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Fossil evidence for a herbaceous diversification of early eudicot angiosperms during the Early Cretaceous

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Eudicot flowering plants comprise roughly 70% of land plant species diversity today, but their early evolution is not well understood. Fossil evidence has been largely restricted to their distinctive tricolpate pollen grains and this has limited our understanding of the ecological strategies that characterized their primary radiation. I describe megafossils of an Early Cretaceous eudicot from the Potomac Group in Maryland and Virginia, USA that are complete enough to allow reconstruction of important life-history traits. I draw on quantitative and qualitative analysis of functional traits, phylogenetic analysis and sedimentological evidence to reconstruct the biology of this extinct species. These plants were small and locally rare but widespread, fast-growing herbs. They had complex leaves and they were colonizers of bright, wet, disturbance-prone habitats. Other early eudicot megafossils appear to be herbaceous rather than woody, suggesting that this habit was characteristic of their primary radiation. A mostly herbaceous initial diversification of eudicots could simultaneously explain the heretofore sparse megafossil record as well as their rapid diversification during the Early Cretaceous because the angiosperm capacity for fast reproduction and fast evolution is best expressed in herbs.

1. Introduction

Molecular phylogenetic studies have converged on a robust model of angiosperm phylogeny that recognizes eudicots as the largest subgroup of angiosperms, comprising approximately 75% of their current diversity and dominating most broadleaf forests [1]. This relatively new model of angiosperm relationships had important implications for palaeobotany and has re-framed hypotheses of early angiosperm evolution (e.g. [2]). The oldest fossil angiosperms are monaperturate and inaperturate pollen grains from Hauterivian (134–130 Ma) deposits in Eurasia [3–5]. Some of these early pollen grains have a reticulate tectum, a synapomorphy of Austrobaileyales + mesangiosperms, indicating that the diversification of crown-group angiosperms was underway by this time [6]. Tricolpate pollen, a synapomorphy of eudicots, first occurs in low-latitude deposits of the latest Barremian (approx. 125 Ma) [4,7–15], giving a minimum age for the origin of the group. Surprisingly, few eudicot megafossils are known from deposits spanning approximately 20 Ma following the first tricolpate pollen; they did not become common until the late Albian (approx. 105 Ma). This has limited our ability to test hypotheses regarding the origin and early evolution of this ecologically important and extraordinarily species-rich group.

Phylogenetic methods reconstruct early eudicots as woody trees or shrubs because extant species in early diverging lineages are woody [16]; and because woody species are common in living outgroups such as magnoliids, Austrobaileyales and *Amborella*. However, there is reason to suspect that early eudicots were herbaceous. Herbs occur in several ‘basal’ eudicot lineages (e.g. Ranunculales, Proteales, Buxales), and the handful of putative eudicot mesofossils and megafossils [17–19] described from Aptian-mid Albian deposits appear herbaceous (electronic supplementary material, S1). Further, angiosperm wood is exceedingly rare in the Lower Cretaceous despite abundant gymnosperm wood in the same deposits [20,21].

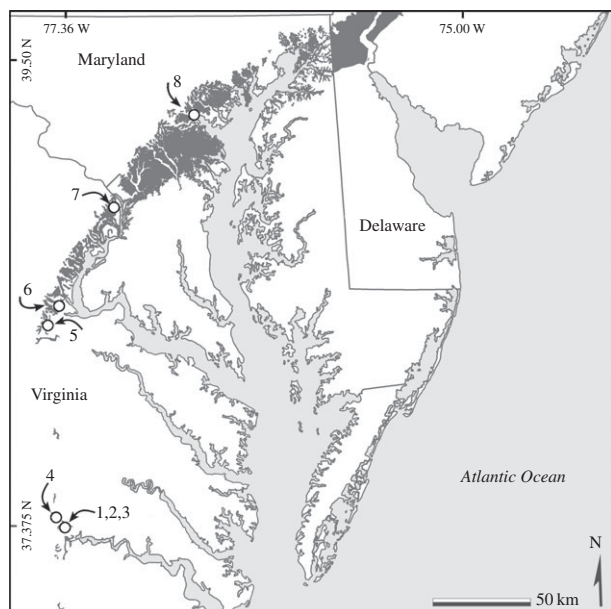


Figure 1. Map of the Lower Cretaceous Potomac Group outcrop in Virginia and Maryland, USA showing the sites from which the fossil specimens described here were collected. (1) Entrance to Trent's Reach, (2) banks of Dutch Gap Canal, (3) base of the bluff at Dutch Gap (LJH JAD 71-117), (4) Fish Hut above Dutch Gap, (5) Fredericksburg, Virginia, (6) roadside near Potomac Run; near Lorton, Virginia, (7) Fairlington, Virginia (USGS 9030), and (8) south of Federal Hill Park in Baltimore, Maryland, USA.

