

***COBBANIA CORRUGATA* GEN. ET COMB. NOV. (ARACEAE):
A FLOATING AQUATIC MONOCOT FROM THE UPPER CRETACEOUS
OF WESTERN NORTH AMERICA¹**

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The fossil record of aquatic flowering plants broadens our understanding of their former diversity and origins from terrestrial ancestors. This paper describes a floating aquatic monocot from 71 whole plants and several isolated leaf fragments from Upper Cretaceous oxbow lake sediments in the Dinosaur Park Formation, Alberta, Canada. The new material is represented by rosettes of leaves and roots attached to short stems that are interconnected by stolons and corresponds to the fossil aroid originally described as *Pistia corrugata* Lesquereux. Up to six plants have been found interconnected on a single slab suggesting that these plants grew in extensive floating mats covering lakes and calm stretches of rivers. Stems have up to six leaves and large numbers of branched aquatic roots. The leaf is trumpet-shaped with an elongate clasping petiole, large aerenchymatous base, and a nearly circular blade rim. Leaf bases are often filled with sediment giving the leaf the appearance of having a basal pouch. Petioles have 6–9 veins that divide into an upper and lower set, and veins converge at an apical notch. A submarginal collective vein and at least two marginal veins with branching veins form the leaf rim. A series of dichotomizing and anastomosing veins characterize the adaxial leaf surface. Tertiary and quaternary veins form polygonal areolae. Leaf surfaces are covered in trichomes that, like those in *Pistia stratiotes*, probably aided in buoyancy. A reconstruction of the plant is presented. Based on unique leaf morphology, these fossil plants are clearly not assignable to the genus *Pistia* and are described as *Cobbania corrugata* (Lesquereux) Stockey, Rothwell et Johnson gen. et comb. nov. Recent systematic analyses using molecular characters resolve two separate origins of floating aquatic aroids included in the duckweeds and the genus *Pistia*. This new fossil genus increases our understanding of colonization of aquatic habitats by revealing a third possible origin of the floating aquatic habit within Araceae.

Key words: aquatic; Araceae; aroids; Cretaceous; Dinosaur Park; fossil plants; *Pistia*.

The fossil record of Araceae goes back to the latest Cretaceous in North America, based mostly on seeds (Mayo et al., 1997), but recently the oldest known probable spadix was identified from the Upper Cretaceous (Campanian) of Alberta (Bogner et al., 2005). Leaves and whole plants of these or other monocots are rare due to their herbaceous and often aquatic growth habit (Herendeen and Crane, 1995; Kvaček and Herman, 2004; Wilde et al., 2005). However, isolated leaves of subfamily Orontioideae (*Orontium* L., *Symplocarpus* Salisb. ex Nuttall and *Lysichiton* Schott) have recently been described (J. Bogner, Munich Botanical Garden, personal communication).

The best and most completely known of the fossil aroids are the floating, aquatic rosettes of *Limnobiophyllum scutatum* (Dawson) Krassilov that were widespread by the Paleocene in western North America (Stockey et al., 1997), but occur from the Late Cretaceous to the Oligocene of North America and the Paleocene of east Asia (J. Bogner, Munich Botanical Garden, personal communication). Another species, *Limnobiophyllum expansum* (Heer) Kvaček, is known from the Miocene of Europe (Kvaček, 1995; Collinson et al., 2001). These plants have been compared to the genus *Pistia* L. and extant

Lemnaceae (Kvaček, 1995; Stockey et al., 1997). Close phylogenetic relationships of *Limnobiophyllum scutatum* to *Pistia stratiotes* L. and to extant Lemnaceae have been suggested on the basis of morphological cladistic analysis (Stockey et al., 1997). However, ovule structure, seed and pollen structure, stamens connate to a synandrium, and DNA analysis (chloroplast restriction site and *trnL-trnF* sequences) remove *Pistia* and the Lemnaceae (= Araceae, subfamily Lemnoideae) to more distantly related clades thus indicating convergent evolution for an aquatic environment rather than sister group relationships (Landolt, 1986; Grayum, 1990; French et al., 1995; Barabé et al., 2002; Cabrera et al., 2003; Rothwell et al., 2003).

In this report, we describe whole plants of an Upper Cretaceous floating aquatic aroid originally described as *Pistia corrugata* Lesquereux (1876, 1878) from isolated leaves and associated roots collected at Point of Rocks, Wyoming, USA. The new material described here consists of stems with attached leaves and roots that are interconnected by stolons in the Upper Cretaceous Dinosaur Park Formation, at Dinosaur Provincial Park, near Brooks, Alberta, Canada. We develop a reconstruction of the plant based on attached organs and compare the fossils with the fossil *Limnobiophyllum* and extant *Pistia*, revealing a greater systematic and ecological diversity of Late Cretaceous Araceae than previously recognized.

MATERIALS AND METHODS

The type material of "*Pistia*" *corrugata* was collected near Point of Rocks Stage Station (41°40'49" N, 108°47'06" W) in Sweetwater County, Wyoming,

¹ Manuscript received 30 June 2006; revision accepted 22 January 2007.

The authors thank D. Braman (Royal Tyrrell Museum of Palaeontology) for access to the collections and for field assistance; P. Currie and E. Koppelhus (University of Alberta) for help in field access; S. Smith, A. Falder, and J. Rothwell for field assistance; G. Hoffman (Norwest Mines, Calgary) and J. Bogner (Munich Botanical Garden) for helpful discussion; and M. Leggitt (Leggitt Design, Denver) for the reconstruction diagrams. This work was supported in part by NSERC grant A-6908 to R.A.S.

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USA (Lesquereux, 1876, 1878; Knowlton, 1900). Modern mapping in this area (Roehler, 1990) defines Point of Rocks itself as the Erickson Sandstone and the overlying mudstone strata as the Almond Formation. The Erickson is a thick massive sandstone and is unlikely the source of Lesquereux's fossils. The overlying Almond Formation is fossiliferous and has yielded "*Pistia*" *corrugata* on the western side of the Rock Springs Uplift (DMNH loc. 1182). The lower part of the Almond Formation is the likely source of the type specimens. Roehler (1990) dated the Almond Formation using the ammonite zonation of Obradovich and Cobban (1975) and Obradovich (1993) and placed the base of the Almond Formation as equivalent to the *Baculites reesidei* Zone. This zone was dated by Obradovich (1993) at 72.36 Ma (million years ago).

A large collection of fossil leaves with attached stems and roots was made during two seasons in Dinosaur Provincial Park in southern Alberta. Fossils are compression/impressions and were being excavated in the 1994 field season by K. Johnson and D. Braman (Royal Tyrrell Museum of Palaeontology) when the most complete skeleton known of the dinosaur *Ornithomimus* was found among the leaves (Keiran, 1999). A large number of fossil leaves were sacrificed in the jacketing of this dinosaur fossil, but a large collection of specimens resulted from this find and further excavations by us in 1998. Among the fossils recovered from the site (now known as the *Ornithomimus* Quarry, DMNH loc. 894) are 71 stems with attached organs.

The Dinosaur Park fossils were preserved in a fine-grained mudstone that was rapidly covered with a coarse-grained sand in an overbank flood. This instantaneous flood of sediment buried the plants where they grew in a small oxbow lake or pond. Sediments are at the base of the Dinosaur Park Formation and are Upper Cretaceous (Campanian) in age. The contact of the Dinosaur Park Formation and the underlying Oldman Formation is approximately 76 Ma (Eberth and Braman, 1993).

Specimens were degaged from the sandy matrix and studied using reflected light. All images were captured with a Microlumina scanning camera (Leaf Systems, Inc., Bedford, Massachusetts, USA) and processed using Adobe Photoshop 7.0, San Jose, California, USA). Dinosaur Park specimens are housed in the Tyrrell Museum of Palaeontology (TMP), Drumheller, Alberta, Canada and in the Denver Museum of Natural History (DMNH), Denver, Colorado, USA. Type and figured specimens of *Pistia corrugata* (Lesquereux, 1878) are housed in the Smithsonian Institution (USNM) collection, specimen numbers USNM P539, P540a, P542, P542a, P543, P548.

RESULTS

Systematics—Order—Arales

Family—Araceae

Generic diagnosis—*Cobbania* gen. nov. Floating aquatic plants with rosettes of trumpet-shaped leaves helically arranged around short stem and numerous elongate roots bearing fine lateral roots. Stems connected by stolons. Leaves pubescent, with inflated base and circular rim with apical notch. Petiole bases clasping, sheath present. Primary veins branch to form adaxial and abaxial series. Adaxial primary veins dichotomize and anastomose; lateral veins branching to form collective veins in rim that meet in or just below apical notch. Secondary veins anastomose, forming tertiary veins at right angles. Quaternary veins form polygonal areolae with freely ending veinlets. Marginal veins in rim at least three, including collective vein and fimbrial vein, connected by series of short secondary veins.

Type species—*Cobbania corrugata* (Lesquereux) Stockey, Rothwell et Johnson comb. nov.

Etymology—The genus *Cobbania* is named for William A. Cobban of the United States Geological Survey whose life's work studying the ammonite biostratigraphy of the Cretaceous Western Interior Seaway has set an unparalleled stratigraphic framework for future study.

Emended specific diagnosis—*Cobbania corrugata* (Lesquereux) comb. nov. Small rosettes with up to six leaves per plant borne on short, stout stems, 1.0–1.7 cm in diameter, connected by stolons, growing in large mats. Stolon surface smooth without indications of vascular tissue. Leaves 1.9–7.0 cm long, 2.4–7.5 cm wide, with six to nine primary veins; lateral veins dichotomize to form collective vein ca. one-third of way from base of blade. Three to four submarginal veins, innermost widely spaced, branching at angles of usually 90° near leaf apex and 45–60° near middle of leaf. Rim thin, up to 5 mm wide.

