EVALUATING RELATIONSHIPS AMONG FLOATING AQUATIC MONOCOTS: A NEW SPECIES OF *COBBANIA* (ARACEAE) FROM THE UPPER MAASTRICHTIAN OF SOUTH DAKOTA

Ruth A. Stockey,[1],* Gar W. Rothwell,*,† and Kirk R. Johnson‡

*Department of Botany and Plant Pathology, Oregon State University, 2082 Cordley Hall, Corvallis, Oregon 97331, USA; †Department of Environmental and Plant Biology, Ohio University, Athens, Ohio 45701, USA; and ‡National Museum of Natural History, Smithsonian Institution, MRC 106, PO Box 37012, Washington, DC 20013-7012, USA

Premise of research. A large number of floating aquatic aroid fossils have been recovered from pond sediments in the Hell Creek Formation (Upper Cretaceous) of South Dakota, providing valuable new data about aquatic vegetation of the uppermost Cretaceous, that are used to describe a new species of the genus *Cobbania*, and to evaluate associated reproductive structures and phylogenetic relationships among floating aquatic monocots.

Methodology. Fossils were uncovered as needed with fine needles to reveal surface features of the specimens. Images were captured with a digital scanning camera, and phylogenetic analyses were conducted with TNT implemented through WinClada.

Pivotal results. The new species, *Cobbania hickeyi* Stockey, Rothwell & Johnson, extends the range of the genus to the uppermost Cretaceous, supports the taxonomic integrity of the genus *Cobbania*, and increases our understanding of structural variation and species richness within the genus. Associated reproductive structures include an aroid spadix, strengthening the assignment of *Cobbania* to the Araceae. Phylogenetic analyses using "total-evidence" data help resolve conflicting results from either morphological or nucleotide sequence analyses of relationships among floating aquatic aroids, and the fossil taxon *Aquaephyllum* does not nest among the other floating aquatic species in any of our results.

Conclusions. Species of the genus *Cobbania* were an important component of aquatic vegetation across the Northern Hemisphere during the Late Cretaceous. In tests of competing hypotheses for relationships among *Pistia stratiotes*, *Cobbania* spp., and species of Araceae subfamily Lemnoideae, the results from a "total-evidence" analysis suggest that specializations for the floating aquatic life form may be overwhelming other characters in the results of morphological analyses alone.

Keywords: Alismatales, aquatic angiosperms, Araceae, *Cobbania*, Cretaceous, fossil.

Introduction

Cobbania corrugata (Lesquereux) Stockey, Rothwell & Johnson was reconstructed in 2007 from interconnected rosettes of floating aquatic monocots preserved in Upper Cretaceous sediments of Dinosaur Provincial Park, near Brooks, Alberta, Canada (Stockey et al. 2007). Isolated roots and leaves of *C. corrugata* were described originally as *Pistia corrugata* Lesquereux from Point of Rocks, Wyoming (Lesquereux 1876, 1878), but the Dinosaur Park fossils revealed the existence of a previously unknown extinct genus of floating aquatic Araceae (Stockey et al. 2007). The organismal concept for *C. corrugata*, developed along with the plant reconstruction (Stockey et al.

2007), was based on attached and dispersed vegetative organs, and the plant was compared with extant *Pistia* L. as well as with *Limnobiophyllum* Krassilov, another extinct genus of floating aquatic Araceae. Recognition of *C. corrugata* as distinct from *Pistia* called into question the accuracy of the fossil record for the genus *Pistia* as a whole.

Stockey et al. (2007) also described and illustrated potential reproductive structures associated with *C. corrugata*, including seeds with a smooth external surface and potential infructescences that were roughly circular in outline. In 2009, Krassilov and Kodrul described additional *C. corrugata* specimens from the Amur Province of the Russian Far East. These specimens were also associated with reproductive structures and dispersed seeds similar to those reported for the North American specimens. The Russian fertile specimens associated with *Cobbania*, named *Cobbanicarpites* Krassilov and Kodrul (2009), were more numerous and better preserved than comparable structures from North America, allowing for a description of the seeds as operculate. Krassilov and Kodrul (2009) concluded

[1] Author for correspondence; e-mail: stockeyr@science.oregonstate.edu.

that these fertile remains associated with *Cobbania* were comparable to some alismatids or aroids, with seeds similar to those of Hydrocharitaceae. The compression/impression preservation of those fossils, however, did not provide for a complete understanding of the morphology or relationships of the reproductive structures.

On the basis of phylogenetic analyses of living and extinct Araceae (Mayo et al. 1997; Cabrera et al. 2008), Stockey et al. (2007) suggested that there have been at least three separate origins of free-floating aquatic plants within the Araceae, with *Pistia* perhaps the most recently derived (a hypothesis also discussed in Bogner 2009). That hypothesis was supported by a systematic analysis of extant Araceae (including subfamily Lemnoideae) using nucleotide sequence characters (Rothwell et al. 2004), but a more recent analysis (Gallego et al. 2014), using morphological characters in a modification of the Stockey et al. (1997) morphological matrix, supported the earlier hypothesis (Stockey et al. 1997) that *Pistia stratiotes*, *Limnobiophyllum* spp., and living species of Araceae subfamily Lemnoideae (formerly Lemnaceae) form a monophyletic group (Gallego et al. 2014).

In this study, we describe a second species of *Cobbania*, *Cobbania hickeyi* sp. nov., based on floating aquatic rosettes with attached leaves and roots that are interconnected by stolons, isolated leaves, and isolated reproductive structures from the uppermost Cretaceous Hell Creek Formation of South Dakota. Among the dispersed specimens is a well-preserved spadix that provides the first convincing evidence for an aroid reproductive structure that may belong to this species. We also present a series of phylogenetic analyses to test the results of previous hypotheses and analyses for the relationships of *Cobbania* to other fossil and living species that have been described as floating aquatics.

Material and Methods

Geologic Setting

In 2002, 2003, and 2004, K. R. Johnson and field crews from the Denver Museum of Nature and Science (formerly the Denver Museum of Natural History, as indicated by the specimen designations) made a large collection of fossil leaves from an unusual Hell Creek Formation site in Harding County, South Dakota. The site, DMNH locality 2703, is known as "Licking Leaves": lat. 45.6°N, long. 103.8°W; Universal Transverse Mercator (UTM) coordinates 13 597500E 5048826N; Pine Spring 7.5′ Quad; northwest quarter of Section 27, Township 19N, Range 3E (landowner: Gary Licking). The exposure crops out to the west of Buffalo at the base of a physiographic feature locally known as the "jump-off." The position of the site, within the 100-m-thick Hell Creek Formation, is not known, since neither the base nor the top of the formation are locally exposed. Given the thickness of adjacent exposures of the Hell Creek Formation, it is reasonable to estimate that the site is in the middle or lower portion of the formation.

The lithology of the site is a light gray claystone that has rare thin (<1-cm), medium-grained sand interbeds that only rarely show evidence of rooted plants. The claystone is not lithified and appears massive but splits along bedding planes. This is quite unusual for the Hell Creek Formation, where pedogenesis

of claystones is the norm. The quality of preservation of the fossils at this site is unusually fine, and the diversity of the flora exceeds 60 taxa, making this one of the most diverse of all Hell Creek fossil plant sites (Johnson 2002). The presence of complete small-bodied fish and abundant and diverse aquatic plants clearly indicates that this was a shallow pond that occasionally saw episodes of turbid flow that deposited sand on the floor of the otherwise placid setting. The co-occurrence of small fish and aquatic plants is unique among the 100+ fossil plant sites known from the Hell Creek Formation in eastern Montana, western North Dakota, western South Dakota, and northeastern Wyoming, where the equivalent strata are known as the Lance Formation (Johnson 2002).

The flora of the site includes cupressaceous conifers, the cycad *Nilssoniocladus* Kimura & Sekido, *Ginkgo* L., a great diversity of angiosperms (e.g., *Erlingdorfia montana* (Brown) Johnson and *"Dryophyllum" subfalcatum* Lesquereux), and an unusually diverse suite of aquatic plants, including *Quereuxia angulata* (Newberry) Kryst. ex Baikovskaja, *Brasenites* Wang & Dilcher, *Hydropteris* Rothwell & Stockey, *Cobbania* Stockey, Rothwell & Johnson, *Limnobiophyllum* Krassilov, and possible species of Nymphaeaceae (Johnson 1992, 2002; K. R. Johnson, personal observation).

The Hell Creek Formation is upper Maastrichtian, Late Cretaceous, in age (Johnson 1996, 2002). It is bounded by Maastrichtian marine deposits (Murphy et al. 2002) and basal Paleocene (Puercan) terrestrial sediments (Moore 1976; Johnson and Hickey 1990). The site from which the new specimens were derived falls in Hell Creek floral zone HC1 (Johnson 2002). On this basis, the site is at least 66.25 Myr old and may be as old as 67 Myr.

Methods and Analyses

Specimens on split surfaces were uncovered as needed with fine needles to reveal surface features of the plants. Images were captured with a Microlumina digital scanning camera (Leaf Systems, Bedford, MA) focused though a Nikkor 105-mm AF Micro lens (Nikon, Melville, NY) and were processed with Adobe Photoshop 7.0 (Adobe, San Jose, CA).

To explore the systematic relationships of *Cobbania hickeyi* and to test competing hypotheses for relationships among floating aquatic Araceae (including Lemnoideae), three types of phylogenetic analyses using either morphological characters only or a combination of nucleotide sequence data and morphological characters have been performed. Analyses of the first type were performed to test the hypotheses (1) that *Cobbania* spp. are assignable to either the Araceae (Stockey et al. 1997) or the Hydrocharitaceae and other alismatalean families (Krassilov and Kodrul 2009), (2) that *Cobbania* spp. form a clade with *Pistia*, the Lemnoideae, and other floating aquatic fossil monocots (Stockey et al. 1997; Gallego et al. 2014) or that the floating aquatic life form has evolved in parallel at least three times within the Araceae (Stockey et al. 2007; Cusimano et al. 2011), and (3) that the fossil *Aquaephyllum auriculatum* Gallego, Gandolfo, Cúneo & Zamaloa is a floating aquatic aroid that nests with *Pistia*, the other fossil floating aquatics, and the Lemnoideae (Gallego et al. 2014). The first set of analyses include living and extinct Araceae + alismatids and uses morphological characters only (appendix). Three variations of this

analysis were employed. The fossil species *A. auriculatum* was coded as either "?" or "1" (present) for aquatic environment (morphological character 1) and as either "?" or "1" (present) for floating aquatic life form (morphological character 2) to test whether those characters influence the position of *A. auriculatum* on the tree. The matrix for these analyses is deposited at Morphobank, http://www.morphobank.org, as Matrix 23,955 of Project 2340.

An analysis of a second type was performed to further test the hypotheses (1) that *Aquaephyllum* is a floating aquatic species of Araceae and (2) that either *Cobbania* spp. form a monophyletic group with *Pistia*, the Lemnoideae, *Limnobiophyllum*, and *Aquaephyllum* or the floating aquatic life form has evolved in two or more clades of Araceae. This analysis was also conducted with morphological characters only (appendix). The matrix for this analysis is deposited as Morphobank Matrix 23,956 of Project 2340.

Analyses of the third type were performed in an attempt to reconcile discordant results of earlier analyses that either utilize morphological characters only for living and extinct species (Stockey et al. 1997; Gallego et al. 2014) or utilize nucleotide sequences or a combination of nucleotide sequences and morphological characters for living species only (Rothwell et al. 2004; Cusimano et al. 2011). The analyses of the third type include a combination of living and extinct Araceae, use a total-evidence matrix (i.e., a combination of all available types of characters for all available categories of taxa; for this study, these are nucleotide sequence and morphological characters for both living and extinct taxa), and were conducted with the same three variations described above for the first set of analyses. Nucleotide sequences for the third type of analyses were taken directly from Cusimano et al. (2011), as supplied by Natalie Cusimano. The matrix for these analyses is deposited in the Documents folder of Morphobank Project 2340.