Here, I describe a common herbaceous angiosperm from the Lower Cretaceous of eastern North America based on specimens collected from at least eight different localities (figure 1) in the lower part of the Potomac Group (figure 2). Comparative morphology, age and phylogenetic analysis suggests that this plant belongs near the base of the eudicot phylogeny. I use functional traits and sedimentological context to draw conclusions about its autecology. Finally, I evaluate the early fossil record of eudicots and argue that the evolution of the herbaceous habit was key to their rapid diversification.

2. Material and methods

The fossils are curated in the Department of Paleobiology at the National Museum of Natural History, Smithsonian Institution in Washington DC; the Yale Peabody Museum in New Haven, CT and the Florida Museum of Natural History in Gainesville, FL. They are preserved as carbonaceous compressions, but cuticular details were not apparent under epiflorescence microscopy. Some of the fossils were prepared by degausing. I photographed the fossils using a Canon EOS digital camera with a 100 mm EF macro lens and a Nikon D70 digital camera with a Macro-Nikkor 65 mm lens and processed the images using whole-image manipulations in ADOBE PHOTOSHOP (San Jose, CA, USA) to improve contrast between the matrix and the fossils. The leaf architecture character definitions are based on those outlined in the *Manual of Leaf Architecture* [22] with some of the modifications developed by Jud & Hickey [23] (electronic supplementary material, S2). I measured leaf area and petiole width from photos of seven complete or nearly complete leaves for which the total area of the blade could be estimated using IMAGEJ [24].

I used the molecular scaffold approach to determine the most parsimonious position of the fossil plant, because the number of taxa included in the analysis is greater than the number of morphological characters [25]. The tree search was constrained by the relationships among the ANA-grade angiosperms, magnoliids

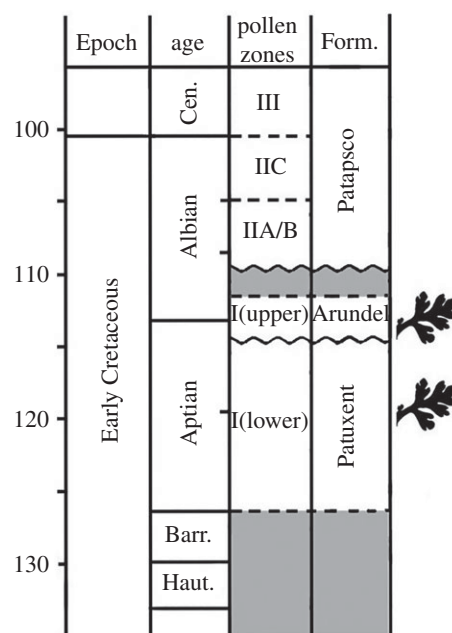


Figure 2. Age of the lower part of the Potomac Group [8,33,75]. Some of the sites where the fossils were collected are in the lower part of Zone I and some are in the upper part of Zone I.

incl. Chloranthales, monocots excl. Commelinidae (the 'basal monocots'), Ceratophyllum and Eudicotyledonae excl. Pentapetales (the 'basal eudicots') [1,26–28]. The sampled genera were chosen deliberately to capture the range of leaf architectural complexity in early diverging angiosperm orders. *Sapindopsis* is included as a stem-genus along the branch leading to modern *Platanus* [29], and *Exnelumbites* is included as a stem-genus along the branch leading to modern *Nelumbo* [30]. I did not include taxa from more derived groups that radiated in the Late Cretaceous and Cenozoic, because many taxa in these groups have characters and character states that are highly divergent from those present in the fossils, making it difficult or impossible to assess homology. I performed parsimony analysis using PAUP* v. 4.0b [31]. I scored 15 characters for 58 genera. If multiple character states are present for a single character within a genus, all were recorded in the matrix. All characters were unweighted and unpolarized, and multistate characters were treated as polymorphic. *Selaginella* served as the outgroup, and the position of the fossil plant was free to vary.

3. Results

Angiosperms (Flowering plants)

unranked – Eudicot clade (Tricolpates)

Order – unknown, cf. Ranunculales, Proteales

Family – unknown

Genus – *Fairlingtonia* gen. nov.