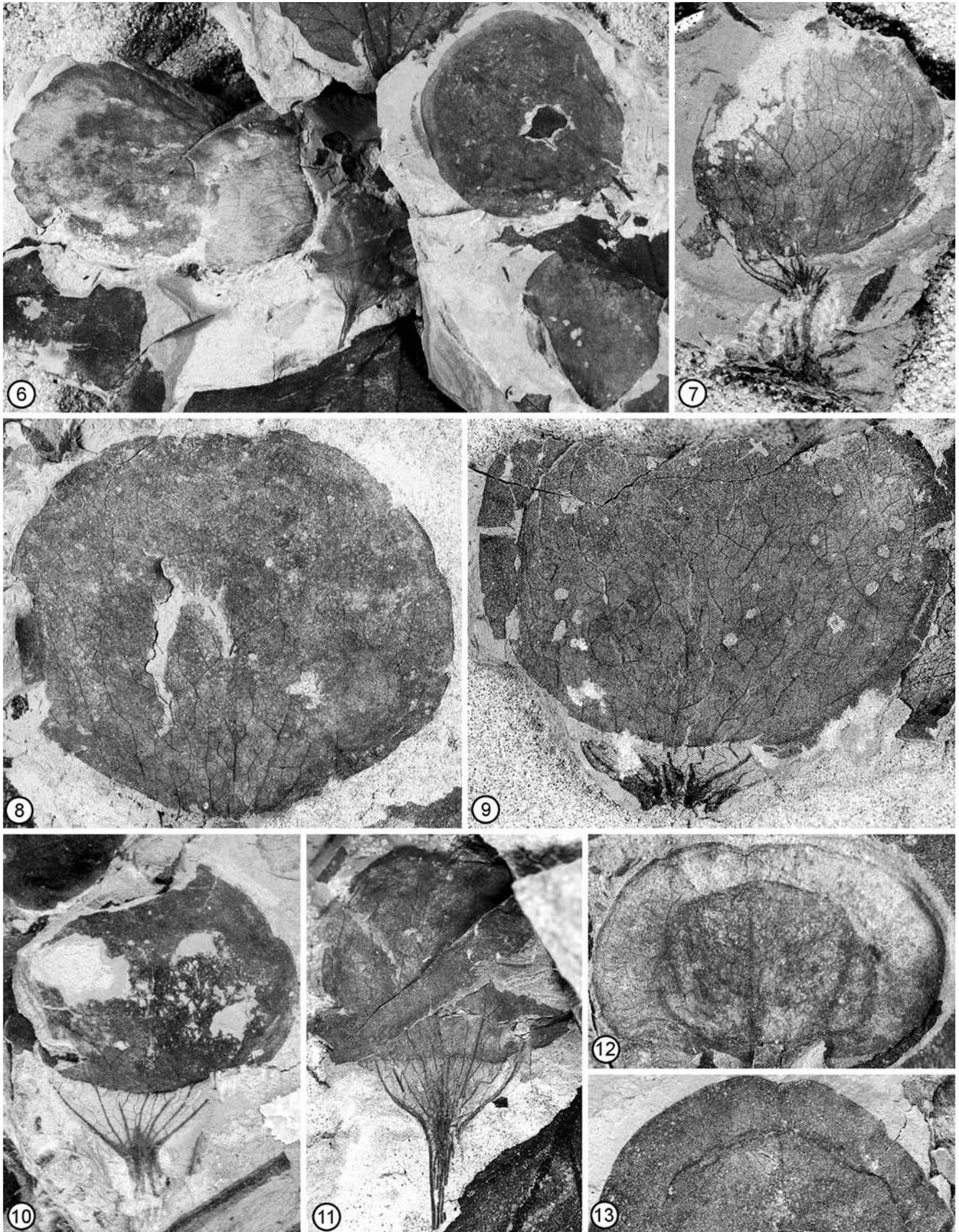
Synonymy—*Pistia corrugata* Lesquereux, 1876, p. 299, *Basionym*; Lesquereux, 1878, p. 103, figs. 1, 3, 4, 6, 7; Knowlton, 1900, p. 31; Knowlton, 1917, pl. 85, fig. 4; Berry, 1935, p. 23; Brown, 1939, p. 248, pl. 49, figs. 7–9, pl. 56, fig. 6a; Dorf, 1942, p. 132, pl. 7, figs. 3, 4, 6; Johnson, 2002, p. 347, pl. 4, fig. 3.

Lectotypification of Cobbania corrugata Lesquereux—Lesquereux, 1878, fig. 1.; USNM P539 (Fig. 22), from Point of Rocks, Wyoming (41°40'49" N, 108°47'06" W), housed in the Smithsonian Institution, National Museum of Natural History, Department of Paleobiology, Washington, D.C., USA. We hereby designate the specimen as the Lectotype, as no holotype specimen was chosen by Lesquereux (1876 or 1878). In the original description (Lesquereux, 1876), no specimens were illustrated. In 1878, the specimen chosen here (Fig. 22) appears as his first figure (Lesquereux, 1878, fig. 1). In addition, several specimens attributed to *Pistia corrugata* as probable roots (Lesquereux, 1878, figs. 9, 10, 11) may belong to this species or other aquatic plants (several of which occur at the type locality) and are not included in our description here. One specimen referred to as *Ottelia americana* (Lesquereux, 1878, fig. 8), may represent a *Cobbania*-like plant, but further investigation is needed.

Description—Seventy-one plants and many isolated leaf fragments have been recovered from the quarry. Most plant specimens extracted on large blocks consist of several stems attached to one another by a horizontal stem or stolon (Figs. 1, 5). Up to five plants have been found attached to one another on a single small slab (Figs. 1, 5) suggesting that these plants grew as an extensive mat covering the lake. These plants were rapidly buried in situ by a rapid influx of coarser grained sand

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Figs. 1–5. *Cobbania corrugata* gen. et comb. nov. **1.** Specimen showing stolon with four attached plantlets bearing roots and attached leaves. Stems indicated by arrows. TMP 95.98.29A ×1.2. **2.** Cross section of stem (near bottom) with attached root. Note dark band of probable vascular tissue and fine lateral roots. TMP 2006.40.01 ×1.6. **3.** Cross section of stem bearing numerous roots, showing one leaf attached. Note several veins in petiole base and small piece of adaxial leaf lamina, at bottom. TMP 2006.40.09 ×1.5. **4.** Cross section of stem with numerous roots and attached petiole bases showing abaxial veins and flattened leaf lamina. TMP 2006.40.03 ×1. **5.** Rock slab showing five plantlets (arrows), with numerous attached roots and one leaf. TMP 95.98.28A ×0.6.



into a lake with a fine-grained muddy bottom, and therefore whole plants are recovered at the interface between the sand and mudstone. Many plants have been found attached to one another in the sediments, bearing helically arranged leaves in rosettes on stout short stems with roots arising on the other side, indicating that these were floating aquatics.

Stems—Upright stems bearing rosettes of leaves are fairly stout measuring 1.0–1.7 cm in diameter. They have persistent leaf bases giving the stem surface a rough appearance in compression and bear up to six leaves per plant. Large numbers of branched roots are borne around the stem base (Figs. 1–5). In addition to the stems of individual plantlets, horizontal stems (stolons) up to 7 mm wide connect the main stems (Fig. 1). Stolon surfaces are relatively smooth and do not show any indications of vascular tissues on their surfaces, but may show folding on some specimens (Fig. 3). Distances between plants vary, with the longest observed internode measuring 3.5 cm (Fig. 1).

Roots—From six up to 12 adventitious roots have been observed attached to each plantlet (Figs. 1–5). Roots are at least 6 cm long and show large numbers of fine, elongate, secondary roots (0.2 mm wide) attached at right angles (Figs. 1–3). Well-preserved roots typically have an elongated dark band, up to 1.2 mm wide, running down the middle, which we interpret as a compression of the root stele (Fig. 2). Due to their placement on the plant and in the rock and to the very delicate nature of the elongated secondary roots, these are interpreted as aquatic roots.

Leaves—Leaves are nearly circular in surface view and vary from 1.9–7.0 cm in length and 2.4–7.5 cm in width at the surface (Figs. 1, 4, 6–9, 12, 14). They have elongate, sheathed petioles that have become compressed from thicker three-dimensional structures (Figs. 3, 7, 10, 11, 16). Petioles show from 6–9 veins entering at the base. These bundles may have been scattered or in a ring in life, but due to compression, they often overlap one another making their numbers difficult to discern. Venation in general is difficult to characterize because of the three-dimensionality and the probable aerenchymatous nature of these leaves.

In general, leaves were trumpet-shaped with a large, hollow, probably aerenchymatous base and a thin blade that may have floated on the surface of the water. Bases are often filled with sediment giving the leaf the appearance of having a basal pouch (Figs. 1, left; 3, 4, 7, 9–11, 16). The venation pattern must be characterized using several specimens and examination of both the abaxial and adaxial leaf surfaces. A series of dichotomizing and anastomosing veins are present on the upper leaf surface (Figs. 14, 16, 17). Tertiary and quaternary veins form areolae that are polygonal in shape (Figs. 16, 17).

Two to three veins at each leaf margin continue along the

margin to the leaf apex (Figs. 14, 16). These veins converge at the apical notch (Fig. 15). Often the inner one of these three veins is the most recognizable depending on leaf preservation and developmental stage (Figs. 12–14, 16). This inner marginal vein branches off near the margin about one-third of the way from the base of the leaf blade (14, 16). All vein orders converge in the inner marginal vein to form an anastomosing pattern of irregularly appearing veins of varying thickness. The inner marginal vein is connected to the outer two marginal veins and a fimbrial vein by a series of smaller veins. The angle is nearly 90° near the leaf apex and about 45–60° near the middle of the leaf (Figs. 15, 16). The apical notch (Figs. 1, 12, 13, 15, 18) is very pronounced in well-preserved leaves and is entered by the three marginal veins and a fourth vein in the center of the leaf that is not strong or straight on the leaf adaxial surface (Fig. 15). A distinct midrib is lacking.