Taxa included in the analyses consist of the fossil monocots *Limnobiophyllum scutatum* (Dawson) Krassilov, *A. auriculatum* Gallego, Gandolfo, Cúneo & Zamaloa, *Cobbania corrugata* (Lesquereux) Stockey, Rothwell & Johnson, and the new species of *Cobbania* described here, as well as genera of Araceae that represent major groups/clades of that family, as resolved by Mayo et al. (1997), Cabrera et al. (2008), and Cusimano et al. (2011), and basal genera of alismatids in clade I (Alismataceae/Limnocharitaceae, Butomaceae, Hydrocharitaceae) of Les and Tippery (2013), also known as the petaloid clade of Ross et al. (2016). Araceous genera used are *Alloschemone* Schott, *Ambrosina* Bassi, *Amorphophallus* Blume ex Decne., *Anadendrum* Schott, *Arisaema* Mart., *Arisarum* Mill., *Arophyton* Jum., *Callopsis* Engl., *Carlephyton* Jum., *Colocasia* Schott, *Cyrtosperma* Griff., *Gorgonidium* Schott, *Gymnostachys* R. Br., *Lemna* L., *Peltandra* Raf., *Philodendron* Schott, *Pistia* L., *Pothos* L., *Protarum* Engl., *Schismatoglottis* Zoll. & Moritzi, *Spathicarpa* Hook., *Spirodela* Schleid., *Wolffia* Horkel ex Schleid., *Wolffiella* Hegelm., *Zomicarpa* Schott, and *Zomicarpella* N.E. Br. Alismatid genera used are *Alisma* L., *Butomus* L., *Hydrocharis* L., *Limnobium* L.C. Rich., *Limnocharis* H.B., *Ottelia* Pers., *Sagittaria* L., and *Stratiotes* L. Trees are rooted with the basal monocot genus *Acorus* L.

Morphological characters (appendix) are modified from the matrices of Stockey et al. (1997), Les et al. (2006), Li and Zhou (2009), and Cusimano et al. (2011), with scorings from Cook

and Lüönd (1982) and Cook and Urmi-König (1983, 1984), and the nucleotide sequences for Araceae are taken directly from the 4494-nucleotide sequence matrix of Cusimano et al. (2011). To render the number of states for each morphological character as four or less in the total-evidence matrix, character states 2 and 3 were combined for character 13 of the morphological matrix.

Maximum parsimony phylogenetic analyses were performed on a custom built DOS-based desktop computer with the Willi Hennig Society edition of TNT (Goloboff et al. 2003, 2008), spawned through WinClada (Asado, ver. 1.1 beta, by K. Nixon). Each of the analyses was conducted with all characters treated as nonadditive (100,000 replicates). Each of the matrices for the various analyses is deposited at Morphobank, http://www.morphobank.org, as part of Morphobank Project 2340.

Results

Systematics

Order—Alismatales

Family—Araceae Jussieu

Genus—Cobbania Stockey, Rothwell & Johnson

Species—Cobbania hickeyi Stockey, Rothwell & Johnson sp. nov. (Figs. 1–6)

Species diagnosis. Small rosettes of up to 5 leaves per plant, borne on short stems 4–7 mm in diameter, connected by stolons, growing in large mats. Up to 5 stolons/stem, 3–5 mm in diameter, with central dark band of presumed vascular tissue. Floating branched aquatic roots 1–2 mm wide, at least 7 cm long, with central vascular zone up to 1 mm wide in largest roots; branch roots numerous, 0.1 mm wide, up to 20 mm long. Adventitious roots simple, unbranched, arising from stems of plantlets, 0.1 mm wide. Leaves 2.5–7.5 cm long (mean = 4.03 cm), 2.5–6.2 cm wide (mean = 4.45) in apical surface view with a central oval, aerenchymatous zone 1.7–3.6 cm × 1.7–3.2 cm and large rim 1–3 mm wide at leaf base, 9–16(20) mm wide at lateral margin. Leaf surface hirsute; trichome bases 150 μm in diameter. Petiole 1 cm long with up to 19 veins branching to form abaxial and adaxial series. One central and two lateral major abaxial veins pinnate with dichotomizing laterals. Lateral primary veins dichotomize to form collective vein in rim and 3 or 4 submarginal veins; innermost widely spaced, branching at angles of 90° near leaf apex and 45°–60° near middle and base of leaf. Collective veins and fimbrial vein converge in and below apical notch.

Holotype. Specimen DMNH 24819 (fig. 1*A*), housed at the Denver Museum of Nature and Science.

Type locality. "Licking Leaves," DMNH locality 2703; lat. 45.6°N, long. 103.8°W; UTM zone 13 597500E 5048826N; Pine Spring 7.5′ Quad; northwest quarter of Section 27, Township 19N, Range 3E.

Stratigraphy. Hell Creek floral zone HC1 of the Hell Creek Formation (Johnson 2002); age: 66.25–67 Myr.

Etymology. The species is named in honor of the late Dr. Leo J. Hickey, Yale University, for his extensive work on
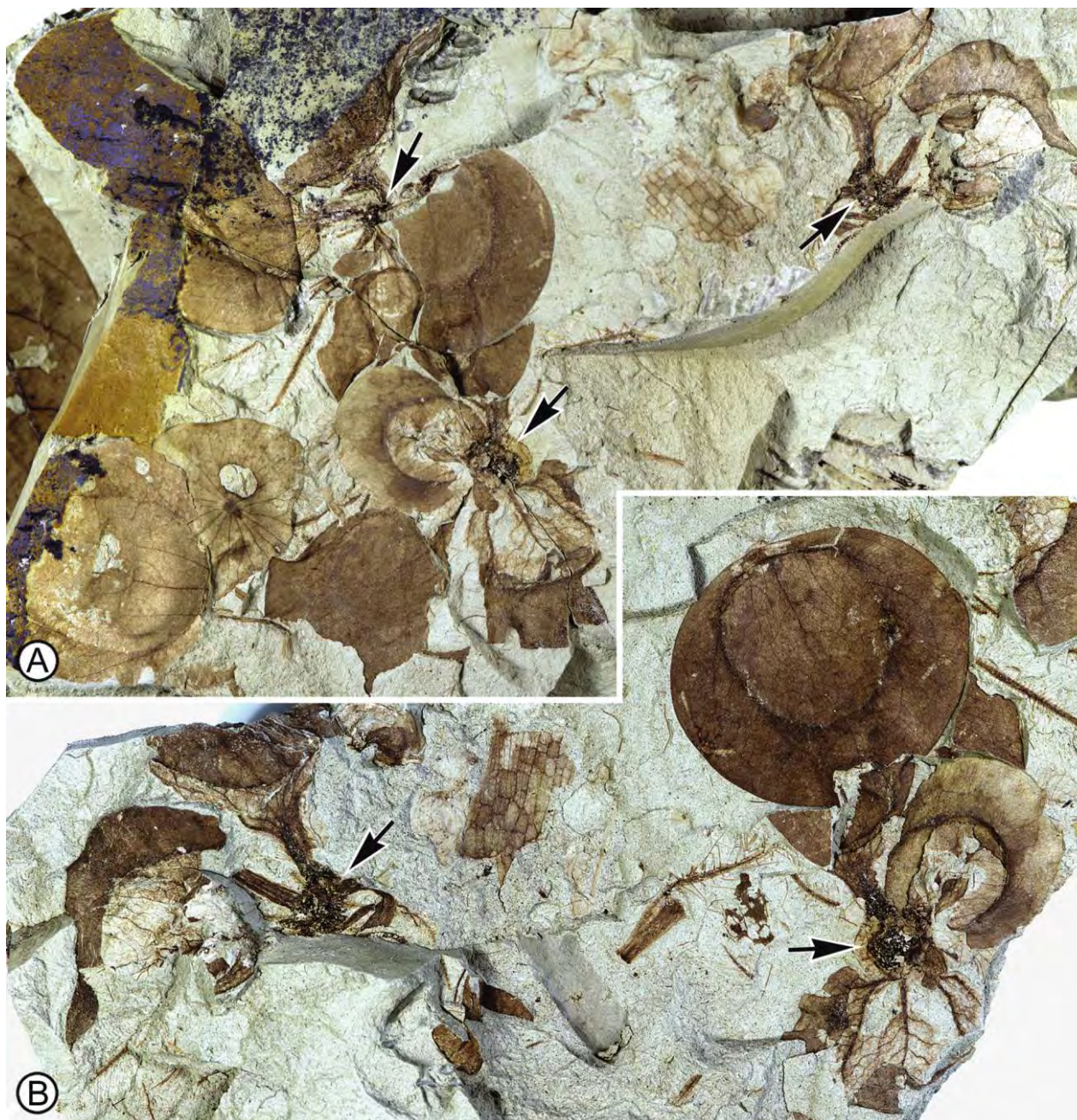
Fig. 1 *Cobbania hickeyi* sp. nov. *A*, Holotype, showing three plants with leaf rosettes (arrows) and an associated peltate *Brasenites* sp. leaf (near left). Specimen DMNH 24819; ×0.9. *B*, Two plants (arrows), with leaves from a third (top right). DMNH 24930; ×1.1.

Cretaceous and Paleogene floras of North America: a friend and mentor, who never let us get away with anything.

Description

Thirteen whole plants (rosettes) and many isolated leaves and roots have been recovered from the Licking Leaves site. These plants were buried rapidly in situ by a rapid influx of very fine-grained mud. Leaves are borne helically on stout, short stems with highly branched roots extending in the opposite di-

rection from the leaves in the sediments, indicating that these floating aquatic plants were buried in growth position. Plants preserved on large blocks show several rosettes interconnected by horizontal stems or stolons (fig. 1). Up to three rosettes have been found attached to one another on a single slab (fig. 1), suggesting that these plants, like those of *Cobbania corrugata* (Stockey et al. 2007), grew in large mats over the pond surface.

Interconnected plants (rosettes). Upright stems bearing up to five helically arranged leaves are 5–7 mm in diameter (figs. 1, 2, 3*A*). They have persistent leaf bases that clasp the stem.
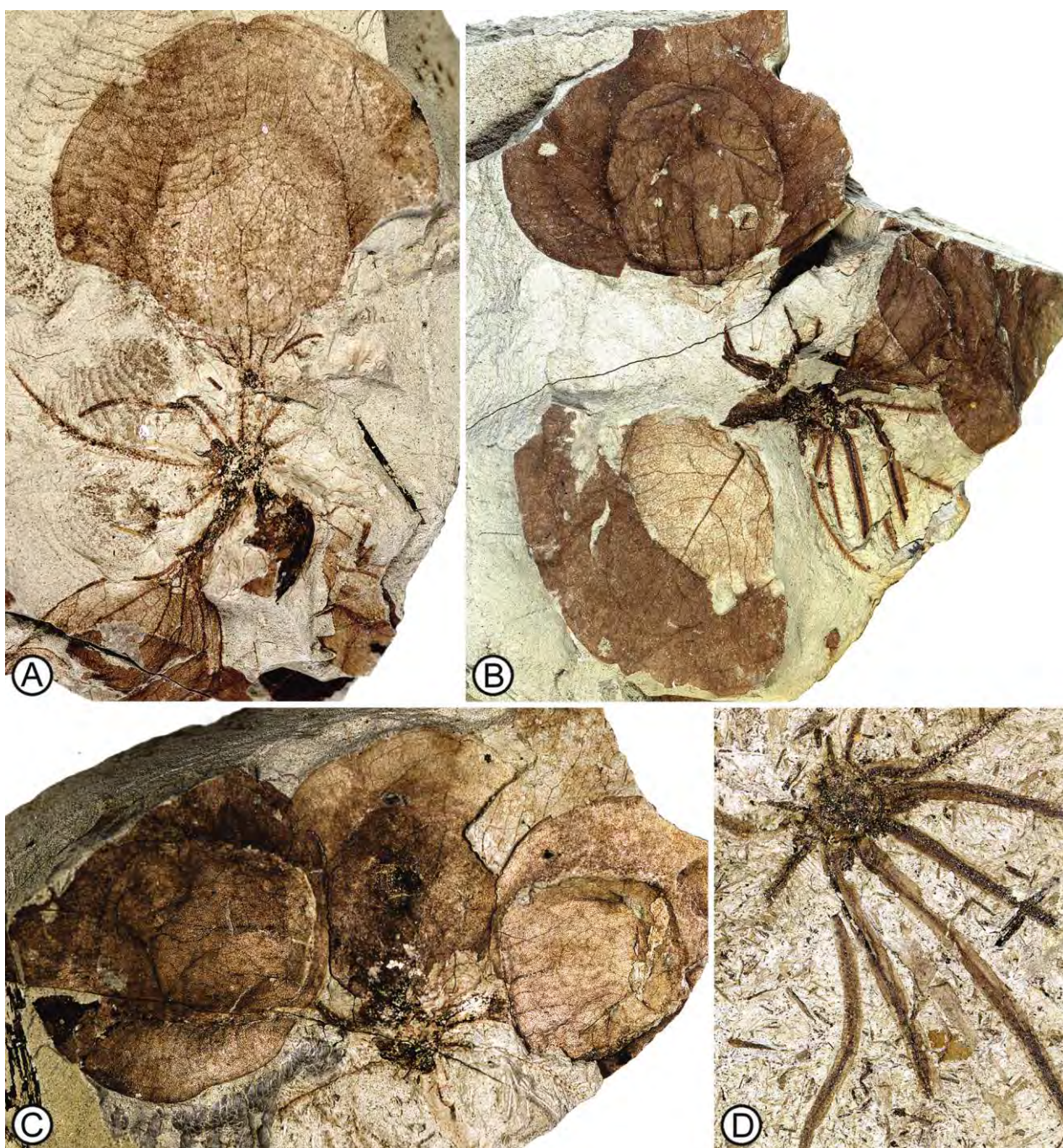
Fig. 2 *Cobbania hickeyi* sp. nov. *A*, Single plants showing at least three attached leaves and several roots. Note banded stain pattern over some areas of bedding plane. Specimen DMNH 24919; ×1.6. *B*, Single plant showing three leaves and dark central stem area with attached roots and stolons. DMNH 30188; ×1.1. *C*, Single plant showing stem cross section and at least five attached leaves. Note roots at bottom. DMNH 24916; ×1.6. *D*, Stem cross section showing stolons (smooth margins) with central dark bands of presumed vascular tissue and lateral roots with secondary roots. DMNH 24712; ×1.7.