Species – *Fairlingtonia thyrsopteroides* (Fontaine) comb. nov. figures 3 and 4 [32]

Basionym – *Sphenopteris thyrsopteroides* [32, p. 89 pl. 25 fig. 3 and pl. 58 fig. 5]

Synonymy – *Sphenopteris spatulata* [32, p. 93 pl. 50 fig. 3]

Sphenopteris pachyphylla [32, p. 93 pl. 50 fig. 5]

Thyrsopteris pachyphylla [32, p. 135 pl. 50 fig. 3]

(See the electronic supplementary material, S1 for a discussion of the history of these names.)

Generic diagnosis – small, stoloniferous herbs with axillary branching and fibrous adventitious roots produced in pairs at nodes. Leaves alternate, resting buds sometimes

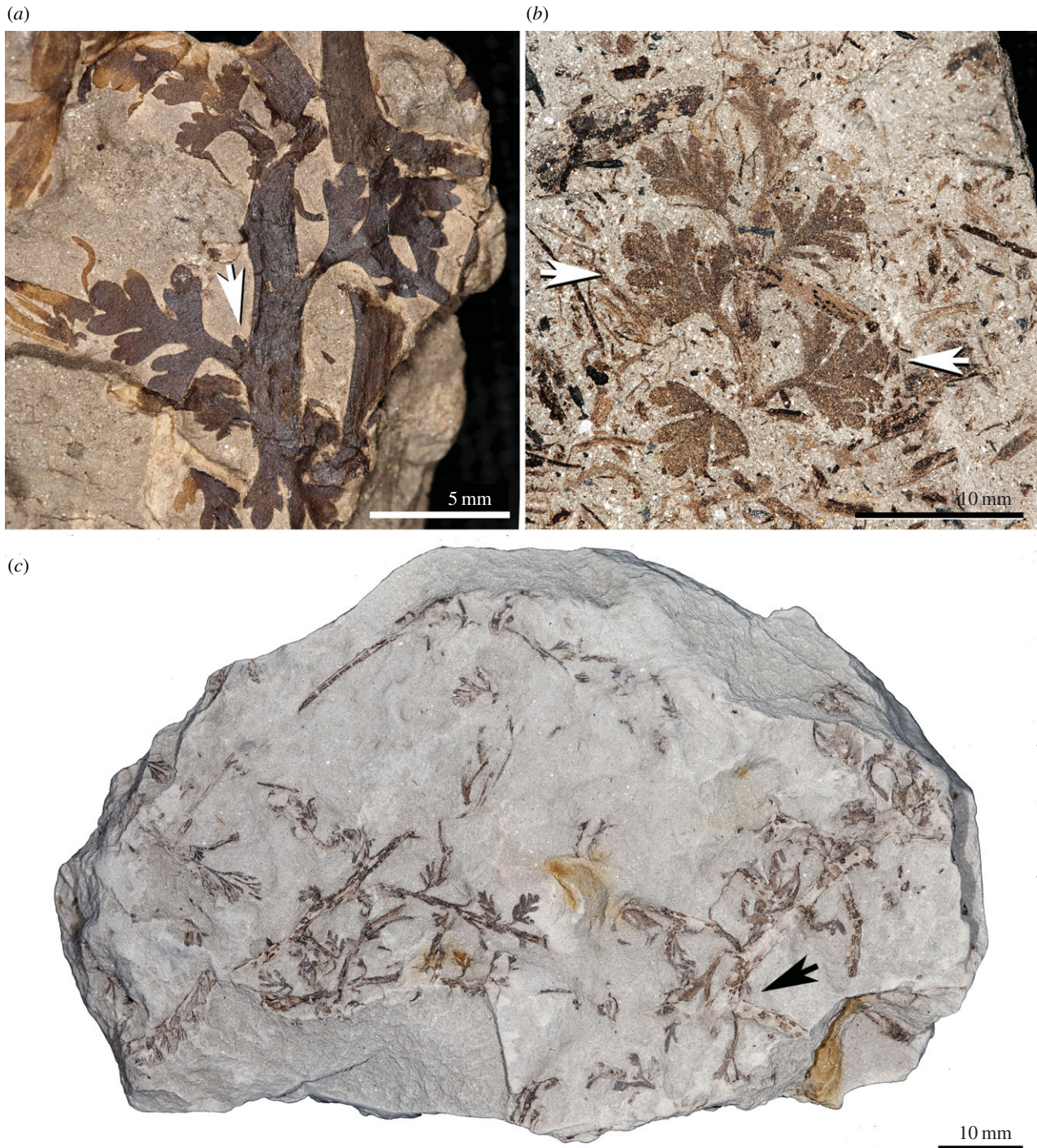


Figure 3. Morphology of the Early Cretaceous eudicot *Fairlingtonia thyrsopteroides* (Fontaine) Jud. (a) Lobed leaves attached to a stem with a bud in the axil of a leaf (arrow). USNM specimen 597570. (b) Variation in leaf morphology from nearly symmetrical (right arrow) to asymmetrical (left arrow). USNM 597571. (c) Branches with subtending leaves (arrow). USNM 597572 = WCB specimen 5975 (see the illustration in the electronic supplementary material, S3). (Online version in colour.)

present. Leaf attachment petiolate, petioles short (less than or equal to 5 mm), petiole base without stipules and decurrent to stem. Petiole width narrows towards blade of leaf. Blade attachment marginal. Leaf size leptophyll, blade ovate and deeply dissected. Apex obtuse, rounded, often slightly asymmetrical. Base obtuse, but not reflex, often slightly asymmetrical. Leaf dissection varies from palmately trilobed and pinnately lobed to twice pinnately lobed. Sinuses rounded. Lobe size and sinus depth both decrease acropetally. Alternate secondary lobes develop acropetally. First and basal most secondary lobe along acroscopic margin of lateral primary lobe or lateral leaflet (analogous to anadromous of pteridology). Major veins (i.e. primary, secondary and minor secondary)

craspedodromous. Perimarginal secondary vein present. Tertiary veins fine, irregular reticulate, areolation poorly developed, freely ending veinlets not present. Margin lobed and smooth, but glandular papillate teeth occur at apices of lobes and are supplied by a medial principle vein and laterally by thickened intra-marginal veins.

Emended specific diagnosis – stems approximately 1–3 mm in diameter, stoloniferous and much-branched. Internodes generally less than or equal to 5 mm. Petioles approximately 2–5 mm long. Blade up to 10 mm long, by up to approximately 13 mm across (but usually much less); leaf area less than 70 mm². Petiole width 0.40–0.70 mm at insertion.