Abaxial leaf views show several strong veins that may have extended straight to the apex after sending branches to the adaxial surface (Figs. 10, 11). The three marginal veins and their branching veins form a fringe or rim around the adaxial leaf surface. Examining compressed leaves from the abaxial surface shows that the aerenchymatous tissue did not extend into the margin of the leaf but was centered under the main circular area within the margins (Figs. 1, 4).

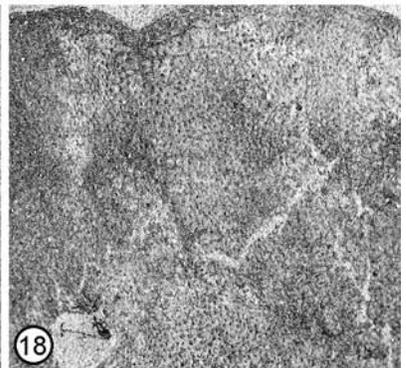
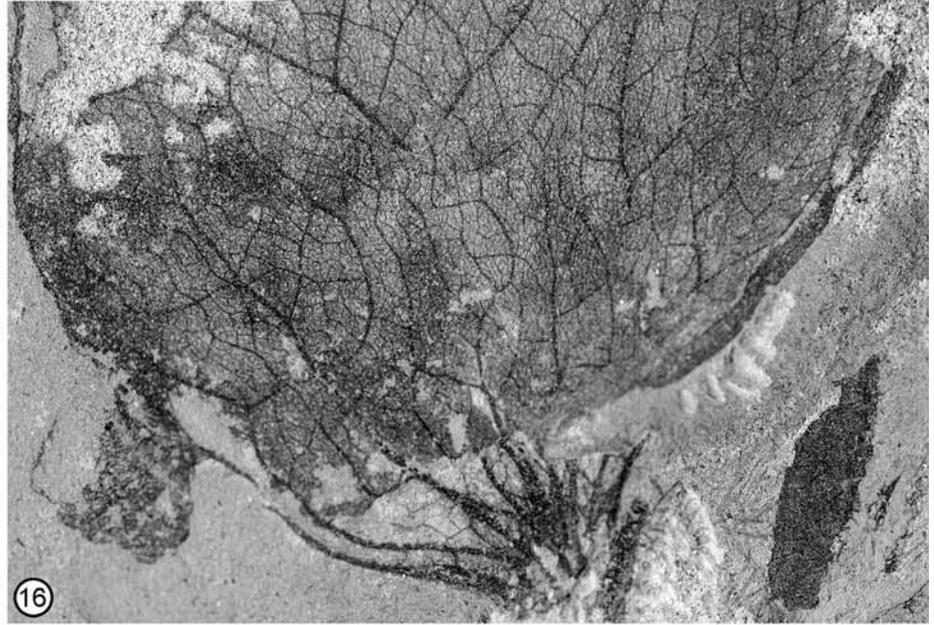
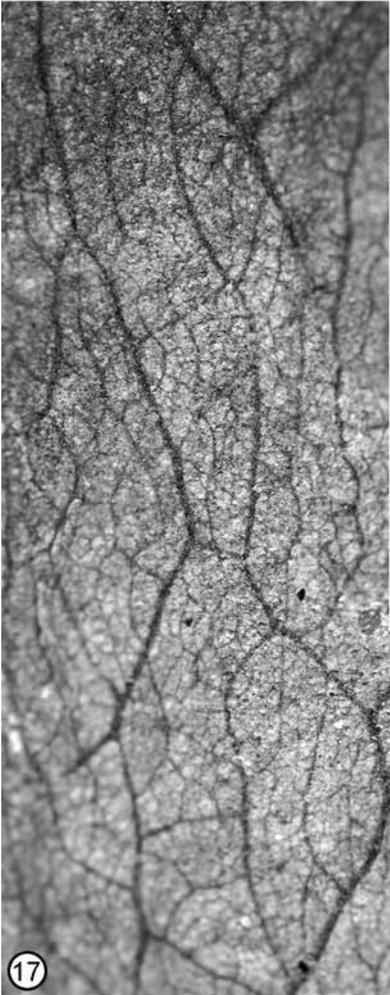
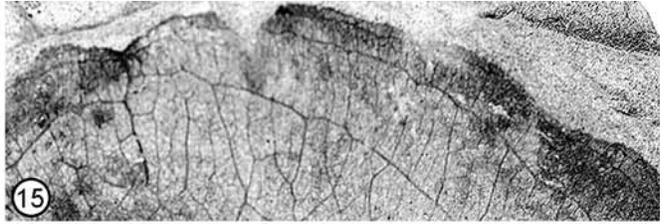
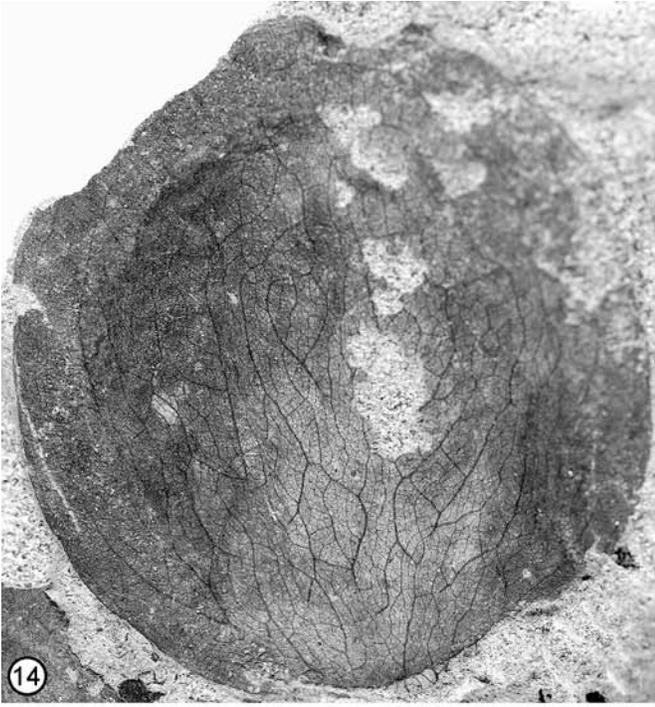
While epidermal cells often can be seen, cuticles are absent from the fossil leaves. Leaf surfaces display a solid covering of trichomes. Compressions that were split along the leaf surface, rather than internally along the veins show the trichome bases most clearly (Fig. 18). These trichomes, like those in *Pistia stratiotes*, probably aided the plant in buoyancy.

Associated fruits—Two clusters of probable fruits with seeds have been found in association with these leaves at Dinosaur Park (Figs. 19, 20). One specimen revealed seed cuticle, the surface of which is smooth (Fig. 21). Seeds are ovoid to ellipsoid, 3–6 mm long and 2.5–4.5 mm wide. One specimen (Fig. 20) shows what might be the remains of surrounding fruit tissue; however, preservation is poor. These fruits are not attached, only associated with the floating plants, and their affinities are uncertain.

Comparison to extant *Pistia stratiotes* L.—*Pistia stratiotes*, like *Cobbania*, reproduces vegetatively by stolons (Fig. 26) that are produced by secondary buds (Lemon and Posluszny, 2000). The leaves of *Pistia* are also borne helically in rosettes, and the plants have dangling branched aquatic roots (Fig. 26). Leaves, like those of *Cobbania*, have an apical notch (Figs. 28–30). Numerous veins enter the petiole (Fig. 28) and split into an abaxial and abaxial series (compare Figs. 29 and 30). A section taken in the basal fourth of a leaf blade shows prominent aerenchyma tissue especially near the middle of the leaf (Fig. 27). However, this thick, spongy tissue does not continue into the upper half of the leaf. Leaves are borne upright above the

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Figs. 6–13. *Cobbania corrugata* gen. et comb. nov. **6.** Six leaves of *Cobbania* with unknown platanoid in center at top. TMP 2006.40.10 × 0.6. **7.** Leaf adaxial view with basal sediment filled pouch in which 9–10 veins enter lamina. TMP 2006.40.02 × 1. **8.** Abaxial leaf surface with trumpet-shaped base buried in sediment. TMP 2006.40.07 × 1.1. **9.** Abaxial leaf surface showing marginal rim, basal pouch (as in 2B) with nine entering veins, and anastomosing venation of upper leaf surface. UAPC-ALTA S59530A × 1.1. **10.** Leaf adaxial view showing basal pouch with seven veins. TMP 2006.40.04 × 1.2. **11.** Leaf abaxial view showing basal bulge and veins entering into central zone of leaf. TMP 2006.40.10 × 1.5. **12.** Immature leaf showing central aerenchymatous zone, marginal rim, and apical notch, at top. TMP 95.98.29A × 2. **13.** Leaf apex showing notch, lateral rim, and convergence of veins near notch. TMP 2006.40.08 × 2.



water surface, the older ones sinking beneath the water on senescence. The leaf surface is covered in trichomes (Fig. 27).

Leaves of *Pistia* clearly differ from those of *Cobbania* in shape, being obovate-cuneate to spatulate (Figs. 26, 27), rather than trumpet-shaped. *Pistia* leaves lack the distinct round rim seen in *Cobbania* and show a more regular and delicate pattern of minor veins on the adaxial surface (Fig. 29), rather than anastomosing dichotomous venation, and have a distinct regular pattern abaxially (Figs. 28, 30). Primary veins in *Pistia*, like those of *Cobbania* also converge at or below an apical notch (Fig. 30). The enlarged trumpet-shaped aerenchyma-filled base (“basal pouch”) of *Cobbania* does not occur in leaves of *Pistia* (Figs. 26–27).

