peltaspermum	?	?	0	?	?	0	0
Cycadales	0	0	1	?	?	0	0
Glossopterids	0	0	1	?	?	1	0
Caytonia	0	?	0	?	?	1	0
Bennettitales	0	0	1	?	?	0	0
Pentoxylon	0	0	1	?	?	0	0
Ephedra	1	0	2	?	?	?	0
Welwitschia	1	0	2	?	?	1	1
Gnetum	1	0	1	0	?	1	1
Amborella	0	1	1	0	1	1	1
core Nymphaeales	0	0/1	1	1	0	1	1
Austrobaileya	1	0	1	0	0	1	1
Trimenia	1	0	1	0	1	1	1
Illicium	0	0	1	0	0	1	1
Schisandraceae	0	0	1	0	1	1	1
Chloranthaceae	1	0	1	0	1	1	1
Saururaceae	0	1	1	1	0	1	1
Asaroideae	0	1	1	1	0	1	1
Winteraceae	0	0	1	0	0	1	1
Hydatellaceae	0	0	3	?	?	?	?
Monocot	0	0/1	1	2	0	1	1
Acaciaephyllum	0	0	1	2	0	1	1

Characters in Table 2. D08 = number of character in Doyle (2008).

1 (D08 26) Phyllotaxis (0) alternate, (1) opposite or whorled.

2 (D08 27) Distichous leaves on at least some branches (0) absent, (1) present.

3 (D08 31, in part). Leaf organization (0) pinnately compound, (1) simple and pinnately veined (with median primary vein) or compound but with parallel-veined leaflets, (2) linear or dichotomous with two or more veins, (3) linear with one vein.

4 (new, D08 31, in part). Secondary venation (0) uniformly pinnate, (1) palmate or basally crowded, (2) low-angle, apically fused. Scored only in taxa with state 1 in character 3.

5 (D08 35). Chloranthoid teeth (0) absent, (1) present.

6 (D08 36). Laminar venation (0) open, (1) reticulate.

7 (D08 37). Laminar vein orders (0) one, (1) two or more.

Explanation to the plates

PLATE 1

A, B. *Liliacidites* sp. A, LM, 1000× (slide 71-8-1d, Trent's Reach, Aptian, Virginia; Hickey and Doyle 1977, figs 4g-h).

C, D. *Liliacidites* sp. F, LM, 1000× (slide D13-545-1b, late Albian, Delaware; Doyle 1973, figs 2h-i).

E. *Liliacidites* sp. F, SEM, ca. 2500× (D13-545, late Albian, Delaware; Doyle 1973, fig. 2g);

F. *Liliacidites* sp. F, TEM, ca. 7000× (D13-535, late Albian, Delaware; Walker and Walker 1984, fig. 91).

G. *Liliacidites* sp. D, LM, 1000× (slide 71-5-1b, White House Bluff, middle Albian, Virginia; Hickey and Doyle 1977, fig. 25a).

H, I. *Similipollis* sp., LM, 1000× (slide D13-540-1c, late Albian, Delaware; Doyle 1973, figs 2n-o).

J. *Acaciaephyllum spatulatum*, 1.5× (USNM 3256A, Fish Hut above Dutch Gap Canal, Aptian, Virginia);

K: detail of same, 5x.

PLATE 2

A. *Welwitschia mirabilis*, venation of cotyledon, 6× (redrawn from Rodin 1953, fig. 7).

B. *Lilium michauxii*, whole leaf showing midvein and longitudinal parallel veins, 1.5× (TXSTATE Herbarium No. 004958).

C. Upper portion of B showing midvein, parallel veins, and cross-veins, 3.5x.

D. *Pandanus* sp., apical part of leaf showing spinose marginal teeth without vasculature and spinose midrib, 2× (TXSTATE Paleobotany, Modern Leaf 276).

E. *Welwitschia mirabilis*, young leaf from second node showing longitudinal parallel veins that thin and form a reticulum at the apex. Note how some veins end blindly along the left margin, resulting in only partial vein closure, 10× (TXSTATE Paleobotany, Modern Leaf 275).