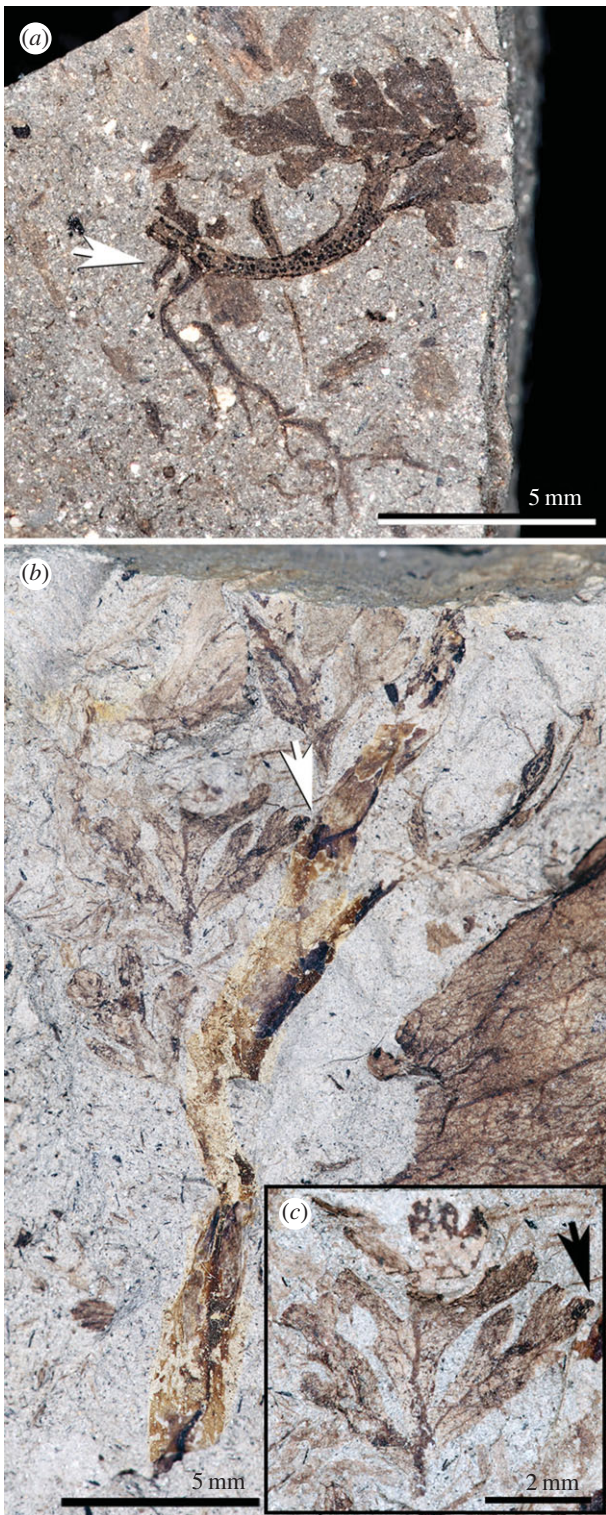


Figure 4. Morphology of the Early Cretaceous eudicot *Fairlingtonia thyrsopteroides*. (a) Leafy shoot with fibrous adventitious roots attached at node (arrow). USNM specimen 597573. (b) Leafy shoot showing sheathing leaf bases (arrow). Composite image of YPM 60054a and 60054b. (c) Close up of the leaf in (b), showing the irregular minor veins and glandular, hydathodal teeth at the lobe apices (arrow). (Online version in colour.)

Holotype – USNM 597566, Department of Paleobiology, Smithsonian National Museum of Natural History, Washington DC. This specimen was illustrated by Fontaine in 1889 (plate XXV fig. 3, LVIII fig. 3C); however, the specimen is severely faded and original illustrations convey the interpretation of this plant as a fragment of a fern frond, rather than a

branching leafy shoot. Other specimens were found in the stratigraphic collections.

Paratypes – USNM 597567, shoot; USNM 597568, shoot; USNM 597569, leaf; USNM 597570, shoot (figure 3a); USNM 597571, shoot (figure 3b); USNM 597572, shoots of *Fairlingtonia thyrsopteroides* mixed with fragments of *Acrostichopteris* sp. (figure 3c); USNM 597573, shoot with attached fibrous adventitious roots (figure 4a); YPM 60054a&b, shoot showing venation of leaves (figure 4b,c).

Etymology – the new generic name *Fairlingtonia* comes from the neighbourhood of Fairlington, VA, USA, where many well-preserved specimens were collected by R. W. Brown in 1944.

Stratigraphic position and age – lower part of the Potomac Group (Patuxent Formation equivalent) and Arundel Clay; pollen Zone I; Aptian-earliest Albian, Early Cretaceous [33]. The fossils occur in collections from both upper and lower Zone I (electronic supplementary material, S1). These two zones are distinguished in part on the presence of tricolpate (eudicot) pollen in upper Zone I and its extreme rarity in lower Zone I [8,10,33].