Large numbers of branched roots are borne around the stem bases (figs. 2, 3*A*). Horizontal stems (stolons) that connect adjacent rosettes are up to 3–5 mm in diameter (figs. 1*A*, 2*D*, 3*A*). There are up to five stolons originating from a single rosette (figs. 2*D*, 3*A*). Stolon surfaces are smooth and can be distin-guished from roots by their horizontal orientation, smooth surfaces, and the absence of lateral roots. A dark band, presum-ably vascular tissue, is preserved at the center of each stolon (figs. 2*D*, 3*A*). Distances between rosettes vary from 5 to 9 cm for the plants that we were able to measure.
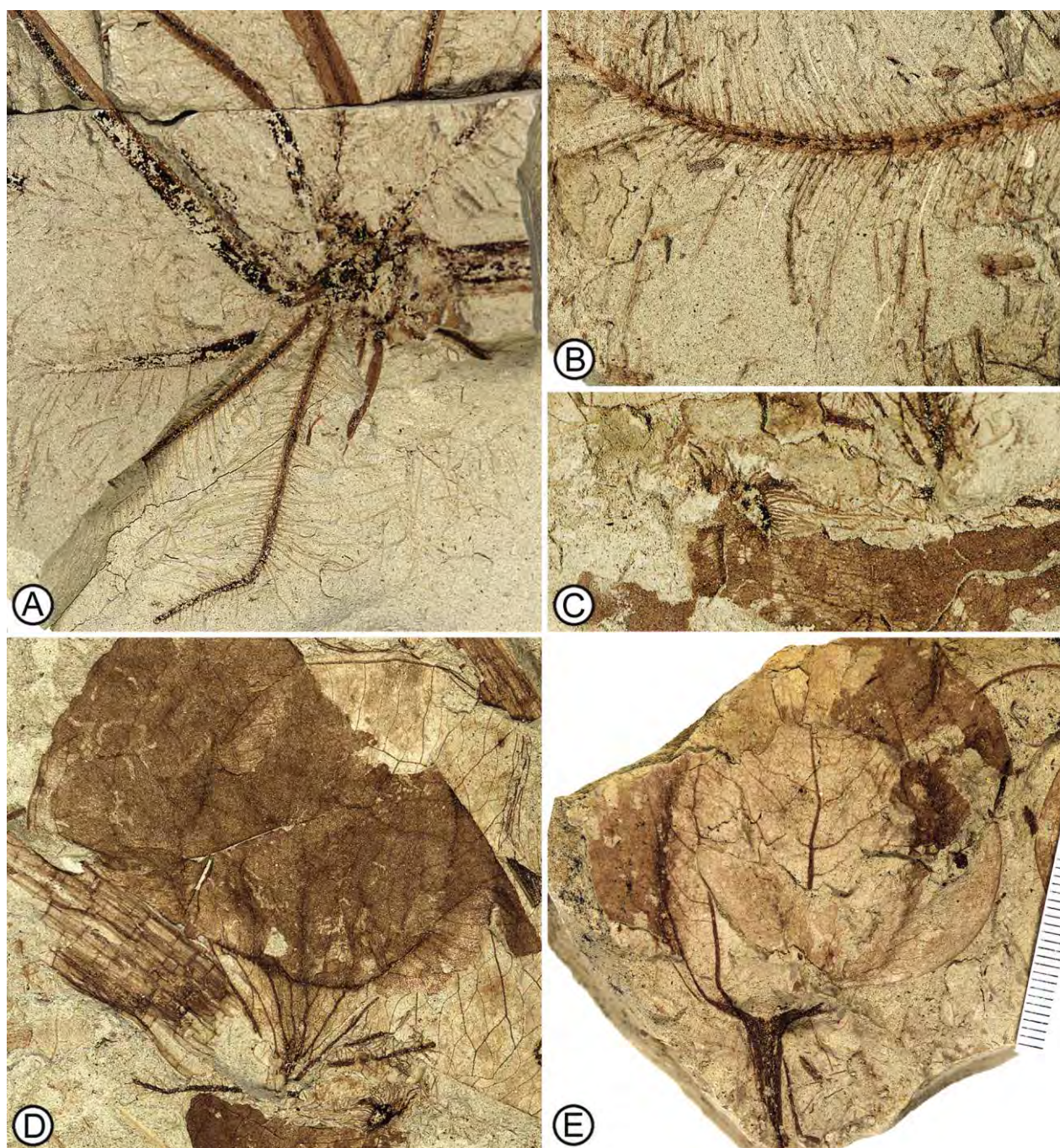
Fig. 3 *Cobbania hickeyi* sp. nov. *A*, Stem cross section, showing numerous attached branching roots and smooth stolons, generally larger with smooth margins. Specimen DMNH 24955; ×1.6. *B*, Lateral root with attached elongate secondary roots. DMNH 24956; ×2.0. *C*, Transverse section of stem, showing simple, unbranched roots arising from the stem (partially obscured by a leaf blade). DMNH 24914; ×2.9. *D*, Leaf from adaxial surface fractured near base, showing seven primary veins and typical morphology of *Cobbania*, including a "basal pouch," or aerenchymatous zone. DMNH 24914; ×1.6. *E*, Leaf fractured through aerenchymatous zone, near abaxial surface, showing petiole and two of three major primary veins that branch pinnately, innermost of two veins at left forming the rim. DMNH 24920; ×1.4.

Leaves. Leaf blades are circular to ovoid at the surface and vary from 2.5 to 7.5 cm long (mean = 4.03 cm, $n = 19$) and from 2.5 to 6.2 cm wide (mean = 4.45 cm, $n = 17$) in surface view (figs. 1, 2*A*–2*C*, 4*A*–4*D*, 5*C*). Leaves have petioles up to 1 cm long that have become compressed from once three-dimensional structures (figs. 1*A*, 3*E*). They are generally trumpet shaped and have a central zone that was aerenchymatous (fig. 6*D*). In leaves that are fractured through this central zone,
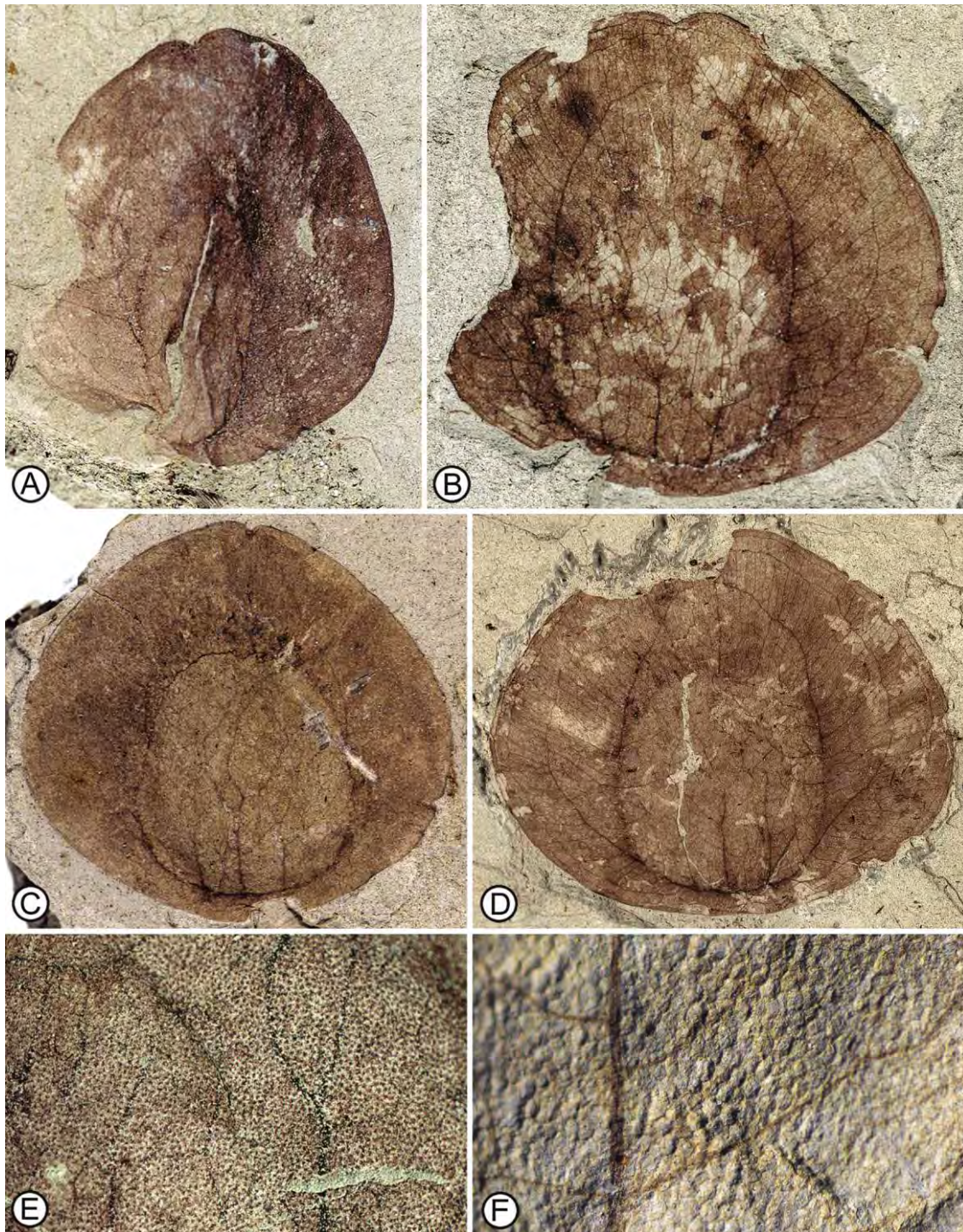
Fig. 4 Leaves of *Cobbania hickeyi* sp. nov. *A*, Small leaf showing apical notch, narrow aerenchymatous zone, and wide rim. Specimen DMNH 24959; ×2.9. *B*, Leaf with excellent venation showing apical notch, wide rim, and general vascular pattern as seen on the adaxial surface. DMNH 24888; ×2.4. *C*, Leaf as viewed from adaxial surface, showing apical notch, nearly circular aerenchymatous zone, slightly sunken below very wide rim, and three stronger veins near leaf base. DMNH 24891; ×2.7. *D*, Leaf with good venation, showing branching of collective veins from vein plexus in base of rim. Note wide collective vein spacing near rim. DMNH 24881; ×1.5. *E*, Leaf adaxial surface, showing numerous dense trichome bases. DMNH 24916; ×5.2. *F*, Leaf fractured through aerenchyma zone, showing pinnately branched major vein. Note hexagonal outlines of aerenchyma tissues. DMNH 30188; ×5.2.