Reevaluation of type material—Specimen *USNM P539a* (Fig. 22) is here chosen as the lectotype because no holotype specimen was designated. It is the original specimen from which the line drawing of Fig. 1 of Lesquereux (1878) was made. Figure 23 is a specimen that is on the same rock as the leaf illustrated in Fig. 22. In addition, several roots and partial leaves also occur on this rock. By contrast, *P540*, Lesquereux (1878) Fig. 2, is a peltate leaf that looks nymphaeaceous with radiating dichotomizing veins rather than *Cobbania*-like and lacks submarginal veins. Specimen *P540a*, Lesquereux (1878) Fig. 4 is a basal part of a leaf of *Cobbania* showing a “pouch.” Specimen *P542*, Lesquereux (1878), Fig. 6 is about three-fourths of a leaf blade showing a basal pouch. Specimen *P542a* and *P543* Lesquereux (1878), Figs. 10 and 11 respectively are roots that may or may not belong to *Cobbania*. Nymphaeaceous remains and *Quereuxia*-like plants also occur at the site. The root specimens are in a slightly coarser and lighter-colored matrix than that bearing *Cobbania* fossils. Rock specimen *P548*, bears additional leaves illustrated in Lesquereux (Figs. 3 and 6 of Lesquereux, 1878), and both are probably *Cobbania* leaves. That illustrated in Lesquereux’s Fig. 3, is now slightly broken as compared to that in the original illustration. Of these specimens the best and most complete is Lesquereux’s fig. 1, *P539a*. While it is slightly smaller than the other leaves in the collection, this leaf falls within the range and has the characteristic apical notch, marginal venation, and major venation patterns seen in the Dinosaur Park specimens. On the reverse side of *P548*, one poorly preserved stem can be observed. Therefore, the Point of Rocks plants and those from Dinosaur Park grew in an identical manner and represent the same species.

DISCUSSION

The fossil material from Dinosaur Park has enabled us to better understand the plants previously included in *Pistia corrugata* and to continue building a context for understanding the colonization of aquatic habitats by a rich assemblage of tracheophytes. Complete vegetative bodies are now known for

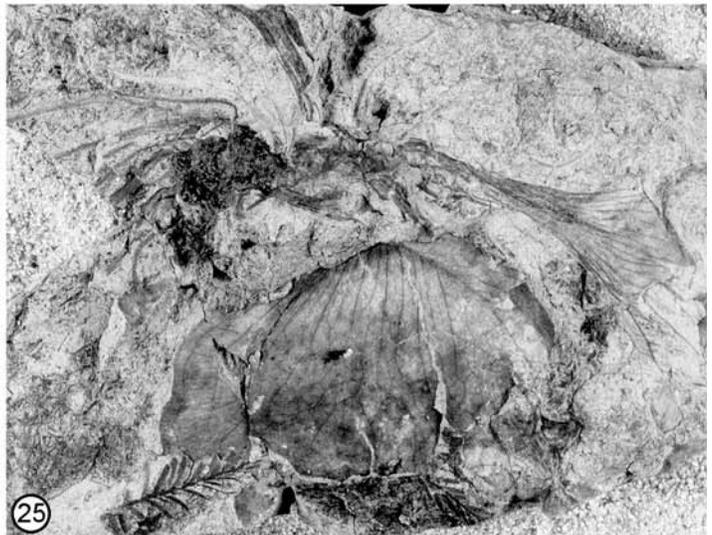
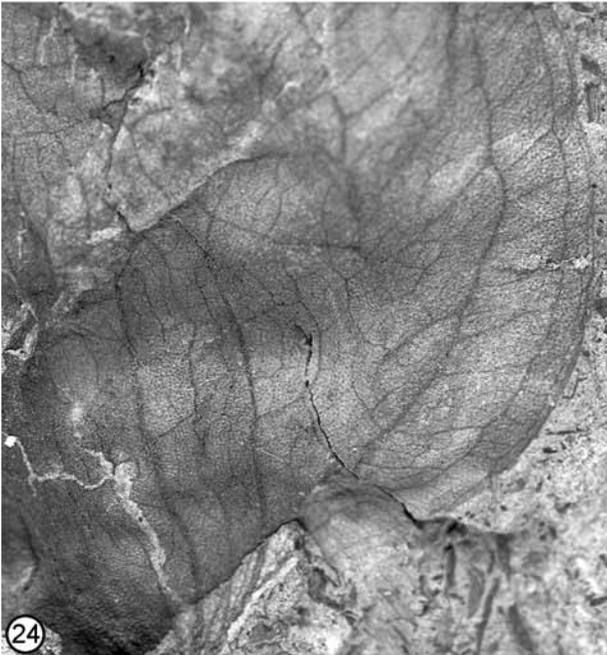
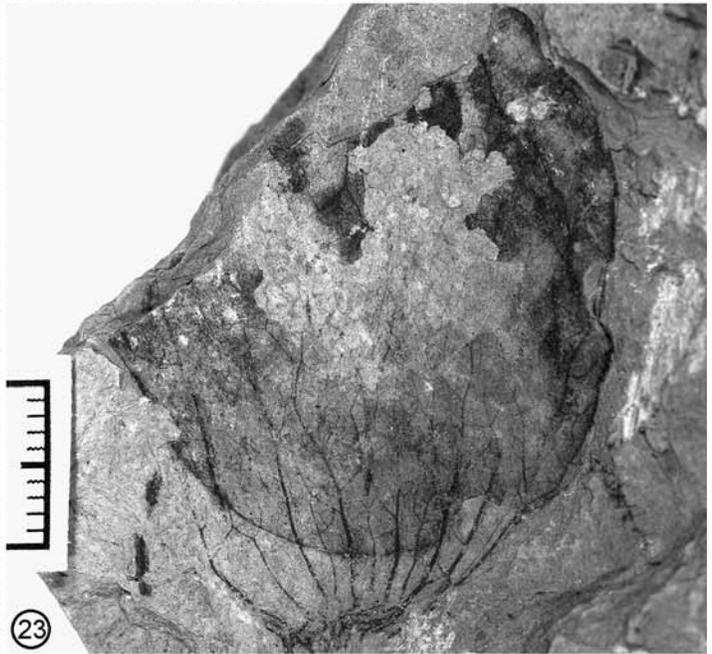
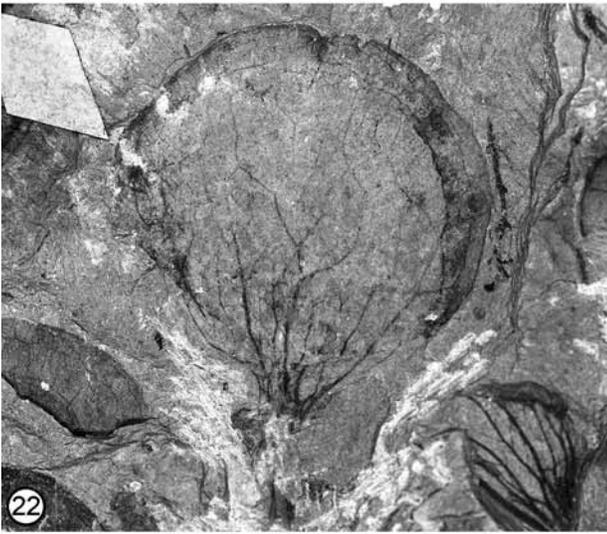
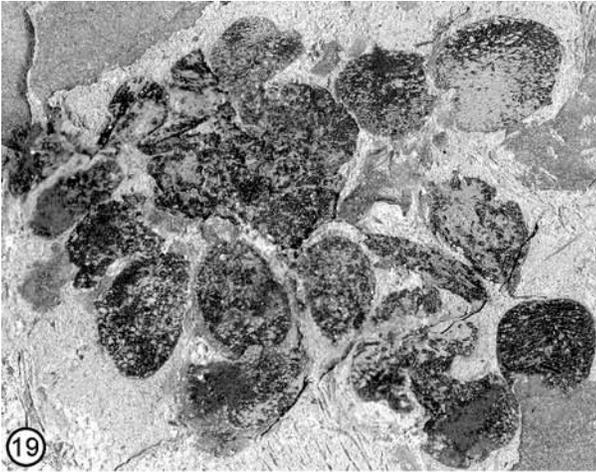
these Cretaceous plants that are common at several localities (Lesquereux, 1876, 1878; Knowlton, 1900, 1917; Berry, 1935; Brown, 1939; Dorf, 1942; Johnson, 2002). *Cobbania* plants grew as floating rosettes of leaves attached to short upright stems with dangling, branched aquatic roots interconnected by stolons. Leaves were petiolate and trumpet-shaped (Figs. 31–33) with an aerenchymatous base and a floating circular rim (Fig. 34).