Description – *F. thyrsopteroides* plants were small, herbaceous, stoloniferous and much-branched. The young stems were flexuous (figure 4a,b), but the older and thicker stems appear generally straight and more robust (figure 3d, at right). Attached branches and buds occur in the leaf axils (figure 3a,c). Fibrous adventitious root systems attached to the stems in pairs at some nodes (figure 4a). The leaves are helically arranged (alternate) along the stem (figure 3b) and comprise a deeply dissected blade, marginal petiole and a decurrent clasping leaf base without stipules (figures 3b and 4b). The petioles are short (less than or equal to 5 mm) and the leaf blade is small (leptophyll). The organization of the dissected leaf blade varies from simple and twice pinnately lobed, to palmately compound (trifoliolate) with pinnately lobed leaflets (figure 3b). The size of the lobes and depth of the sinuses decreases smoothly towards the apex. The secondary lobes are alternate but not pedate (figure 3a,b). The laminar length: width ratio is 1–1.25:1; the overall shape is ovate, but the lobes are obovate. The apex is obtuse and rounded; and the base is obtuse and concave to decurrent. The insertion of the petiole to the blade is often asymmetrical. The primary venation is either pinnate or palmate with three primary veins. The major secondary veins are craspedodromous; secondary vein spacing decreases distally and the secondary vein angle smoothly decreases proximally (figure 4c). The minor secondary veins are craspedodromous. A perimarginal vein is visible in the distal parts of the lobes (figure 4c). The tertiary vein framework is irregular reticulate, forming irregular areoles without freely ending veinlets (figure 4c). Vein density is unknown because the minor veins are rarely preserved. Glandular teeth are present at the apices of the lobes. The teeth terminate in papillate that resemble hydathodes of some extant herbs. The teeth are vascularized by a medial principal vein that terminates at the apex and thickened lateral accessory veins that are continuous with the perimarginal vein (figures 3a and 4c). Figure 5 provides a generalized diagram of the leaf architecture. I measured petiole width and leaf area on five complete leaves (electronic supplementary material, S1) and estimated leaf mass per unit area (LMA) at $75.4 \text{ g} \times \text{mm}^{-2}$ with a prediction interval of 49.2–