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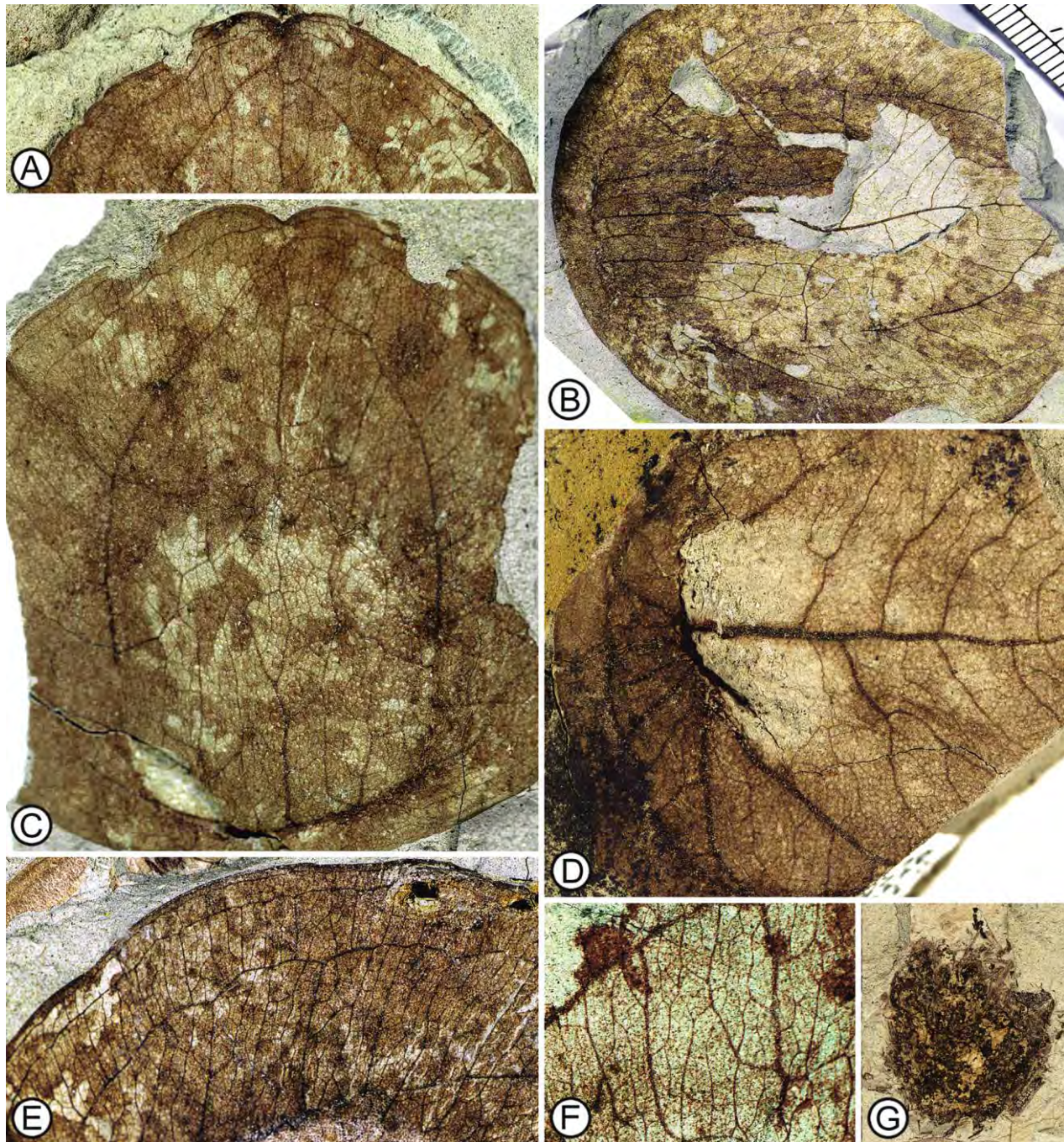
Fig. 5 *Cobbania hickeyi* sp. nov., leaf venation and associated reproductive structure. *A*, Leaf apex, showing convergence of primary and collective veins of rim merging in and below the apical notch. Specimen DMNH 24882; ×3.5. *B*, Leaf adaxial surface with fracture into the aerenchyma zone, showing pinnate central primary vein with dichotomizing lateral veins that end in inner-rim vein. DMNH 24934; ×1.8. *C*, Venation of central aerenchymatous zone as seen from the adaxial surface. Note dichotomizing and anastomosing veins. DMNH 24920; ×3.2. *D*, Unusual fractured leaf surface through aerenchyma zone. Note central primary vein with pinnate secondary veins that dichotomize, two lateral primary veins, and a basal confluence of seven other veins. Note basal rim at left. DMNH 24964; ×3.7. *E*, Venation in the leaf rim, showing rim edge vein (bottom right), three collective veins, and a fimbrial vein. Note wide spacing of inner collective veins and smaller veins that connect them, some of which branch at 90° angles. DMNH 24929; ×2.8. *F*, Areolation seen on adaxial leaf surface, showing elongate anastomoses and some dichotomous venation. DMNH 24893; ×5.5. *G*, Associated reproductive structure with ovoid dark bodies. DMNH 24924; ×1.5.

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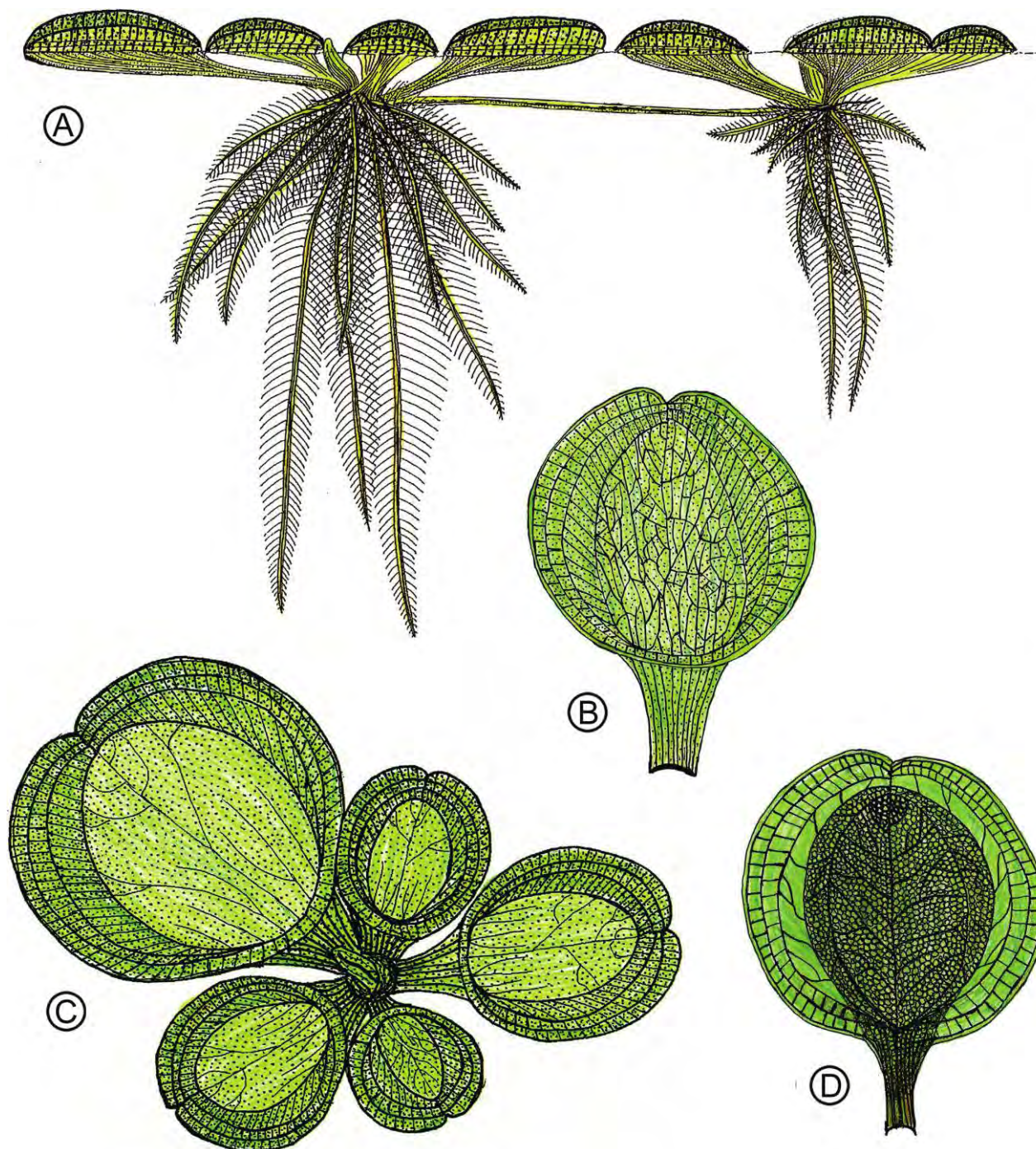
Fig. 6 Reconstructions of *Cobbania hickeyi* sp. nov. by R. Stockey. *A*, Growth habit of two floating rosettes connected by a stolon, as seen from side. *B*, Adaxial view of leaf, showing overall shape and the major venation of the petiole, central zone, and rim. *C*, Top view of a single rosette, showing helically arranged leaves. *D*, Abaxial view of leaf, showing overall shape and major venation of the petiole, central zone, and rim. Circular areas in the central zone represent arenchyma.

the actual structure of aerenchymatous tissues is preserved in the fine-grained matrix (fig. 4*F*). The central aerenchymatous zone of the leaf is round to oval in outline, 1.7–3.6 cm × 1.7–3.2 cm (figs. 1, 2*A*–2*C*, 4*A*–4*D*, 5*B*, 5*C*). In smaller, younger leaves, the aerenchyma zone is narrower laterally (e.g., fig. 4*A*, 4*C*), while this zone is wider in older leaves (e.g., fig. 1*B*). Occasional breaks through a leaf, as in figure 3*D*, show the appearance of a "basal pouch," as has been described for *C. corrugata*

(Stockey et al. 2007), but because of the wide rims in the Hell Creek specimens, leaves are more often exposed in the matrix, with the complete adaxial surface showing.

Where they can be counted, leaves show eight major petiolar veins at the base (fig. 3D), and these branch, forming up to 19 veins near the base of the leaf blade. The most prominent feature of the leaves is the broad, thin rim that encircles the thickened leaf (figs. 1, 2A–2C, 4A–4D). As the major veins enter the leaf blade from the petiole, they branch. The centrally located vein on the abaxial surface has pinnate secondary veins (figs. 2B, 3E, 5B, 5D). In addition, two lateral primary veins (figs. 1A [bottom right], 3E, 5D) show a similar branching pattern. The secondary veins arising from these three veins dichotomize several times. Several leaves in the collection show these three stronger veins on the midabaxial surface in addition to the veins in the rim edge (e.g., figs. 1A, 2B). Two of these three veins are present in the broken leaf in figure 3E. This appearance is not consistent, however, for all leaves examined, and the number of exposed veins depends on how the leaves were broken open during collecting.

The two lateral abaxial primary veins dichotomize on the abaxial surface to form the strongest lateral collective vein, which in turn dichotomizes several times to form the venation in the rim (figs. 3E, 4D). Because of the three-dimensional nature of these leaves, the overall venation pattern is difficult to determine and can be discerned and pieced together only by examining leaves that are broken at various places and in different planes (fig. 6B–6D).

What appear to be five adaxial primary veins also dichotomize as they reach the adaxial leaf surface (fig. 4C). These major veins dichotomize and anastomose in the leaf, forming tertiary and quaternary veins with polygonal, sometimes elongate, areolae (fig. 5A–5C, 5F). One leaf (fig. 5D) is fractured so that the central primary vein from the abaxial surface can be seen as well as the adaxial veins, and in this leaf veins appear to come from a central line or point (?peltate venation) and the rim still appears near the leaf base. However, in other leaves, such as those illustrated in figure 5B, 5C, the adaxial primary veins extend into the matrix and only the rim venation shows at the adaxial leaf surface; i.e., a confluence of primary veins does not appear to be present. While most of the central primary vein seems to be submerged in aerenchymatous tissue (see leaves in figs. 3E, 4F, 5B, 5D), this vein probably sends branches to the adaxial surface. The central vein itself appears to come to the adaxial surface near the apex, beneath the notch (fig. 5A–5C), joining with other, smaller veins at the surface. Leaves in figure 5B, 5D show the typical adaxial venation. The cut through the leaf in figure 5B shows the underlying primary vein. This primary vein is also seen in figure 5D. In figure 5B, the primary vein shows dichotomizing secondaries that are joining the inner rim margin (upper right). The central primary vein shows a somewhat sinuous course near the leaf apex, where the collective veins join at the notch.