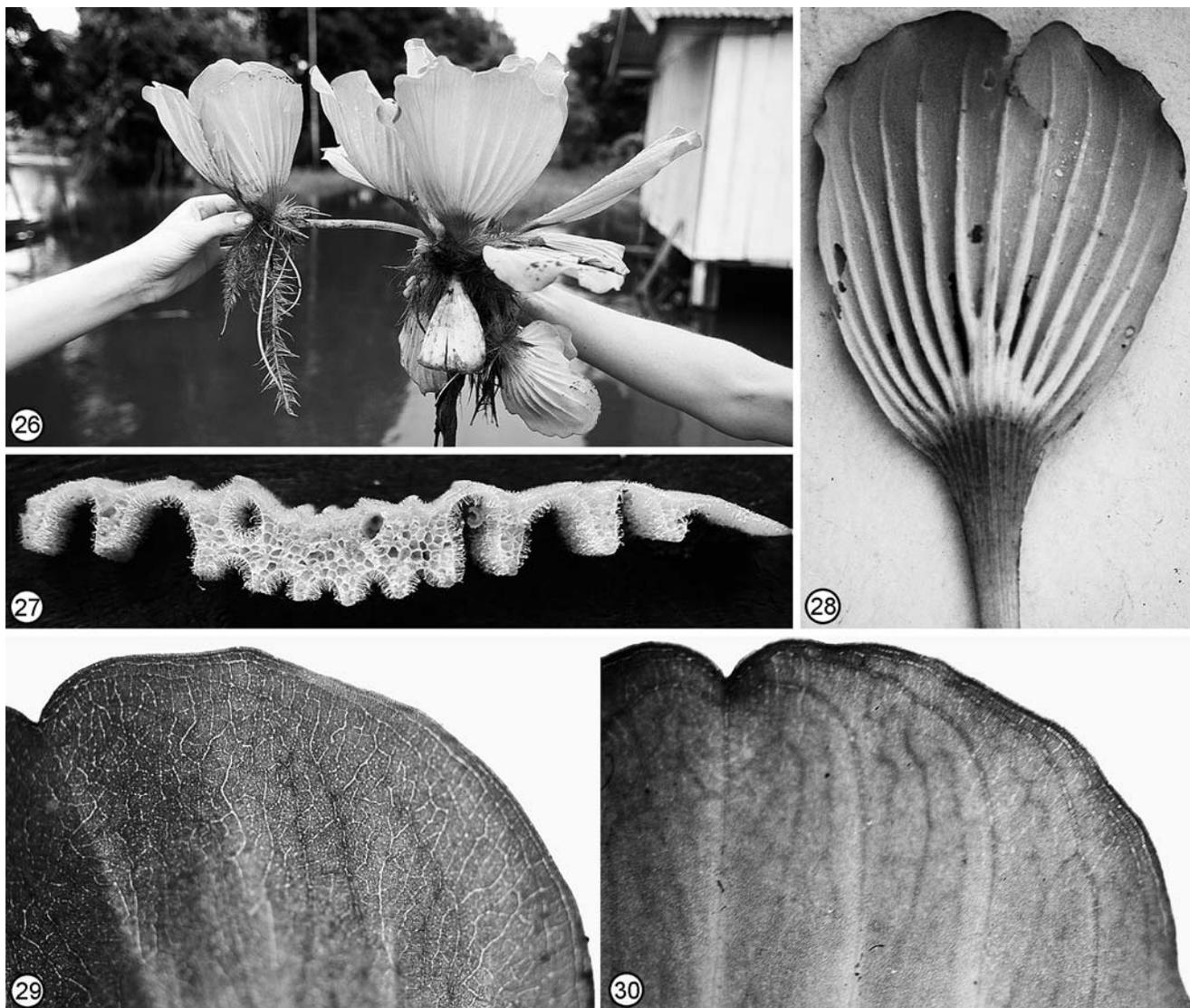
Comparison to *Pistia*—It is clear to us from comparisons to extant *Pistia stratiotes* that the plants described as “*Pistia*” *corrugata*, while they have a similar growth habit, clearly do not represent another species of *Pistia*. Shoot development in extant *Pistia* has a complex system of supernumerary buds that develop in the axils of prophylls rather than the foliage leaves as was previously believed (Arber, 1920; Lemon and Posluszny, 2000). Because of the compression/impression nature of the fossils, it is difficult to compare this developmental facet of *Pistia* to that of *Cobbania* shoots. Comparisons of leaf morphology and venation, however, are possible, and several differences are apparent. Because both taxa are aquatics, leaves contain aerenchyma. Both have short petioles, compared to other aroids, and clasping leaf bases. While leaves of *Pistia* are aerenchymatous at the base, they lack the basal “pouch” or trumpet-shaped base seen in *Cobbania*. *Pistia* leaves lack a distinct midrib that gives rise to secondary veins, as in many other aroids (Mayo et al., 1997) and are vascularized by a series of bundles that are prominent on the abaxial surface as in *Cobbania*. However, they lack the widely spaced, submarginal collective veins and distinct rim seen in *Cobbania*. *Pistia* leaves are generally rounded at the apex and have an apical notch as in *Cobbania*, and both taxa have pubescent leaf surfaces, but major vein patterns within the leaf are different in the two taxa. *Pistia* has reticulate higher order veins that are much finer and have smaller areoles than those seen in *Cobbania* (compare Figs. 14–17 vs. Figs. 29, 30). Primary veins in *Pistia* do not have the prominent and extensive dichotomizing seen in leaves of *Cobbania*. *Pistia* leaves have fairly regular rows of minor veins that run longitudinally near the adaxial surface that run parallel to the major veins on the abaxial surface, a much more regular venation pattern than that seen in *Cobbania*. Both taxa show freely ending veinlets in the areolae.

Thus, while growth habits of *Pistia* and *Cobbania* are similar, their leaf shape and venation patterns differ dramatically. *Pistia* leaves also lack a distinct rim such as that which characterizes *Cobbania*. These characters support recognition of the fossil plants formerly treated in *Pistia corrugata* as a new genus. The vegetative growth of *Cobbania* has been reconstructed in Figs. 31–34 (see also Appendix). The prominent rim in leaves of *Cobbania* is thin and does not appear to have been aerenchymatous, suggesting that it may have rested on the water surface.

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Figs. 14–18. *Cobbania corrugata* gen. et comb. nov. **14.** Leaf abaxial view showing anastomosing vein pattern. Note branch of lateral vein into rim, lower left. TMP 2006.40.05 \times 1.4. **15.** Venation of leaf rim near notch showing convergency of veins near notch. TMP 2006.40.10 \times 3. **16.** Abaxial leaf venation and veins entering basal pouch. Note dichotomous, anastomosing pattern of veins in center of leaf and three major veins in margin interconnected by cross veins. TMP 2006.40.02 \times 2.7. **17.** Higher magnification of leaf in 3A showing anastomosing primary veins and polygonal areolae formed by secondary, tertiary, and quaternary veins. TMP 2006.40.05 \times 5.2. **18.** Leaf apex showing apical notch and densely packed trichome bases on leaf surface. TMP 2006.40.06 \times 4.5.





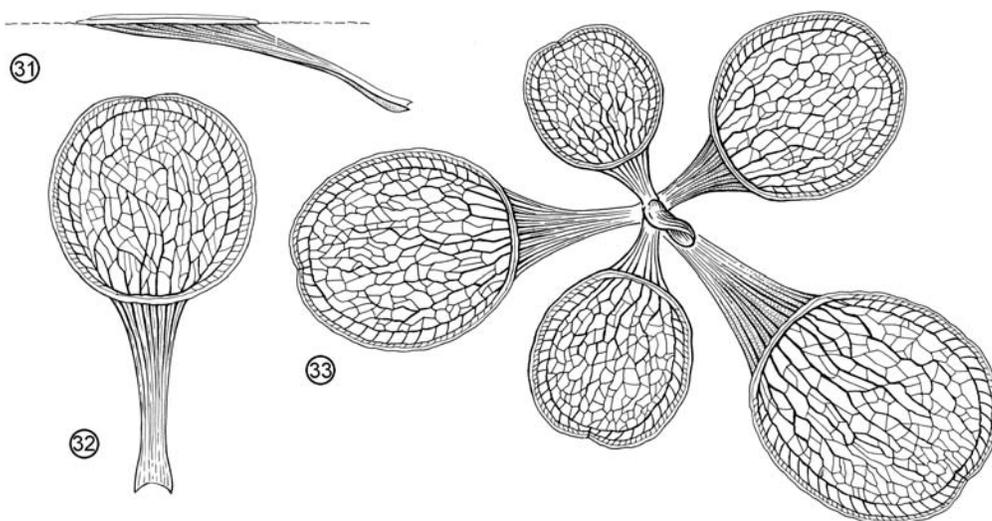
Figs. 26–30. *Pistia stratiotes* L. **26.** Whole plant with two plantlets, connecting stolon, and adventitious roots with laterals. $\times 0.13$. **27.** Section through fresh leaf near base of blade showing internal aerenchymatous tissue and trichome covered surface. $\times 1.3$. **28.** Whole leaf in abaxial view. $\times 0.6$. **29.** Apex of leaf showing notch and adaxial venation. $\times 1.1$. **30.** Apex of leaf showing notch and more abaxial venation. $\times 1.1$.

Comparison to other aroids—While *Cobbania corrugata* has been compared to *Pistia stratiotes* in the past, a broader look at extant and fossil aroids was necessary to determine if this plant should actually be classified within family Araceae (Fig. 35). Wilde et al. (2005) recently reviewed the fossil record of Araceae leaves and their table 1 compares fossil Araceae leaves to those of extant taxa based on blade shape, lateral veins, cross veins and areoles, and venation near the leaf

margin. Aroids have a wide diversity of leaf forms but most commonly have lanceolate to elliptic or widely ovate to cordate, peltate, hastate, and sagittate leaf forms (Mayo et al., 1997; Wilde et al., 2005). Leaves of Araceae are mostly all petiolate, sometimes with a geniculum or pulvinus (a swelling on the petiole at or below the junction with the lamina) (Mayo et al., 1997; Wilde et al., 2005). Preservation of *Cobbania* clearly shows leaves attached to stems with a clasping leaf base

←

Figs. 19–25. 19–21. Specimens from Dinosaur Provincial Park. **19.** Cluster of ovoid to ellipsoid seeds associated with *Cobbania corrugata*. TMP 95.98.27A $\times 3.6$. **20.** Structure bearing fruits/seeds. TMP 95.98.13A $\times 2$. **21.** Isolated ellipsoid seed (or one-seeded fruit?) with smooth outer surface. TMP 95.98.13A $\times 10$. Figs. 22, 23. *Cobbania corrugata* gen. et comb. nov., Point of Rocks, Wyoming. **22.** Lectotype specimen from Point of Rocks, Wyoming, USA originally illustrated by Lesquereux, 1878, fig. 1. USNM P539a. $\times 1.7$. **23.** Specimen on same slab as lectotype, showing abaxial venation and trumpet-shaped base. USNM P539b. $\times 2.2$. Figs. 24, 25. Specimens from Mosquito Butte (Hell Creek Fm.). **24.** Close-up of submarginal collecting vein and widely spaced submarginal veins interconnected by lateral veins. DMNH 8654 $\times 1.2$. **25.** *Cobbania corrugata* plant showing stem with attached petiole bases, roots, and large rim on one leaf. DMNH 8656B $\times 0.6$.