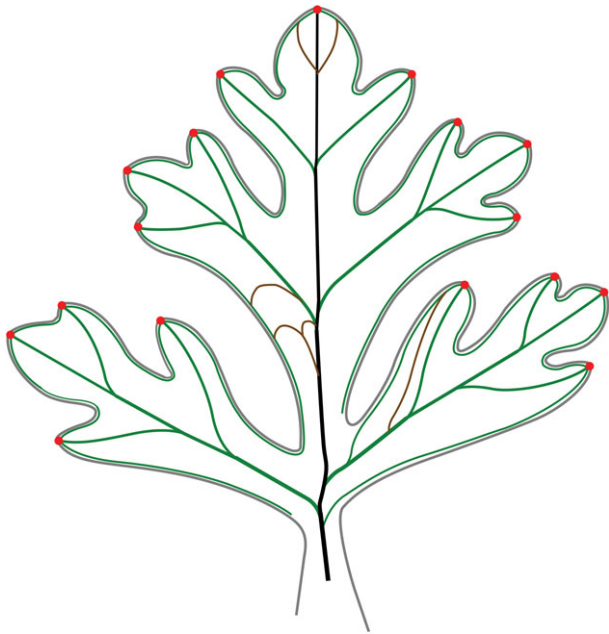


Figure 5. Line drawing of a leaf of *Fairlingtonia* based on several specimens. Major veins run to lobe apices and are shown thicker than minor veins. The dots at the apices of the lobes represent glandular teeth. (Online version in colour.)

$115.4 \text{ g} \times \text{mm}^{-2}$ using the equation of Royer *et al.* [34] for angiosperm herbs.

4. Discussion

(a) Phylogenetic implications

Fairlingtonia thyrsopteroides can be confidently assigned to the seed plant clade based on its axillary branching [35,36]. Attached leaves subtend branches (figure 3c) and resting buds occur in the leaf axils (figure 3a). It is not a fern, as originally described [36]. The combination of five other vegetative characters: (i) herbaceous habit, (ii) petiole base that at least partially encircles the stem, (iii) hierarchical reticulate venation, (iv) glandular (hydathodal) teeth, and (v) the mode of complex leaf dissection, allow for more precise identification and indicate that this plant is a eudicot angiosperm.

Eudicot megafossils are expected to co-occur with tricolpate pollen grains. In the Potomac Group, tricolpate pollen grains occur in upper Zone I, but they are exceedingly rare in lower Zone I [8]. They have not been documented from any of the lower Zone I localities where *Fairlingtonia* was collected. This pattern raises three possibilities. First, tricolpate pollen might be present at the lower Zone I sites with *Fairlingtonia*, but so rare that it has not been detected [23]. Second, *Fairlingtonia* may belong to a eudicot stem lineage that predates the evolution of tricolpate pollen, but post-dates the origin of eudicot-like leaves [6]. Finally, *Fairlingtonia* might belong to an entirely extinct group of plants unrelated to eudicots but with convergent morphology. I suggest that the first possibility is the most likely.

The most parsimonious positions for *Fairlingtonia* were all within the eudicot clade, either nested among the Proteoideae (Proteaceae) or near the base of Papaveroideae (Papaveraceae) (figure 6). These two subfamilies share the herbaceous habit, hydathodal teeth, perimarginal veins, and simple leaves that are deeply dissected. The two positions for *Fairlingtonia* were favoured by different characters. Successive