Leaf margins are vascularized by a series of collective veins, derived from veins at the base of the rim (fig. 5E). There are two or three veins derived near the leaf base that divide to form up to four veins, including a fimbrial (marginal) vein in the rim (figs. 3E, 4B–4D, 5A, 5C, 5E). These collective veins in the rim are connected by small, closely spaced branching veins that arise at angles of about 90° near the leaf apex and from 45°

to 60° near the base of the leaf or near the strongest vein of the rim (fig. 5C, 5E). Collective veins converge near the apex in the apical notch (figs. 2A, 4A–4C, 5A, 5C). The inner marginal veins converge with the central primary vein below the notch, often at different points (fig. 5A, 5C).

Leaf surfaces are covered in a dense indumentum of trichomes (fig. 4E). Trichome bases, 150 µm in diameter, are also preserved on leaves that are fractured at the actual surface (fig. 4E). Because of the strong collective vein at the base of the rim and their concave surfaces when the rock is broken open, we believe that these leaves may have been slightly cup shaped on the surface of the water (fig. 6A). The trichomes, in addition to the aerenchyma, as seen in other aquatic plants, such as *Pistia stratiotes* L., helped the leaves to float on the water surface.

Roots. Up to 10 lateral roots have been observed attached to the bottom of the rosettes. These branched roots, some at least 7 cm long, produced large numbers of lateral roots up to 20 mm long at nearly right angles to the main root (fig. 8). In addition, one specimen (fig. 3C), shows small, unbranched roots arising directly from the stem itself. The large roots are up to 2 mm wide and have a dark central strand, presumably vascular, that is up to 1 mm wide (figs. 2D, 3A, 3B). The smaller lateral roots are about 0.1 mm wide. Because of their placement on the plant and orientation in the rock and the very delicate nature of the elongated secondary roots, we interpret these as aquatic roots (fig. 6A).

Associated fertile structures. An oval structure, similar to what has been reported at the *C. corrugata* sites (Stockey et al. 2007; Krassilov and Kodrul 2009), has been found at the Licking Leaves site (fig. 5G). That structure measures 22.7 mm × 20.0 mm. It is difficult to interpret because of its compressed nature and incomplete preservation, but it looks like a globular fruit with several seeds (fig. 5G).

One shortly stipitate, cylindrical, spadix with helically arranged units has been found associated with the Hell Creek plants (fig. 7A, 7C). The inflorescence/infructescence axis is 6 mm wide and at least 12 mm long, borne on a larger axis at least 33 mm long and 9 mm wide, which might also include the base of a broken spathe (fig. 7A). There are at least 60 helically arranged, coalified structures arranged in nearly vertical rows on the surface of the exposed spadix (fig. 7A, 7B). Whether these represent flowers, fruits, or fruit scars is uncertain. The structures are hexagonal in outline and 0.8–1.0 mm in diameter and sometimes show a dark central spot (fig. 7C), which could possibly be the stigma. In other parts of the spadix, this tissue has been ripped away, possibly when the specimen was exposed. The uniform structure of the hexagonal compressions suggests that this spadix produced flowers of only one morphology, which is characteristic of aroid species with bisexual flowers.

On one side of the axis, below the spadix, there is a cluster of seeds and associated tissues (fig. 7A–7C) that may represent a fruit similar to the one described earlier in this article and those that have been found in association with previously described specimens of *C. corrugata* (Stockey et al. 2007; Krassilov and Kodrul 2009). This squashed cluster measures 13 mm across and either is extending from behind the main axis or is located directly adjacent to the axis (fig. 7A, 7C). The ovoid seeds are ca. 3.5 mm wide and have a shiny surface (fig. 7C). It is possible that this material fell off the spadix above. Alternatively, this
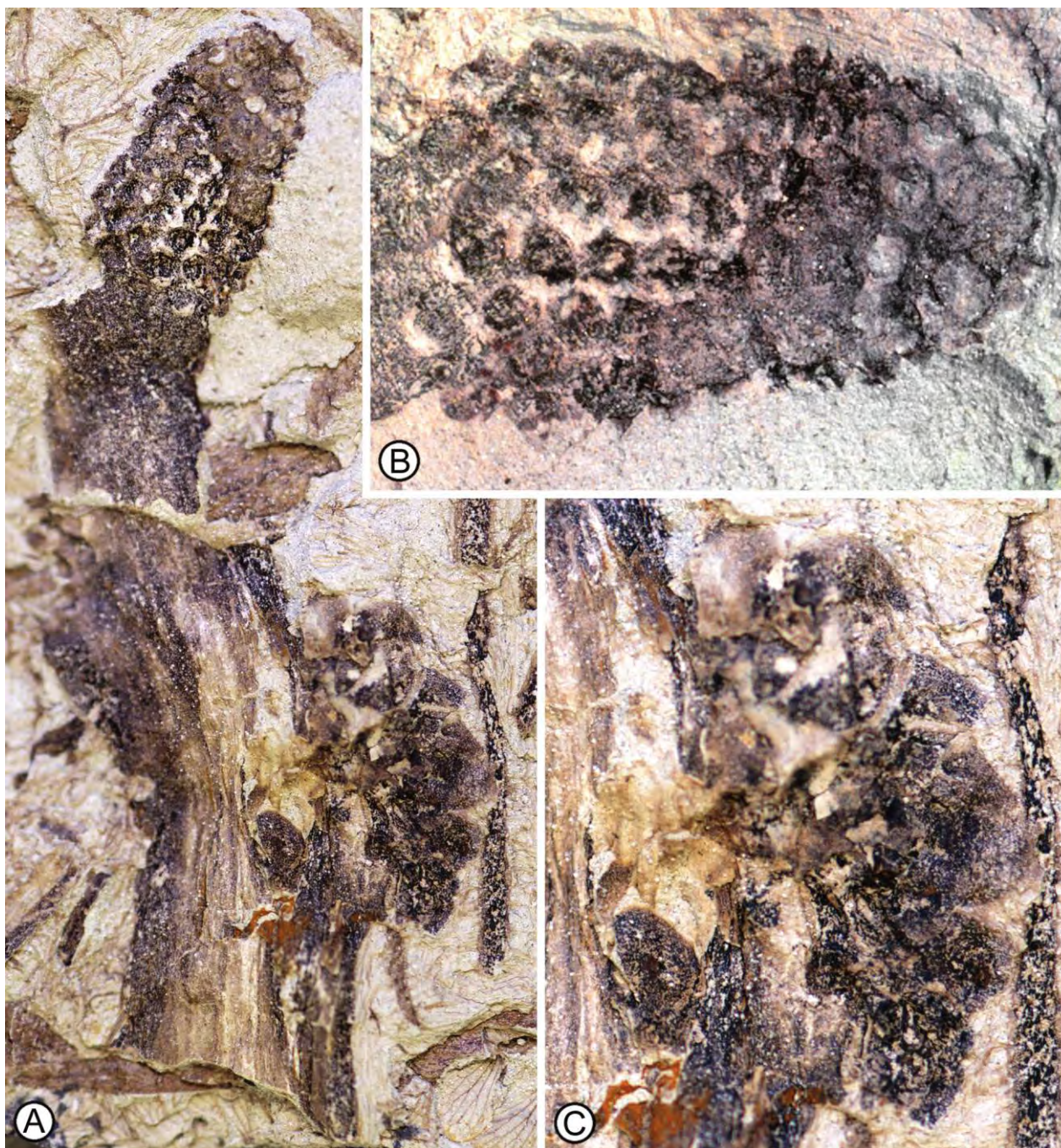
Fig. 7 Spadix and reproductive structure associated with *Cobbania hickeyi*. Specimen DMNH EPI.35479. *A*, Longitudinal view of shortly stipitate spadix with helically arranged scars. Note reproductive structure with cluster of seeds beneath lower portion of axis; ×4. *B*, Surface of spadix, showing at least 60 helically arranged hexagonal scars; ×8.5. *C*, Reproductive structure, showing at least one ovoid seed (lower left); ×8.

could be a completely separate structure (see the small portion of matrix showing between two axes in fig. 7*A*, 7*C*). A spathe could not be demonstrated with certainty, and there is a break in the specimen below the attachment of the actual spadix (fig. 7*A*). This break is taphonomic, as it occurs across the entire rock and through several other tissues of nearby plants (fig. 7*A*). The tissues of the axis that continue into the spadix are of the same texture and appearance as those below the break (fig. 7*A*).

The specimen ends at the rock edge, and a possible attachment was not collected.

Phylogenetic Analyses

As detailed in "Material and Methods," several phylogenetic analyses have been performed to help clarify relationships of *Cobbania* to other fossil and living species of monocots and

to test several previously proposed hypotheses for relationships among the included taxa.

Analyses of type 1. The first group of analyses were conducted to test the hypotheses presented earlier in this article that *C. hickeyi* is closely related to *C. corrugata*, that *Cobbania* is a genus of either the Araceae (Stockey et al. 2007) or the alismatids (Krassilov and Kodrul 2009) in clade I (Alismatales) of Les and Tippery (2013), and that *Aquaephyllum auriculatum* is a floating aquatic monocot that nests among the other floating aquatic species of Araceae (Gallego et al. 2014). The morphological matrix for these analyses consists of 40 taxa and 46 systematically informative morphological characters (Morphobank Matrix 23,955).

Results of the first form of analysis 1 (i.e., with characters 1 [habitat of growth] and 2 [floating aquatic life form] coded as "?") yield 20 most parsimonious trees of 185 steps (consistency index [CI] = 41, retention index [RI] = 71). Sixteen nodes collapse in the strict consensus tree (SCT) of those results, producing a tree (fig. 8*A*) that consists of a fully resolved clade of alismatids (blue branches in fig. 8*A*) arranged as *Butomus* + (*Stratiotes* + (*Ottelia* + *Thalassia*)) + ((*Alisma* + *Sagittaria*) + (*Limnocharis* + (*Hydrocharis* + *Limnobium*))) that is the sister group to a large polytomy of Araceae (fig. 8*A*). Within the Araceae polytomy, almost all of the taxa are attached either individually or as small clades of two or three. The only larger clade in this polytomy is fully resolved and consists of the eight species of floating aquatic Araceae (green branches in fig. 8*A*). As in the results of earlier phylogenetic analyses of morphological characters (Stockey et al. 1997; Gallego et al. 2014), the floating aquatic clade (green branches in fig. 8*A*) is arranged with *Pistia* at the base, the Lemnoideae at the apex (i.e., *Spirodela* + (*Lemna* + (*Wolffia* + *Wolffiella*))), and the extinct species attached to the stem in between. In our results, the extinct species consist of the small *Cobbania* clade (i.e., *C. corrugata* + *C. hickeyi*), and *Limnobiophyllum scutatum* attached at adjacent nodes on the stem of the floating aquatic Araceae clade between the nodes where *Pistia* and the Lemnoideae are attached (green branches in fig. 8*A*). *Aquaephyllum auriculatum* occurs within the aroid polytomy as a single species (fig. 8*A*, red, with arrow) and is not a member of the clade of floating aquatics (fig. 8*A*).

Although one must have much lower confidence in the results represented by the majority-rule consensus tree (MRCT) of these results, that tree is almost fully resolved (i.e., only five nodes collapse). This tree (fig. 8*C*, not figured in full) differs from that in figure 8*B* only by the position where *Aquaephyllum* attaches to the stem of the tree (cf. fig. 8*B*, 8*C*; see fig. 8 legend for further explanation).

In the second form of analysis 1, *A. auriculatum* is recoded as occupying an aquatic habitat (i.e., state 1 for character 1) but remains equivocal for growth form (i.e., coded as "?" for character 2). The results of the second form of analysis 1 yield fewer (i.e., 6) most parsimonious trees of the same length as in the first analysis, but the SCT of those results has the same topology as found in the first analysis (fig. 8*A*).