Figs. 31–33. Line diagrams of *Cobbania corrugata* gen. et comb. nov. 31. Leaf from side view showing adaxial surface floating at surface of water. 32. Adaxial view of leaf venation patterns. 33. Single floating plant as seen from top view.



Fig. 34. Side view of two plants at surface of water interconnected by stolon.

(or sheath of petiole), but the three-dimensional nature of the compressions makes further comparisons difficult.

The marginal venation in *Cobbania* provides some characters that are useful taxonomically. While many Araceae have marginal veins, submarginal veins are less common, and those with several submarginal and collective veins are even fewer. Table 1 shows a list of the subfamilies and tribes of Araceae that are reported to have marginal collective veins (Mayo et al., 1997; Wilde et al., 2005). The positions of these taxa in current phylogenies are indicated in Fig. 35. All of these Araceae differ in leaf shape from *Cobbania* and have distinct midribs (Keating, 2002). *Cobbania* shows 3–4 submarginal and

collective veins in the rim, and spacing between these veins is wide.

Subfamily Pothoideae, tribe Anthurieae, genus *Anthurium* Schott has a wide variety of leaf shapes that are rarely orbicular or peltate but all have a distinct midrib and usually 1–2 submarginal veins, but some species may have as many as three (Mayo et al., 1997). These veins, however, fuse with the fimbrial (marginal) vein prior to reaching the apex (see Mayo et al., 1997, Plate 8), unlike those in *Cobbania* that continue to the apex.

Subfamily Monsteroideae, tribe Anadendreae, genus *Anadendrum* Schott has several orders of submarginal veins (Wilde

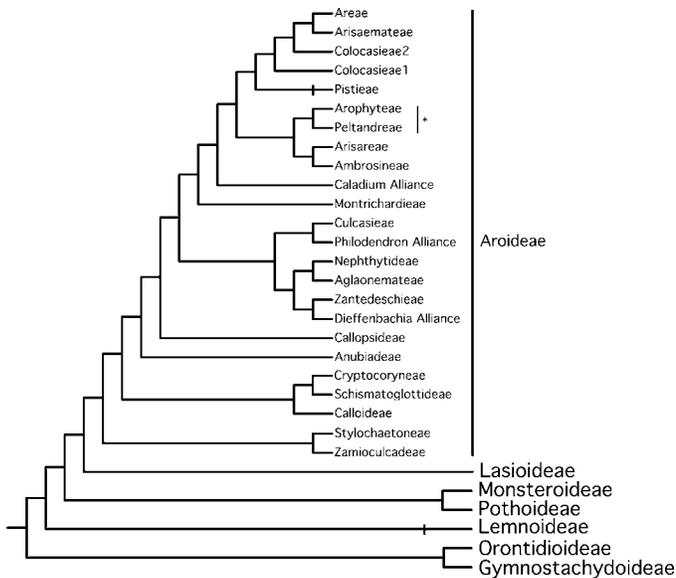


Fig. 35. Cladogram of Araceae derived from Mayo et al. (1997) with modifications from Cabrera et al. (2003): J. Bogner, Munich Botanical Garden, personal communication. Asterisk indicates possible placement of *Cobbania*.

et al., 2005). The primary veins are acrodromous (Leaf Architecture Working Group, 1999) but run into the marginal vein successively (Mayo et al., 1997), unlike the distinct submarginal veins in *Cobbania* that meet at or just below the apical notch. *Anadendrum* also has large irregular areolae (see Mayo et al., 1997, plate 11) unlike the regular polygonal areolae in *Cobbania*.

Subfamily Aroideae, *Aglaonema* Schott (tribe Aglaonemateae) has veins that are acrodromous and can have two submarginal veins, the inner of which is formed by the confluent ends of laterals (Wilde et al., 2005), and higher order veins that are parallel-pinnate unlike the polygonal areolae seen in *Cobbania*. *Arisarum* P. Miller (tribe Arisareae) has one lateral collective vein and two marginal veins near the leaf apex, but the collective veins arise from branches of the primary laterals that merge back with other laterals in a series of arches (Mayo et al., 1997) reminiscent of brochidodromous loops in dicots (Leaf Architecture Working Group, 1999).

Homalomena Schott (*Philodendron* alliance; tribe Homalomeneae) sometimes has two closely spaced (sometimes fused) veins in the margin, but these are not widely spaced collective veins of the type seen in *Cobbania*. Some species of *Homalomena* have only a marginal (fimbrial) vein (Mayo et al., 1997; Wilde et al., 2005). Tribe Thomsoniaee (*Philodendron* alliance) with *Amorphophallus* Blume ex Decaisne and *Pseudodracontium* N.E. Brown (Cabrera et al., 2003) has large “dracontiid” blades, that are trisect with one marginal collective vein and one marginal vein (Mayo et al., 1997) unlike the circular blades of *Cobbania*. *Zomicarpa* Schott, *Zomicarpella* N.E. Brown, *Ulearum* Engler, and *Filarum* Nicolson (*Caladium* alliance; tribe Zomicarpeae), which have one submarginal collective vein and usually one, sometimes two, marginal veins (Mayo et al., 1997). Tribe Caladieae contains taxa with one marginal collective vein and usually 1–2 marginal veins (Mayo et al., 1997). *Xanthosoma* Schott and *Chlorospatha* Engler (Tribe Caladieae) have one marginal

TABLE 1. Extant aroids with marginal collective veins.

Subfamily Pothoideae
Tribe Anthuriaeeae
Subfamily Monsteroideae
Tribe Anadendreae
Subfamily Aroideae
Tribe Homalomeneae
Tribe Zomicarpeae
Tribe Caladieae
Tribe Aglaonemateae
Tribe Thomsoniaeeae
Tribe Arophyteae
Tribe Peltandreae
Tribe Arisareae
Tribe Areae
Tribe Colocasieae

Note: Classification according to Mayo et al. (1997)

collective vein and one or more submarginal veins (Mayo et al., 1997), but none of these taxa have the widely spaced submarginal veins with connecting veins as in *Cobbania*.

Tribe Areae contains taxa with marginal collective veins, and several taxa including *Arum* L., *Theriophonum* Blume, *Typhonium* Schott, *Sauromatum* Schott, *Pinellia* Tenore, and *Arisaema* Martius have 1–2 marginal veins and reticulate higher order veins (Mayo et al., 1997). While this group contains a variety of leaf forms from cordate-sagittate, hastate, trifid, pedatifid or pedatisect, to linear or narrowly lanceolate to elliptic and oblong (Mayo et al., 1997), none have the widely spaced submarginal veins with connecting veins seen in *Cobbania*. Tribe Colocasieae has leaves with one submarginal collective vein and one to two marginal veins (Mayo et al., 1997). Areolation in this tribe is distinct from that in *Cobbania*, as most taxa of Areae have elongate and exmedially ramified higher order venation forming elongate meshes (Mayo et al., 1997).

In Tribe Peltandreae, in addition to the submarginal collective vein, there are two or more (*Peltandra* Raf.) or three to four (*Typhonodorum* Schott) marginal veins (Mayo et al., 1997). Connecting veins also occur between the collective and the inner submarginal veins in both of these taxa as in *Cobbania*. However, higher order venation is densely parallel-pinnate in *Typhonodorum* and parallel near the midrib in *Peltandra* but reticulate near the margin (Mayo et al., 1997), unlike the dichotomous venation forming a reticulum with polygonal areolae seen in *Cobbania*. In addition, the marginal veins are fairly close together in Peltandreae (Mayo et al., 1997) unlike the widely spaced veins in *Cobbania*. Wilde et al. (2005) describe these marginal veins as “obliquely anastomosing.”

On the other hand, tribe Arophyteae has taxa with a submarginal collective vein and that may have several marginal veins (Wilde et al., 2005). Three to four widely spaced submarginal veins with densely anastomosing connecting veins have been reported in *Carlephyton* Jumelle and *Arophyton* Jumelle (Wilde et al., 1997). These marginal veins are very similar to those seen in *Cobbania* (see Wilde et al., 1997, fig. 51). *Colletogyne* Buchet has a distinct venation pattern with secondary and tertiary laterals mostly parallel-pinnate (Mayo et al., 1997). While leaves of *Arophyton* can be cordate, hastate,

trifid to trisect or pedatifid, those of *Carlephyton* and *Colletogyne* are cordate. All of these taxa of Arophyteae have distinct midribs with equivalent to secondary veins arising at angles of about 45°, rather than the numerous dichotomizing and anastomosing veins that characterize *Cobbania*. It is interesting that all three of these genera of Arophyteae, have ellipsoidal seeds with a thin, smooth testa (Mayo et al., 1997) like those associated with *Cobbania*.

Therefore, while leaves of *Cobbania corrugata* have some similarities to those of aroids in subfamily Aroideae, Tribe Arophyteae, these endemics to northern and northeastern Madagascar survive on limestone outcrops or rainforests as forest floor herbs rather than in the aquatic realm. Without a connection of fruits and seeds to whole plants, it is difficult to more precisely place *Cobbania* among these extant aroids.