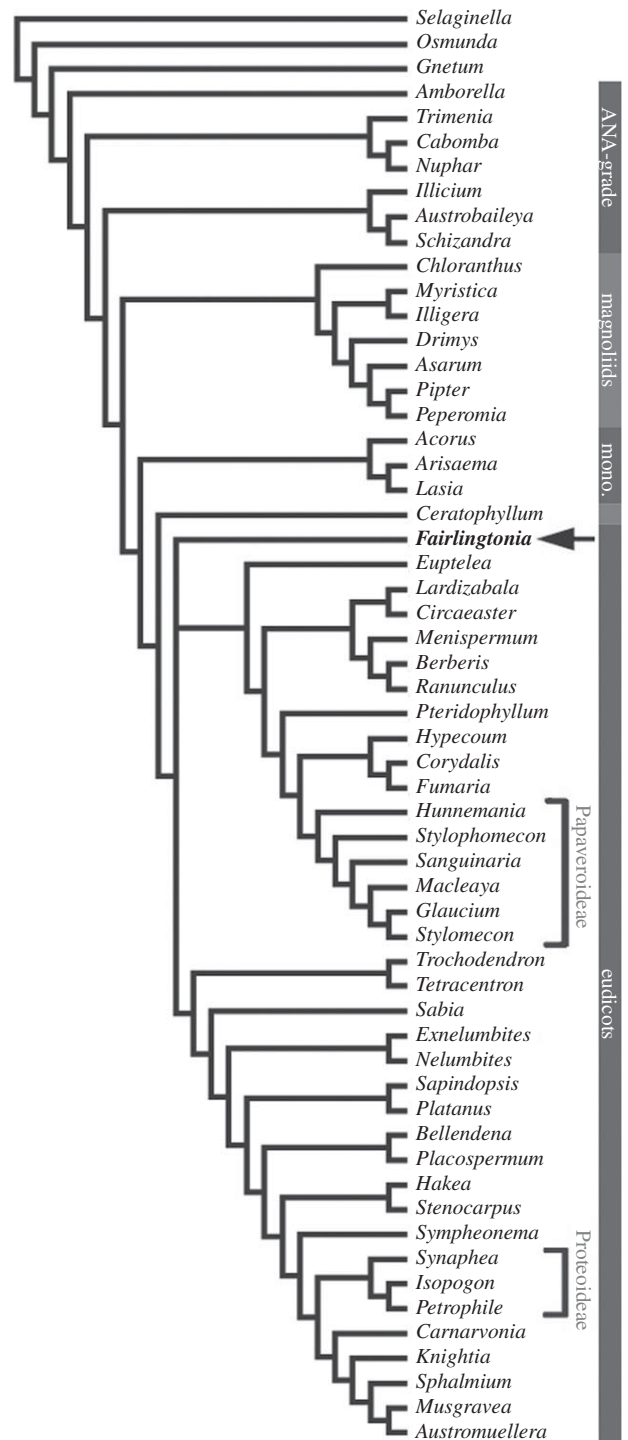


Figure 6. Adam's consensus of 10 best trees showing the position of *Fairlingtonia* as part of a polytomy the base of the eudicot clade (arrow). Angiosperm groups are marked by shaded bars (mono = Monocotyledonous angiosperms). The most parsimonious positions of the fossil are nested either among the Papaveroideae or the Proteoideae.

apical fusion of the veins at the apex of the leaf is seen in some herbaceous Papaveraceae, but not in Proteaceae. By contrast, the arrangement and relative size of the lobes in *Fairlingtonia* leaves serve as a developmental fingerprint for a mode of leaf dissection that today is restricted to Proteaceae (e.g. *Isopogon*, *Petrophile*, *Grevillea*), though it also occurs rarely in more derived lineages (e.g. *Bidens*, Asteraceae (N. A. Jud 2014, personal observation)). It is not known in Papaveraceae or other Ranunculales. Given the age of the *Fairlingtonia* fossils, the similarities with Papaveroideae and

Proteoideae probably reflect ecological similarity and the retention of ancestral features in the modern groups rather than membership in the extant subfamilies.

The placement of *Fairlingtonia* near the base of the eudicot phylogeny, below Eupteleaceae, suggests that eudicot angiosperms were ancestrally herbaceous even though they are reconstructed as woody when extant plants alone are considered [16]. Other previously described Aptian-mid Albian eudicot fossils also have features of herbs rather than of trees and shrubs (electronic supplementary material, S1), despite the taphonomic megabias against herbs and in favour of woody plants [37]. Extant eudicots may not fairly represent the initial habit of the group [38], and this provides a new framework for thinking about the ecological role of the earliest eudicots generally.

(b) Ecological implications

Some of the same features used to assess the phylogenetic position of *Fairlingtonia* also provide information about its ecological strategy. The slender and flexuous stems of *Fairlingtonia* show that it was herbaceous (figures 3*b* and 4*a,b*). The presence of lobed leaves with glandular teeth and short marginal petioles, rather than cordate, peltate or filiform leaves with long petioles and entire margins, support the conclusion that *Fairlingtonia* was a terrestrial herb rather than an aquatic one [39,40]. Furthermore, the small size, adventitious roots (figure 4*a*) and abundance of resting buds (figure 3*a*) suggests a potential for vigorous opportunistic growth, typical of creeping or scrambling herbs adapted to colonizing freshly disturbed substrates [41–43].