In the third form of analysis 1 (i.e., when *A. auriculatum* is recoded both as growing as a floating aquatic and occupying an aquatic habit [i.e., state 1 for characters 2 and 1, respectively]), results of the analysis yield only four most parsimonious trees of the same length as in the previous analyses. In the SCT from the third form of analysis 1, only four nodes collapse, yielding a tree

(fig. 8*B*) that is similar to the MRCT from the second form of analysis 1, but with one fewer unresolved node. As stressed above, the MRCT from the second form of analysis 1 is nearly identical to the SCT from the third form of analysis 1 (fig. 8*B*). The two trees differ only by the position of *A. auriculatum*, which occurs at the base of the Araceae as part of an *Anadendrum–A. auriculatum–Pothos* polytomy in the MRCT from the first form of analysis 1 (fig. 8*C*) and at the base of a clade of floating aquatic aroids in the SCT from the third form of analysis 1 (fig. 8*B*).

Analysis 2. In analysis 2, relationships among all of the aroid taxa from analysis 1 (including *A. auriculatum* but with all of the alismatid taxa omitted) are analyzed with the same morphological characters as in analysis 1, with *A. auriculatum* coded as "?" for characters 1 and 2 (Morphobank Tree 33,956). Results of that analysis yielded two most parsimonious trees of 128 steps (CI = 51, RI = 75), yielding an almost fully resolved SCT in which only three nodes collapse. In this tree (fig. 8*D*), *A. auriculatum* is attached to the stem near the base of the tree, and the floating aquatic aroids form the same fully resolved clade at the tip of the tree as in the results of all three forms of analysis 1 (fig. 8*A*, 8*B*, 8*D*). The remaining aroids are arranged in nearly the same order as in the SCT from the second form of analysis 1 (but contrast the relationship between *Anadendrum* and *Pothos* in fig. 8*B*, 8*D*).

Analyses of type 3. In type 3 analyses, relationships among the all of the living and extinct aroid taxa from analysis 2 are analyzed with a combination of the 4494-nucleotide sequence characters of Cusimano et al. (2011) and the 46 morphological characters from analyses 1 and 2 (matrix deposited in the Documents folder of Morphobank Project 2340). For this "total-evidence" matrix, all of the morphological characters have a maximum of four character states. To achieve this constraint, only one character required modification; for character 13, character states 2 and 3 were combined.

Results of that analysis yielded 50 most parsimonious trees of 2720 steps (CI = 71, RI = 68). In the SCT of those results, *Gymnostachys* attaches to the stem at the node above the root (*Acorus*), a fully resolved clade of floating aquatic extinct taxa and living Lemnoideae occurs at the next node on the stem, and the remaining aroids form a large polytomy at the apex of the tree (fig. 8*E*). That polytomy includes the extinct aroid *A. auriculatum* (fig. 8*E*). The fully resolved clade of floating aquatics consists of the extinct aroids (i.e., *L. scutatum* + (*C. corrugata* + *C. hickeyi*)) as the sister group to the lemnoid Araceae (i.e., *Spirodela* + (*Lemna* + (*Wolffia* + *Wolffiella*))). The remaining aroid taxa (including *Pistia* and *Aquaephyllum*) form a large polytomy of single species and small clades at the last node on the stem of the tree (fig. 8*E*).

When *A. auriculatum* is coded as having an aquatic habitat (i.e., state 1 of character 1), the analysis yields 18 trees of 2720 steps (CI = 71; RI = 86). In the SCT of those results, only 12 nodes collapse, but the topology of the SCT is the same as that in the previous results (fig. 8*E*). When *A. auriculatum* is coded as having an aquatic habitat and a floating aquatic life form (i.e., state 1 for both characters 1 and 2) the analysis yields 30 trees of 2721 steps (CI = 71; RI = 86). In the SCT of those results, 12 nodes collapse, producing the same topology as the previous results from variations of analysis 3 (fig. 8*E*). The MRCT of those results (fig. 9) is far more highly resolved than the SCT topology (fig. 8*E*). This tree (fig. 9) is generally concor-
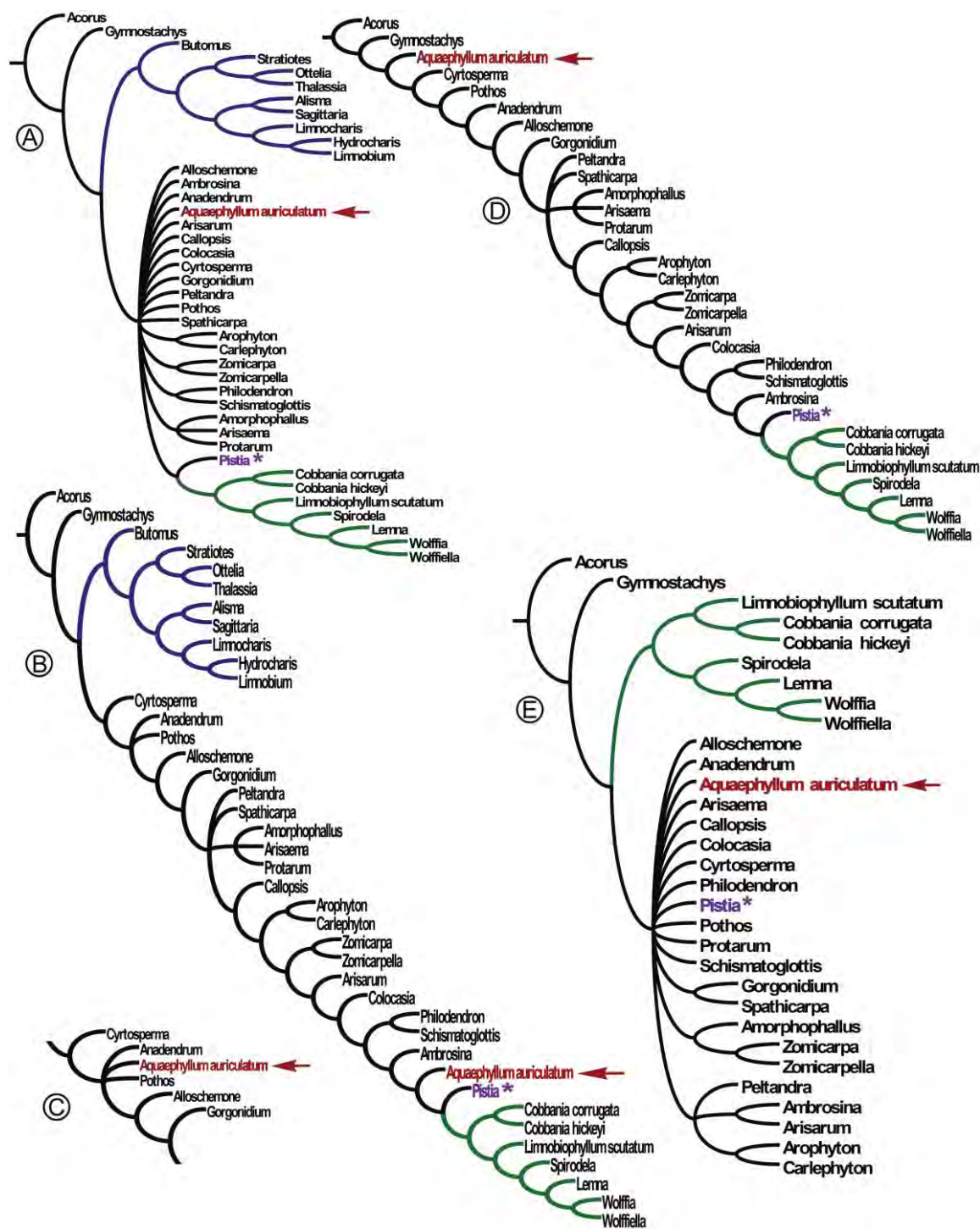
Fig. 8 Phylogenetic trees showing relationships among *Cobbania* spp., *Aquaephyllum auriculatum* (in red, with arrow), *Pistia* (in purple, with asterisk), other living and extinct floating aquatic monocots of Araceae (including Lemnoideae), and representative genera of major clades of Araceae and clade I alismatids of Les and Tippery (2013). See text for discussion of details of all trees. *A*, Strict consensus tree (SCT) from the first form of analysis 1. Alismatids (blue branches) form a fully resolved clade near the base of the tree, and Araceae occur in a large polytomy. Note *Pistia* (in purple, with asterisk) as sister to remaining extinct floating aquatic plus genera of Lemnoideae (green branches) in a fully resolved clade within the polytomy. Note that *A. auriculatum* (in red, with arrow) also occurs in the large aroid polytomy but does not nest with floating aquatic aroid taxa. *B*, SCT of third form of analysis 1, where *A. auriculatum* is coded as a floating aquatic (characters 1 and 2) to strengthen possible relationships of that species to floating aquatic Araceae. Note that the tree is much more fully resolved than that from first form of analysis 1. *Aquaphyllum auriculatum* is attached to the stem near the base of the tree, whereas floating aquatic taxa form a clade at the tip of the tree. *C*. Small segment of majority rule consensus tree from first form of analysis 1, wherein *A. auriculatum* forms a polytomy with

dant with the maximum likelihood results of Cusimano et al. (2011) but is somewhat less fully resolved. In addition, both trees of our results show the positions on the tree that are occupied by the extinct species, which are not included in the Cusimano et al. (2011) results.

Discussion

The fossil plants described here from the Hell Creek Formation are preserved in growth position, exhibit a novel combination of characters, and clearly represent a new species of the genus *Cobbania* Stockey, Rothwell & Johnson. The plants were aquatics that grew in a small pond before becoming entombed by a fine-grained mud. These plants consist of rosettes interconnected by stolons, individual rosettes having floating aquatic roots and helically arranged trumpet-shaped leaves. Leaf blades are characterized by the vascularized rim and apical notch that are characteristic of *Cobbania* (Stockey et al. 2007), but they also show several differences from the previously described species (table 1).

Cobbania hickeyi stems are only about half the diameter of those in the previously described species, *Cobbania corrugata*. (Stockey et al. 2007; table 1). In addition, petioles in *C. corrugata* are longer than any reported for the new species described here (table 1). The number of primary veins entering the petiole is difficult to distinguish in both of these species because of the fleshy nature of the leaves and fossilization by compression, and it cannot be determined from observation of any single specimen. The two species probably had a similar number of major veins arising from the main stem. The three most noticeable characters that distinguish the two species include the wider leaf rims, vascularized stolons, and three abaxial major veins with pinnate secondary venation that occur in leaves of the Hell Creek *Cobbania* (table 1). While in *C. corrugata* the rim is only 5–7 mm wide, the Hell Creek leaves have rims at least 16 mm wide, in one case 20 mm near the leaf apex (table 1). In *C. corrugata*, the stolons do not show a darkened central zone, while the large floating roots do (Stockey et al. 2007). In *C. hickeyi*, both stolons and large roots show a darkened central band, which may represent the stele (table 1). It could be supposed that the presence (*C. hickeyi*) or absence (*C. corrugata*) of a dark central area that represents vascular tissue in the stolons could be due to differential preservation between plants from the two localities. However, all of the other vascular tissues are preserved in a comparable fashion for both species, and the stolon is the only organ to show this type of difference in preservation of putative vascular tissues. Therefore, it is unlikely that this difference is of taphonomic origin.

Perhaps the most striking difference between the new *Cobbania* leaves and those of *C. corrugata* is the presence of three centrally located, abaxial major veins in *C. hickeyi* that show a pinnate pattern of branching secondaries (table 1). This does not occur in any of the *C. corrugata* leaves that have been studied. One specimen of *C. corrugata*, illustrated by Stockey et al.

(2007, fig. 12), a young leaf from one of the rosettes, shows what might be a pinnately branched abaxial vein. However, this leaf was exposed on the adaxial surface, and this character cannot be confirmed. None of the abaxial breaks through *C. corrugata* leaves show pinnate divisions (cf. fig. 12 and fig. 11 in Stockey et al. 2007). In this regard, the Campanian material of *Cobbania* from the Amur Region of Russia described by Krassilov and Kodrul (2009) and similar specimens from the Santonian-Campanian of China (Quan and Sun 2008) appear to be similar in all respects to *C. corrugata*. Thus, we describe the Maastrichtian Hell Creek specimens as the new species *C. hickeyi* Stockey, Rothwell & Johnson.