Comparisons to fossil aroid leaves—The fossil record of aroids is best known from remains of seeds, and leaf remains are usually scanty or incomplete (Wilde et al., 2005; Stockey, 2006). Wilde et al. (2005) reviewed the fossil aroid leaf record and reanalyzed *Caladiosoma* Berry (1925), *Aracaeophyllum* Kräusel (1929) and *Nitophyllites* Iljinskaja (1963). These authors describe *Araciphyllites tertarius* (Engelhardt, 1922) Wilde, Z. Kvaček & Bogner, comb. nov., 2005; and new species of the other genera from the Eocene of Messel, Germany.

Caladiosoma leaves are broadly ovate, cordate with a thick midrib and widely spaced higher order veins that form an irregular network of interprimary veins. Areolae are irregular and elongate, and leaves have several submarginal veins that are irregularly anastomosing (Wilde et al., 2005). Higher order venation is described as “colocasoid” and shows several exmedial veins as well as interprimaries (see fig. 7D of Wilde et al., 2005), differing considerably from the higher order venation in *Cobbania*. The affinities of *Caladiosoma* are thought to be with subfamily Aroideae, tribes Caladieae or Colocasieae.

The leaves of plants now known as *Araciphyllites* (= *Amomum*, = *Aracaeophyllum*) (see Wilde et al., 2005 for the taxonomic history of this genus) are known from four species from the Neogene of Sumatra and the Paleogene of Messel (Kräusel, 1929). These leaves are lanceolate elliptic with lateral veins that are weakly differentiated (Wilde et al., 2005). Some of the described species are represented by incomplete specimens, but have areolae that are elongate and differ considerably from those seen in leaves of *Cobbania*.

Nitophyllites leaves are known from three species *N. limnestis* (Dilcher et Daghljan) Wilde, Z. Kvaček et Bogner, *N. bohemicus* Wilde, Kvaček et Bogner, and *N. zaisanicus* Iljinskaja emend. Fedotov from the Eocene of North America and Europe (Iljinskaja, 1963; Fedotov 1975; Dilcher and Daghljan, 1977; Wilde et al., 2005). These leaves are cordate, hastate, or broadly ovate with robust midribs and have higher order veins that are almost the same thickness with parallel-pinnate arrangement (Wilde et al., 2005). Areolation is dense and isodiametric, oblique to perpendicular, some partly narrow and elongate, and several submarginal veins have obliquely anastomosing connecting veins (Wilde et al., 2005). These leaves are thought to have affinities with subfamily Aroideae, tribes Peltandreae or Arophyteae. The marginal venation of *Nitophyllites* and *Cobbania* have similarities, but the higher order venation of the two genera is distinctly different (see fig. 10C of Wilde et al., 2005).

Fossil monocots included in *Limnobiophyllum scutatum* (Dawson) Krassilov emend. Kvaček (1995) and *L. expansum* (Heer) Kvaček (1995) are floating rosettes of small leaves attached to short stems, interconnected by stolons (Stockey et al., 1997). Like plants of *Cobbania*, these monocots also bore branched aquatic roots. However, the leaves of *Limnobiophyllum* are sessile rather than petiolate and generally much smaller than those of *Cobbania*. Leaves of *Limnobiophyllum* have several primary veins that converge toward an apical notch and have a fimbrial vein but lack any rim with submarginal veins as in *Cobbania*. In addition to elongate roots with laterals, simple unbranched roots are also borne on the stems of *L. scutatum* (Stockey et al., 1997). While *Limnobiophyllum* probably also had aerenchymatous leaves, they do not have the trumpet shape with a basal pouch as in *Cobbania*. *Limnobiophyllum* plants are clearly related to Araceae, subfamily Lemnoideae based on the occurrence of *Pandaniidites* Elsik pollen in the anthers of their flowers (Sweet, 1986; Stockey et al., 1997).

Occurrences of *Cobbania corrugata*—In addition to the type locality near Point of Rocks, Wyoming, USA and Dinosaur Park in Alberta, Canada, plants similar to *Cobbania corrugata* have been reported from the Hell Creek Formation in Slope County, North Dakota, USA (DMNH loc. 571) where they are located approximately 65 m below the K-T boundary. These sediments are dated by magnetostratigraphy and the downward extrapolation of sediment accumulation rate at 66.3 Ma (Hicks et al., 2002). Plants also occur in nine other localities in Slope and Bowman counties, the highest of which (DMNH loc. 2097) is 29 m below the K-T boundary and corresponds to an estimated age of 65.95 Ma. The uppermost Hell Creek Formation in this area is intensely sampled and has yielded no *C. corrugata* despite the presence of appropriate ponded-water facies. Other examples of *Cobbania* fossils from the upper Maastrichtian are known from the Hell Creek Formation of Harding County, South Dakota, USA (DMNH loc. 2703); the Lance Creek Formation of Converse and Weston Counties, Wyoming, USA (Dorf, 1942; and DMNH loc. 1564); the Fox Hills Formation near Glendive in Dawson County, Montana, USA (Brown, 1939); and the Whitemud Formation of southern Saskatchewan, Canada (Berry, 1935).

The occurrence of “*Pistia*” *corrugata* in the Paleocene Ravenscrag Formation of Saskatchewan (McIver and Basinger, 1993) is here rejected, because the Ravenscrag leaves do not have the characteristic collective veins or the inflated trumpet-shaped bases seen in *C. corrugata*. Based on this evidence, it appears that *C. corrugata* became extinct approximately half a million years before the end of the Cretaceous.

The uppermost Campanian occurrences in addition to those in the Almond Formation include numerous unpublished sites (Yale Peabody Museum) in the Meeteetse Formation near Meeteetse and Elk Basin in Park County, Wyoming, USA and two sites in the St. Mary River Formation, Saskatchewan, Canada (Bell, 1949). The Meeteetse Formation has been dated at 71.77 Ma by Wing et al. (1993). Recently, fossils referable to *Cobbania* have been discovered in the Campanian-Maastrichtian? strata in the Kundur and Tsagayan formations in the Zea Bureya Basin, Amur region in the Russian Far East (Sun, 2002; E. Bugaeva and T. Kodrul, Geological Institute, Russian Academy of Sciences, personal communication, 2002).

Middle Campanian occurrences in addition to those at Dinosaur Park include the Judith River and Belly River

formations from northern Montana, southern Alberta and Saskatchewan (mentioned in Dorf, 1942); the Kirtland Formation in the San Juan Basin, New Mexico, USA (Knowlton, 1917; Lisa Boucher, University of Nebraska, Omaha, personal communication); and the Neslen Formation in the Book Cliffs of Grand County, Utah, USA (DMNH loc. 649). Roberts and Kirschbaum (1995) and Hettinger and Kirschbaum (2002) have constrained the age of the Neslen to the *Baculites scotti* Zone or approximately 76 Ma, roughly coeval with the Dinosaur Park material. Based on all of these occurrences, the first appearance of *Cobbania* is approximately 76 Ma and its last appearance is 65.95 Ma. The geographic distribution ranges from New Mexico to the Russian Far East.

Taxonomic implications—The genus *Pistia* traditionally has been classified in the Order Arales, Family Araceae (Mayo et al., 1997). While interpretations of its systematic relationships to the Lemnaceae and within Araceae s.s. have differed with various authors (French et al., 1995; Kvaček, 1995; Mayo et al., 1997; Stockey et al., 1997; Renner and Weerasooriya, 2002; Cabrera et al., 2003; Rothwell et al., 2003; Renner and Zhang, 2004; Stockey, 2006), it is now clear that Lemnaceae are nested within Araceae and that *Pistia* is nested within the subfamily Aroideae (French et al., 1995; Mayo et al., 1997; Barabé et al., 2002; Cabrera et al., 2003). A clade containing subfamilies Gymnostachyoideae and Orontioideae is sister to the rest of the Araceae, with Lemnaceae (now included as subfamily Lemnoideae) occurring at the next node along the stem of the tree (Cabrera et al., 2003).

The Aroideae is a large subfamily of about 74 genera (Mayo et al., 1997) that contains most of the derived taxa of Araceae (Fig. 35). *Cobbania corrugata* has similarities in marginal venation to Tribe Arophyteae (and to a lesser extent Tribe Peltandreae) in this subfamily, while *Pistia* nests as the basal member of a clade that also includes Areae, Arisaemateae, and two Colocasiae clades (Fig. 35). Because previous studies have shown that the floating aquatic life history pattern has evolved separately in subfamily Lemnoideae and tribe Pistieae, subfamily Aroideae (French et al., 1995; Renner and Weerasooriya, 2002; Cabrera et al., 2003; Renner and Zhang, 2004; Rothwell et al., 2004; Stockey, 2006), our reconstruction of *Cobbania* reveals a third separate origin of the floating aquatic habit within Araceae (Fig. 35).

Colonization of aquatic habitats—From the earliest evidence of land plants onward, the fossil record documents that wetland communities have been an important component of continental biotas (Martín-Closas, 2003; DiMichele and Greb, 2006). The most ancient wetland communities of vascular plants occupied swampy habitats during the latest Early Silurian and Early Devonian (e.g., Hotton et al., 2001; Fayers and Trewin, 2004), with a majority of wetland species representing extinct lineages of rhizomorphic lycophytes and equisetophytes from the Carboniferous through the Jurassic (Stewart and Rothwell, 1993; Pigg, 2001). Some species of ferns probably also occupied paleowetlands (Scheckler, 1986; DiMichele and Phillips, 2002). A few plants of these types could have been rooted in open standing water, but most represent either swampy/marshy habitats or periodically inundated sites (DiMichele and Greb, 2006) as they do today (Sculthorpe, 1967; Cook, 1990).