Fairlingtonia has flexible stems, very short petioles and small, dissected leaves. This combination of features indicates that it was able to photosynthesize under bright conditions. Short petioles and small leaves are more common in herbs that colonize freshly disturbed substrates where competition for light is not a factor. This is because structural petiole tissue provides no advantage for plants that could otherwise invest in photosynthetic area and reproduction [44]. Lobed leaves are generally associated with adaptation to shade [45]; however, in very small leaves lobes are associated with high density of major veins that maintain equable water potential across the leaf under bright conditions [46,47]. Small dissected leaves also enable rapid convective cooling, protecting the leaves from overheating in high light and still air [46,48–50]. Furthermore, the relatively low inferred LMA of *Fairlingtonia* (electronic supplementary material, S1) is a value typical of herbaceous plants in riparian habitats [34]. Plants with rapid resource acquisition typically have high mass-based photosynthetic and respiration rates, short leaf lifespans, fast growth rates and low LMA; whereas plants with slower resource acquisition typically have a low mass-based photosynthetic rate, longer leaf lifespans, slow growth rates and high LMA [51,52].

Glandular hydathodal teeth like those in *Fairlingtonia* (figures 3*a* and 4*c*) are common among plants that grow in wet soils and periodically experience high humidity, indicating that *Fairlingtonia* was adapted to wet substrates. Teeth of this type are sites of guttation; the loss of water at tooth apices prevents flooding of the leaf mesophyll under conditions of high soil moisture, high humidity and low evaporative demand [53–55]. Environments such as forest understory and riparian corridors in tropical and temperate climates typically host plants with hydathodal teeth [49,56–61]; but hydathodal teeth also occur in some marginally or semi-aquatic ranunculalean herbs that grow under bright, subareal conditions [39].

The fossils discussed here were collected from massive to poorly laminated beds of mudstone and siltstone that typically alternate with poorly sorted, cross-laminated, coarse-grained beds [36]. This pattern of sedimentation is typical of variable flow regimes and rapid, near-channel deposition associated with crevasse-splay events [62,63]. The preservation of *Fairlingtonia* with leaves and roots attached to slender stems suggests minimal transport, and therefore that its depositional environment also represents its environment of growth. *Fairlingtonia* was a riparian herb.

The distribution, morphology and sedimentological context of the fossils suggest that *Fairlingtonia* was a widespread fast-growing eudicot (or stem-eudicot) herb that colonized bright, wet, riparian habitats in subtropical eastern North America during the Aptian-earliest Albian (approx. 113 Ma). Many of the features that support this conclusion are typical of putative Lower Cretaceous eudicot megafossils in general (electronic supplementary material, S1). Rather than being woody plants restricted to under-sampled regions, or to 'upland' environments not represented in the fossil record [64,65], early eudicots were generally small herbaceous plants that grew near depositional settings; their fossils may be widespread but small and locally rare in fine-grained, low-energy deposits with minimally transported plant fossils. This finding could explain the paucity of eudicot megafossils in existing Aptian to middle Albian collections, but also suggests that new early eudicots will emerge with sufficient sample sizes and the proper search image.

5. Conclusion

Fairlingtonia thyrsopteroides was an herbaceous angiosperm that belongs near the base of the eudicot phylogeny. This plant was capable of fast growth under bright conditions and was a colonizer of disturbed microsites in wet, riparian habitats. This discovery contributes to an emerging pattern of early eudicots and eudicot-like plants as small herbs rather than woody plants as previously thought. An initially herbaceous radiation of eudicots that included the origin of the crown-group makes sense in the context of angiosperm reproductive innovations that promote short seed-to-seed time [66–68], because herbs tend to reach reproductive maturity earlier, have higher nucleotide substitution rates and have faster rates of climate niche evolution compared to their woody counterparts [69–74]. Therefore, the herbaceous habit may have been a key trait allowing eudicots to diversify in Early Cretaceous communities that were still dominated by gymnosperms and ferns.

Data accessibility. The character matrix and settings used for the phylogenetic analysis is available as part of the electronic supplementary material, S2. The file is named Jud_Supplement 2.nex and can be opened with a text editor.

Competing interests. I declare no competing interests.

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