Krassilov and Kodrul (2009) described reproductive structures found in association with the *C. corrugata* specimens from Russia. These structures, like those of *C. corrugata* from western North America (Stockey et al. 2007), are preserved as compression/impressions of dispersed infructescences with fruits and/or seeds that were not preserved in attachment to specimens of *Cobbania*. Krassilov and Kodrul (2009) named their isolated reproductive material *Cobbanicarpites amurensis* Krassilov & Kodrul. The fruits were described as emerging from a spathulate bract that detached at maturity, with persistent laminar appendages and numerous elliptical to obovate seeds with caps or opercula. The seed integument is two-layered and contains papillae between the layers, presumably interpreted as "endotegmen tuberculae," as have been reported in Hydrocharitaceae (Shaffer-Fehre 1991*a*, 1991*b*). Krassilov and Kodrul (2009) compared the reproductive structures with those of *Hydrocharis* (Hydrocharitaceae) and other alismatalean families, including Araceae. However, the interpretation of the reproductive structures described by Krassilov and Kodrul is difficult to confirm because of the mode of preservation (i.e., highly flattened compression/impression). It is clear that seeds are operculate, with an apparently two-layered integument with what appear to be papillate cells in the inner integumentary layer. Micropylar caps are known in a number of angiosperm families (Baskin and Baskin 2001), often in plants that have seeds with an impermeable layer. In *Pistia* L. (Araceae), seeds are orthotropous and operculate, as in the fossil material from Amur and North America, but are barrel shaped, with an irregular surface (Seubert 1993) that is described as reticulate-aveolate with small pits (see fig. 14 of Bogner 2009). However, the germination valve in *Pistia* seeds is similar to that described for *Keratosperma* Cevallos-Ferriz & Stockey (1988; also Smith and Stockey 2003) and other extant lasioids (Araceae) in which there is a thin micropylar cover (Seubert 1993; Kvaček and Bogner 2008). By contrast, the Krassilov and Kodrul (2009) seeds show an operculum similar to that seen in some Nymphaeales (Collinson 1980; Cevallos-Ferriz and Stockey 1989; Taylor et al. 2006; DeVore et al. 2015).

Leaves of Hydrocharitaceae, such as those of *Hydrocharis* L. and *Limnobium* L.C., do show a centrally located aerenchymatous zone; however, they usually have a cordate or reniform base with a basal "sinus" (Cook and Lüönd 1982). They are

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Anadendrum and *Pothos*. *D*, SCT of results from analysis 2 (Araceae), showing topology largely concordant with Araceae from SCT of third form of analysis 1. The most important difference for the purposes of this article is the position of *A. auriculatum*, which does not nest with fully resolved terminal clade of floating aquatics. *E*, SCT of results from "total-evidence" analysis of Araceae, in which floating aquatic living and extinct aroids are sister groups of a fully resolved clade that occurs near the base of the tree. Note that *A. auriculatum* does not nest with floating aquatic aroids in these results.
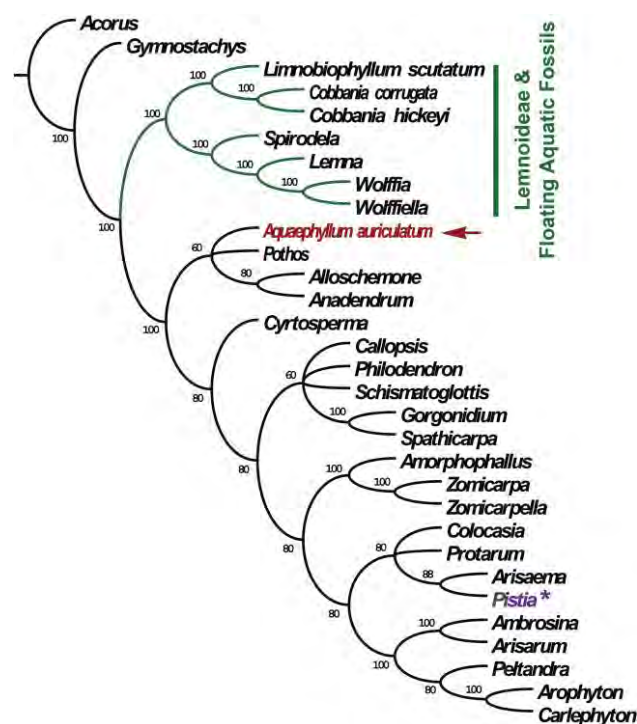
Fig. 9 Majority rule consensus tree of results from the "total-evidence" analysis of Araceae, showing much more resolution than the strict consensus tree from same analysis (fig. 8E). Results are generally concordant with those from analysis of nucleotide sequences for living taxa only (Cusimano et al. 2011). Note the positions of floating aquatic Lemnoideae + extinct floating aquatic aroids, *Aquaephyllum auriculatum*, and *Pistia* on the tree that imply three separate origins of floating aquatic Araceae. Numbers indicate the percentage of trees in which each node is resolved. Color coding as in figure 8. See text for details.

rolled in bud and have two basal stipules (Wilder 1974; Cook and Lüönd 1982; Cook and Urmi-König 1983; Les et al. 2006). While leaves of both species of *Cobbania* do show clasping petiole bases, we have been unable to demonstrate the presence of stipules, and leaf bases are not cordate but inflated. Structure of the leaves in bud could not be demonstrated in any of the specimens of either *Cobbania* species.

Neither the *C. amurensis* reproductive structures nor the spadix illustrated here were found in attachment to the *Cobbania* rosettes at any of the known localities. Until such attachments are found, we cannot be sure of the affinities of either of these reproductive structures, as either or both could have been produced by other aquatic plants that are present at the localities. We are still inclined, however, to regard *Cobbania* as a member of Araceae because of the venation pattern in the leaves and the clasping leaf bases without stipules. Moreover, our interpretation is supported by the position of the two *Cobbania* species in the results of our phylogenetic analyses (fig. 8A, 8B).

Recently, a new genus and species of fossil Araceae, *Aquaephyllum auriculatum* Gallego, Gandolfo, Cúneo & Zamaloa, was described from the Upper Cretaceous (Maastrichtian) of Patagonia, Argentina (Gallego et al. 2014). *Aquaephyllum* leaves are described as petiolate, with an inflated leaf base and aerenchymatous tissue; however, they differ from those

of *Cobbania* in leaf venation and leaf margin (Gallego et al. 2014). Leaf margins are crenate in *Aquaephyllum*, with occasional glands, while leaf margins in *Cobbania* are smooth. Submarginal collective veins and rims like those of *Cobbania* spp. are absent in *Aquaephyllum* (Gallego et al. 2014). In addition, *Aquaephyllum* leaves are described as being auriculate, a feature lacking in *Cobbania*, and they lack an apical notch like that of *Cobbania* species. While the venation that forms areolae in *Aquaephyllum* is dichotomizing and anastomosing, as in *Cobbania*, it does not form elongate meshes and has a clearly different aspect.

Although *A. auriculatum* is represented by only four more or less complete specimens of dispersed leaves and smaller disarticulated fragments (Gallego et al. 2014; R. A. Stockey and G. W. Rothwell, personal observation, 2015), the specimens do occur in an aquatic depositional setting along with dispersed roots and pollen from the same formation (Cúneo et al. 2014; Gallego et al. 2014). Therefore, while those specimens could possibly represent floating aquatic plants, there is currently no evidence that they consist of rosettes with attached leaves and roots that are interconnected by stolons (as suggested by Gallego et al. 2014) like those of *Cobbania* spp. and *Limnobiophyllum* spp. (Kvaček 1995; Stockey et al. 1997). Alternatively, the small number of leaves from disarticulated plants of *A. auriculatum* that have thus far been found could be from individuals that grew near (but not in) the water and were merely deposited in sediments of aquatic origin. Currently, there is no evidence to confirm that isolated roots and dispersed pollen from the same deposits with leaves of *A. auriculatum* actually are from *A. auriculatum* plants.

Limnobiophyllum scutatum (Dawson) Krassilov (Araceae) is another extinct floating aquatic species with a minor-vein pattern like that of *Aquaephyllum*. However, unlike those of *Aquaephyllum*, *L. scutatum* leaves have smooth margins and marginal veins, and *L. scutatum* lacks elongate petioles (Stockey et al. 1997). In 1997, Stockey et al. described *Pandaniidites* Elsik pollen grains (long thought to be pollen of Pandanaceae) in the flowers of *L. scutatum* from the Paleocene Joffre Bridge locality of Alberta, Canada, thus demonstrating that this pollen type is indicative of aquatic habitats rather than of frost-free environments. As indicated by Gallego et al. (2014), *Pandaniidites* grains also occur in the same geological formation as the *Aquaephyllum* leaves (i.e., the Maastrichtian La Colonia Formation) and were ascribed to *Aquaephyllum* in their analysis. However, because such grains are not known to occur in reproductive structures attached to the leaf specimens of *Aquaephyllum*, we consider the affinities of *Pandaniidites* in the La Colonia Formation to remain equivocal.

Systematic Relationships among Floating Aquatic Species of Araceae (including Lemnoideae)

Until the mid-1990s, systematic relationships of the Lemnaceae, now considered the subfamily Lemnoideae of the Araceae (Cabrera et al. 2008; Bogner 2009; Cusimano et al. 2011; Nauheimer et al. 2012; Mayo et al. 2013; Henriquez et al. 2014), and the floating aquatic aroid *Pistia stratiotes* were poorly resolved (Mayo et al. 1995). However, the phylogenetic analysis of morphological characters accompanying the description of the Paleocene fossil *L. scutatum* resolved *Pistia* at the base of a clade

Table 1

Comparison of *Cobbania* Species Based on Contrasting Morphological Characters

Species	Stem diameter (mm)	Maximum petiole length (cm)	Primary veins entering petiole[a]	Widest rim width (mm)	Vascularized stolons	Three pinnate abaxial veins
C. corrugata[b]	10–17	1.5	6–9	5–7	No	No
C. hickeyi	5–7	1.0	8	16–20	Yes	Yes

[a] Exact number difficult to determine because of compression of veins in fossilization.

[b] Data for *C. corrugata* from Stockey et al. (2007).

of floating aquatic species within the Araceae that included all of the living genera of Lemnoideae (Stockey et al. 1997). A concurrent treatment of the family Araceae placed *Pistia* within the subfamily Aroideae and discussed similarities and differences between *Pistia* and Lemnaceae but did not include Lemnaceae within phylogenetic analyses (Mayo et al. 1997). Because molecular analyses at the time were inconclusive for the placement of Lemnaceae within Aracaeae, Stockey et al. (1997) suggested that *Limnobiophyllum* and *Pistia* may be closely associated in the results of their analysis because of their floating aquatic habit, rather than from close systematic affinities. Among the cladistic analyses conducted by Stockey et al. (1997) was one test in which characters that were associated with the floating aquatic growth form were removed (Stockey et al. 1997), but *Pistia* and *Limnobiophyllum* still grouped together despite their differences in pollen morphology, leaf form, and so on (Mayo et al. 1997).

Rothwell et al. (2004) analyzed relationships among a larger number of aroid/lemnoid taxa, using the chloroplast *trn*L-*trn*F intergenic spacer to test the hypothesis of close relationships between Lemnoideae, *Pistia*, and other Araceae. This and other, more recent studies using nucleotide sequence characters (e.g., Cabrera et al. 2008; Cusimano et al. 2011; Henriquez et al. 2014) point to two origins of the floating aquatic habit within living Araceae. During the subsequent description of *C. corrugata* (Stockey et al. 2007), that whole-plant species of fossils was not included in a morphological matrix, since preliminary analyses resolved relationships with *Pistia* and the Lemnoideae similar to those found by Stockey et al. (1997). We suggested at the time that *Cobbania* probably represented a third group of floating aquatic aroids because of the major differences in leaf venation and general structure, as compared to the leaves of *Pistia* and species of Lemnoideae (Stockey et al. 2007).

More recently, Gallego et al. (2014) performed a phylogenetic analysis of morphological characters to help establish the systematic relationships of *Aquaephyllum*. The results of that analysis found essentially the same relationships among floating aquatic aroids as did Stockey et al. (1997), except that *C. corrugata* and *Aquaephyllum* were added to the clade of floating aquatic aroids. Their analysis was modified from that of Stockey et al. (1997) by the addition of *C. corrugata* and *A. auriculatum* and with some modification and a small reduction in the number of characters. More importantly, several characters that we consider to be equivocal for *Aquaephyllum* were coded in that analysis (Gallego et al. 2014). The equivocal characters of Gallego et al. (2014) that we recoded as "?" in our analysis are aquatic habit of growth (character 1), floating aquatic habit (character 2), roots present (character 25), pollen shape ellipsoid (character 42), pollen monosulcate (character 43), and ex-

ine sculpturing echinate (character 46 in the appendix; Morphobank Matrix 23,955).