F. *Lilium michauxii*, detail of leaf in B and C showing sequential fusion of parallel veins (arrows) and complete vein closure at apex, 10x.

PLATE 1

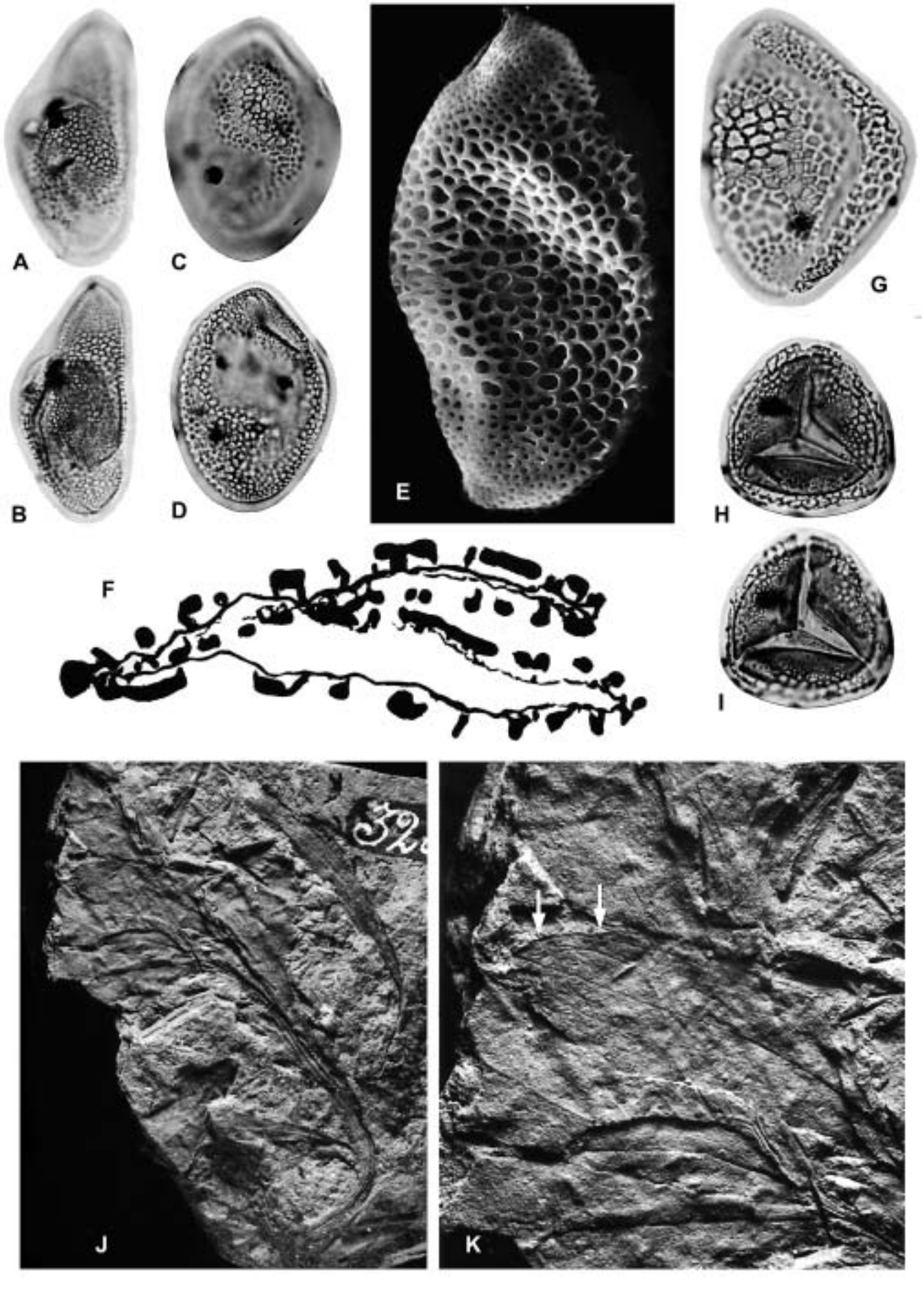

PLATE 2