We (R. A. Stockey and G. W. Rothwell) reexamined the type specimens of *A. auriculatum* at the Museo Paleontológico Egidio Feruglio (MEF), Trelew, Argentina, and confirmed that (1) the species is represented primarily by only four specimens of more or less complete leaves, (2) there is no evidence of pollen or flowers attached to *Aquaephyllum*, and (3) there is no evidence of stem and/or root attachment (i.e., the leaves are from disarticulated plants). These specimens consist of leaves whose venation patterns and crenate margins differ markedly from those of other extant and extinct aquatic aroids. Leaves appear to be thin but may have contained some aerenchyma near the center. However, they also lack the basal pouch or trumpet-shaped base of *Cobbania* and the trichomes and venation patterns of *Pistia*. With the equivocal characters of *Aquaephyllum* recoded as "?," that genus attaches to the stem of the tree among the other aroids in the analysis of the morphological matrix (fig. 8*A*) and is not closely related to the floating aquatic species of monocots in our current analysis. Only when *Aquaephyllum* is coded as being a floating aquatic monocot (i.e., state 1 for characters 1 and 2) does that species nest with a clade of floating aquatic aroids (fig. 8*B*). However, even when coded as a floating aquatic monocot, *Aquaephyllum* does not nest with that clade in the results of the "total-evidence" analysis (figs. 8*E*, 9).

Although the depositional environments represented by the La Colonia Formation are well characterized and the fossils clearly are from aquatic sediments Cúneo et al. (2014), only a small number of isolated specimens of *A. auriculatum* from disarticulated plants have thus far been discovered (Gallego et al. 2014). This suggests that, like the conifer remains that also occur in the deposits (Cúneo et al. 2014), *Aquaephyllum* plants may have grown on land adjacent to the aquatic environments in which they are deposited. If this supposition is correct, this difference in growth environment may help explain why some features of *A. auriculatum* are unlike those of typical floating aquatic aroids and why *A. auriculatum* does not nest with the floating aquatics in the results of most of our analyses (figs. 8, 9).

Although the occurrence of aquatic plants in the fossil record is relatively uncommon in Mesozoic and Paleogene deposits, such floras reveal communities of aquatic vegetation that consist of a continuously changing combination of lycopods, ferns, equisetophytes, conifers, dicots, and monocots, some of which are rooted wetland plants while others are floating aquatics (e.g., McIver and Basinger 1994; Hoffman and Stockey 1997; Kvaček et al. 2004; Riley and Stockey 2004; Cúneo et al. 2014). Such floras document a greater diversity of extinct Araceae/Lemnaceae than is represented in the modern flora, but the in-

completeness of many extinct species and the infrequency of occurrences leave the systematic relationships of many fossils in doubt. Assignment of species of *Cobbania* and *Limnobiophyllum* to the family Araceae as the sister group to the subfamily Lemnoideae is relatively firm, but the paucity of attached flowers and fruits (but see Stockey et al. 1997 for an exception) render their relationships to each other uncertain and their placement among the more highly resolved species of living Araceae and Lemnoideae tentative.

As Cusimano et al. (2011) point out, aquatic life forms of several kinds occur within all major clades of Araceae, and a major theme in the phylogeny of Araceae involves a complex evolution to and from water-associated life forms (Cook 1999). The genus *Pistia* and taxa of the Lemnoideae represent extreme aquatics, as do the fossils of *Limnobiophyllum* and *Cobbania*. The discovery of *C. hickeyi* in the Hell Creek Formation of South Dakota reveals the presence of a second species of the *Cobbania* and extends the range of the genus to near the Cretaceous-Paleogene boundary. More importantly, the new species adds additional data about possible fertile structures of the genus and provides an opportunity to test competing hypotheses for the pattern of evolution among floating aquatic monocots.

Phylogenetic Relationships of Cobbania spp.

While our understanding of aroid/lemnoid evolution and phylogeny remains incomplete, analyses of morphological characters in living and extinct species that include the new data on *C. hickeyi* continue to support the hypothesis that the floating aquatic lemnoids *Cobbania* spp., *Limnobiophyllum* spp., *P. stratiotes*, and species of the Lemnoideae form a monophyletic group (fig. 8*A*, 8*D*). Concurrently, the most recent phylogenetic analyses of living species using nucleotide sequence characters (Cusimano et al. 2011) continue to contradict those results by resolving trees that show that free-floating aquatics have evolved

at least two times among living araceous alismatids (Cabrera et al. 2008; Cusimano et al. 2011). Our analyses that test these competing hypotheses, by employing several analyses of the same taxa that use either morphological characters or a combination of morphological and nucleotide sequence characters for both living and extinct species, continue to produce a variety of topologies, but results from the total-evidence analysis (i.e., including both living and extinct taxa and both morphological and molecular characters) are highly compatible with aroid trees derived from analyses of nucleotide sequences for living species only (figs. 8*E*, 9). Results of the latter analyses suggest that morphological specializations for the floating aquatic growth form in plants like *Cobbania*, *Limnobiophyllum*, and *Pistia* could possibly be overwhelming other morphological characters in the results of analyses that integrate living and extinct Araceae. These data highlight the difficulties of using aquatic fossil plants in phylogenetic analysis of living plus extinct species, even when whole plants are reconstructed, thus emphasizing the need for denser sampling of the fossil record and for the thorough evaluation of the available anatomical and morphological data.

Appendix

Description of morphological characters scored in the data matrix. Characters modified from Stockey et al. (1997), Les et al. (2006), Li and Zhou (2009), Cusimano et al. (2011), and Gallego et al. (2014).

1. Habitat of growth; (0) not aquatic, (1) fresh water or brackish, (2) marine; modified from character 1 of Stockey et al. (1997) and character 35 of Cusimano et al. (2011)
2. Aquatic habit; (0) helophytes, (1) floating aquatics, (2) submerged aquatics, (3) rheophytes, (4) amphibious; modified from character 2 of Stockey et al. (1997) and character 35 of Cusimano et al. (2011)
3. Phyllotaxy; (0) distichous, (1) helical, (2) subdistichous; character 7 of Cusimano et al. (2011)
4. Stem; (0) with nodes and internodes, (1) as centrum, (2) apparently absent; character 3 of Stockey et al. (1997)
5. Budding from pouch; (0) absent, (1) present; character 4 of Stockey et al. (1997)
6. Vegetative reproduction by fragmentation; (0) absent, (1) present; character 5 of Stockey et al. (1997)
7. Vegetative reproduction by stolons; (0) present, (1) absent; character 6 of Stockey et al. (1997)
8. Stem stele; (0) atactostele, (1) protostele or strand, (2) absent; character 16 of Stockey et al. (1997)
9. Prickles on stem or petiole; (0) absent, (1) present; character 30 of Cusimano et al. (2011)
10. Petiole; (0) present, (1) absent; character 9 of Stockey et al. (1997)
11. Leaf; (0) simple, (1) compound; character 7 of Gallego et al. (2014)
12. Trumpet-shaped leaves with inflated aerenchymatous petiole; (0) absent, (1) present; new character
13. Leaf (blade) shape; (0) linear to strap shaped, (1) sagittate or cordate (may be deeply lobed), (2) circular to reniform, (3) ovate to ovate linear, (4) pedatisect/radiatisect; modified from character 10 of Stockey et al. (1997); replaces character 8 of Gallego et al. (2014)

14. Blade base shape; (0) acute, cuneate, obtuse, or rounded, (1) cordate-sagittate, (2) peltate, (3) equitant; new character
15. Leaf division; (0) not lobed, (1) lobed; character 9 of Gallego et al. (2014)
16. Leaf margin; (0) entire, (1) not entire (serrate, dentate, crenate); modified from character 27 of Cusimano et al. (2011); character 10 of Gallego et al. (2014)
17. Leaf blade with apical notch; (0) absent, (1) present; new character
18. Auricle; (0) absent, (1) present; character 11 of Gallego et al. (2014)
19. Leaves with distinct abaxial pad or zone of aerenchyma; (0) absent, (1) present; new character
20. Major venation in leaf/frond, (0) pinnate, (1) not pinnate; character 12 of Stockey et al. (1997)
21. Marginal vein; (0) present, (1) absent; character 14 of Stockey et al. (1997)
22. Anastomosing veins reticulate; (0) present, (1) absent; character 13 of Stockey et al. (1997)
23. Differentiated conducting cells in leaf/frond venation; (0) present, (1) absent; character 11 of Stockey et al. (1997)
24. Pubescence; (0) largely absent, (1) as trichomes, (2) as papillae; character 15 of Stockey et al. (1997)
25. Roots; (0) present, (1) absent; character 7 of Stockey et al. (1997)
26. Lateral roots; (0) present, (1) absent; character 8 of Stockey et al. (1997)
27. Vessels in root; (0) present, (1) absent; character 17 of Stockey et al. (1997)
28. Spathe; (0) present, (1) absent; character 19 of Stockey et al. (1997)
29. Spadix/inflorescence with; (0) numerous flowers, (1) fewer than five flowers; character 18 of Stockey et al. (1997); character 1 of Cusimano et al. (2011)
30. Spadix zonation; (0) no zonation, (1) male-female, (2) female-sterile-male, (3) female-male-sterile, (4) female-sterile-male-sterile; character 44 of Cusimano et al. (2011)
31. Flowers; (0) bisexual, (1) unisexual; character 20 of Stockey et al. (1997); replaces character 18 of Gallego et al. (2014)
32. Perianth/perigonium; (0) present, (1) absent; character 21 of Stockey et al. (1997)
33. Number of ovules per locule; (0) six or more, (1) five or less; modified from character 22 of Stockey et al. (1997); replaces character 21 of Gallego et al. (2014)
34. Placentation; (0) axile or strongly intrusive placentae, (1) apical, (2) parietal, septa very reduced, (3) basal, basal-parietal, or basal-axile, (4) basal and apical, (5) laminar; modified from character 23 of Stockey et al. (1997); character 56 of Cusimano et al. (2014)
35. Ovule type; (0) anatropous and hemianatropous, (1) amphitropous, (2) orthotropous and hemiorthotropous, (3) campylotropous; character 29 of Stockey et al. (1997)
36. Operculate seed; (0) absent, (1) present; character 30 of Stockey et al. (1997)
37. Number of stamens; (0) four to six, (1) fewer than four or more than six; character 24 of Stockey et al. (1997)
38. Stamen connation; (0) free, (1) connate (and connate at base); reworded from character 25 of Stockey et al. (1997); character 24 of Gallego et al. (2014)
39. Sporangia per anther; (0) four, (1) two, (2) three; character 26 of Stockey et al. (1997)
40. Position of anther dehiscence; (0) lateral, (1) apical; character 27 of Stockey et al. (1997)
41. Anther dehiscence; (0) by longitudinal slits, (1) by oblique pore-like slits, (2) by apical pores or apical slits, (3) by single continuous slit; modified from character 28 of Stockey et al. (1997); character 51 of Cusimano et al. (2011)
42. Pollen shape; (0) ellipsoid, (1) boat-shaped, (2) globose or spheroidal; modified from character 31 of Stockey et al. (1997) and character 10 Cusimano et al. (2011)
43. Pollen aperture type; (0) monosulcate, (1) monoporate, (2) zonate, (3) inaperturate, (4) ulcerate, (5) polyaperturate, (6) foraminate; modified from character 32 of Stockey et al. (1997) and character 8 of Cusimano et al. (2011); character 27 of Gallego et al. (2014)
44. Sporopollenin; (0) present, (1) absent; character 75 of Cusimano et al. (2011)
45. Pollen wall ultrastructure; (0) granular, (1) alveolar, (2) atectate, (3) tectate/columellate; modified character 34 of Stockey et al. (1997)
46. Exine sculpturing; (0) foveolate-reticulate, (1) spinose, (2) striate, (3) psilate, (4) echinate; modified from character 33 of Stockey et al. (1997); character 28 of Gallego et al. (2014)

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