While the majority of wetland species continued to occupy marshy habitats at the margins of lakes and streams into the

Cenozoic (e.g., Wilde, et al., 2005; DiMichele and Greb, 2006), by the end of the Mesozoic other species began to invade ecological space that was previously unoccupied by vascular plants. These species, that were both submerged and floating, probably displaced aquatic algal macrophytes (Martín-Closas, 2003). Colonization of open water by rooted and unrooted floating aquatic vascular plants appears to have originated with the evolution of herbaceous flowering plants (e.g., Friis et al., 2000, 2001; Sun et al., 2002; Wang and Dilcher, 2006) and heterosporous leptosporangiate ferns (i.e., Hydropteridales sensu Rothwell and Stockey, 1994) near the Jurassic/Cretaceous boundary (Collinson, 1996; Yamada and Kato, 2002). While there is evidence for rooted heterosporous fern species by the end of the Jurassic (e.g., Batten and Kovach, 1993; Collinson, 1996; Yamada and Kato, 2002), the first unrooted floating aquatic plant remains appear to be from mid-Cretaceous deposits (Wang and Dilcher, 2006). By the Late Cretaceous aquatic vascular plants were widespread and diverse, including both dicotyledonous and monocotyledonous flowering plants (Stockey and Rothwell, 1997; Stockey et al., 1997; Martín-Closas, 2003; Gandolfo and Cuneo, 2005) and the hydropteridalean ferns *Salvinia* and *Azolla* (Collinson, 1991).

The recognition of *Cobbania corrugata* as distinct from *Pistia* calls to question the fossil record of the genus *Pistia* as a whole. Knowlton (1917) discusses the four or five species that have been described worldwide. Preservation does not allow for detailed characterization of these fossil taxa as species of *Pistia* at the present time, and their confusion with other known aquatics requires future research at localities such as Dinosaur Park where more whole plants may be collected. The reconstruction of *C. corrugata* increases our understanding of unrooted floating aquatic plants in the Upper Cretaceous and reveals a previously underappreciated food source for herbivorous dinosaurs and other large reptiles of the late Mesozoic. As a result of the growing phylogenetic resolution of Araceae, *Cobbania*, *Limnobiophyllum*, and *Pistia* reveal that there have been at least three separate origins of free-floating aquatic plants within the family, with true *Pistia* as perhaps the most recently derived of these taxa.

LITERATURE CITED

- ARBER, A. 1920. The vegetative morphology of *Pistia* and the Lemnaceae. *Proceedings of the Royal Society of London, B, Biological Sciences*. 91: 96–103.
- BARABÉ, D., A. BRUNEAU, F. FOREST, AND C. LACROIX. 2002. The correlation between development of atypical bisexual flower and phylogeny in the Aroideae (Araceae). *Plant Systematics and Evolution* 232: 1–19.
- BATTEN, D. J., AND W. L. KOVACH. 1990. Catalog of Mesozoic and Tertiary megaspores. American Association of Stratigraphic Palynologists Contributions Series No. 24: 1–227.
- BELL, W. A. 1949. Uppermost Cretaceous and Paleocene floras of western Alberta. *Canadian Geological Survey Bulletin* 13: 1–231.
- BERRY, E. W. 1935. A preliminary contribution to the floras of the Whitemud and Ravenscrag formations. *Canada Department of Mines, Geological Survey Memoir* 182: 1–107.
- BOGNER, J., G. L. HOFFMAN, AND K. AULENBACK. 2005. A fossilized aroid infructescence, *Albertarum pueri* gen. nov. et sp. nov., of Late Cretaceous (Late Campanian) age from the Horseshoe Canyon Formation of southern Alberta, Canada. *Canadian Journal of Botany* 83: 591–598.
- BROWN, R. W. 1939. Fossil plants from the Colgate Member of the Fox Hills Sandstone and adjacent strata. *U. S. Geological Survey Professional Paper* 189-I: 239–275.

- CABRERA, L. I., G. A. SALAZAR, M. W. CHASE, AND S. J. MAYO. 2003. Phylogenetics of Araceae and Lemnaceae: evidence from multiple plastid DNA data sets. Conference on the Comparative Biology of the Monocotyledons and Fourth International Symposium on Grass Systematics and Evolution, Ontario, California, USA, 2003, 11 (abstract). Rancho Santa Ana Botanic Garden, Claremont, California, USA.
- COLLINSON, M. E. 1991. Diversification of modern heterosporous pteridophytes. In S. Blackmore and S. H. Barnes [eds.], *Pollen and spores*, 119–150. Systematics Association Special Volume No. 44. Clarendon Press, Oxford, UK.
- COLLINSON, M. E. 1996. "What use are fossil ferns?"—20 years on: with a review of the fossil history of extant pteridophyte families and genera. In J. M. Camus, M. Gibby, and R. J. Johns [eds.], *Pteridology in perspective*, 349–394. Royal Botanic Gardens, Kew, UK.
- COOK, C. D. K. 1990. *Aquatic plant book*. SPB Academic Publishing, The Hague, Netherlands.
- DILCHER, D. L., AND C. P. DAGHLIAN. 1977. Investigations of angiosperms from the Eocene of southeastern North America: *Philodendron* leaf remains. *American Journal of Botany* 64: 526–534.
- DI MICHELE, W. A., AND S. GREB [EDS.]. 2006. Wetland paleoecology through time. Geological Society of America Special Paper 399.
- DI MICHELE, W. A., AND T. L. PHILLIPS. 2002. The ecology of Paleozoic ferns. *Review of Palaeobotany and Palynology* 119: 143–159.
- DORF, E. 1942. Upper Cretaceous floras of the Rocky Mountain region. II. Flora of the Lance Formation at its type locality, Niobrara County, Wyoming. *Carnegie Institution of Washington Publication* 508: 83–168.
- EBERTH, D. A., AND D. R. BRAMAN. 1993. Selected Upper Cretaceous sections of the southern Alberta plains: the Judith River Group, Horseshoe Canyon Formation, Whitemud, Battle and Scollard formations, and the Cretaceous-Tertiary boundary. Geological Association of Canada/Mineralogical Association of Canada Joint Annual Meeting, Fieldtrip Guidebook, Edmonton, Alberta, Canada.
- ENGELHARDT, H. 1922. Die alttertiäre Flora von Messel bei Darmstadt. *Abhandlungen der Hessischen Geologischen Landesanstalt zu Darmstadt* 7: 17–128.
- FAYERS, S. R., AND N. H. TREWIN. 2004. A review of the palaeoenvironments and biota of the Windyfield Chert. *Transactions of the Royal Society of Edinburgh, Earth Sciences* 94: 325–339.
- FEDOTOV, V. V. 1975. On systematic assignment of the genus *Nitophyllites*. *Paleontologiskii Zhurnal* 1: 133–136 (in Russian).
- FRENCH, J. C., M. G. CHUNG, AND Y. K. HUR. 1995. Chloroplast DNA phylogeny of the Ariflorae. In P. J. Ruddall, P. J. Cribb, D. F. Cutler, and C. J. Humphries [eds.], *Monocotyledons: systematics and evolution*, 255–275. Royal Botanic Gardens, Kew, UK.
- FRIIS, E. M., K. R. PEDERSEN, AND P. R. CRANE. 2000. Reproductive structure and organization of basal angiosperms from the Early Cretaceous (Barremian or Aptian) of western Portugal. *International Journal of Plant Sciences* 161: S169–S182.
- FRIIS, E. M., K. R. PEDERSEN, AND P. R. CRANE. 2001. Fossil evidence of water lilies (Nymphaeales) in the Early Cretaceous. *Nature* 410: 357–360.
- GANDOLFO, M. A., AND R. N. CUNEO. 2005. Nelumbonaceae from the La Colonia Formation (Campanian-Maastrichtian, Upper Cretaceous), Chubut, Patagonia, Argentina. *Review of Palaeobotany and Palynology* 133: 169–178.
- GRADSTEIN, F., J. OGG, AND A. SMITH. 2004. *A geologic time scale 2004*. Cambridge University Press, Cambridge, UK.
- GRAYUM, M. 1990. Evolution and phylogeny of the Araceae. *Annals of the Missouri Botanical Garden* 77: 628–697.
- HERENDEEN, P. S., AND P. R. CRANE. 1995. The fossil history of the monocotyledons. In P. J. Ruddall, P. J. Cribb, D. F. Cutler, and C. J. Humphries [eds.], *Monocotyledons: systematics and evolution*, 1–21. Royal Botanic Gardens, Kew, UK.
- HETTINGER, R. D., AND M. A. KIRSCHBAUM. 2002. Stratigraphy of the Upper Cretaceous Mancos Shale (upper part) and Mesaverde Group in the southern part of the Uinta and Piceance Creek Basins, Utah and Colorado. U.S. Geological Survey Series, Geological Investigations Series I-2764.
- HICKS, J. F., K. R. JOHNSON, L. TAUXE, D. CLARK, AND J. D. OBRADOVICH. 2002. Magnetostratigraphy and geochronology of the Hell Creek and basal Fort Union Formations of southwestern North Dakota and a recalibration of the Cretaceous-Tertiary boundary. In J. Hartman, K. R. Johnson, and D. J. Nichols [eds.], *The Hell Creek Formation and the Cretaceous-Tertiary Boundary in the northern Great Plains: an integrated Continental record of the end of the Cretaceous*, 35–56. Geological Society of America Special Paper 361.
- HOTTON, C. L., F. M. HUEBER, D. H. GRIFFING, AND J. S. BRIDGE. 2001. Early terrestrial plant environments: an example from the Emsian of Gaspé, Canada. In P. G. Gensel and D. Edwards [eds.], *Plants invade the land*, 179–212. Columbia University Press, New York, New York, USA.
- JOHNSON, K. R. 2002. The megafloora of the Hell Creek and lower Fort Union Formations in the western Dakotas: vegetational response to climate change, the Cretaceous-Tertiary boundary event, and rapid marine transgression. In J. Hartman, K. R. Johnson, and D. J. Nichols [eds.], *The Hell Creek Formation and the Cretaceous-Tertiary Boundary in the northern Great Plains: an integrated Continental record of the end of the Cretaceous*, 329–392. Geological Society of America Special Paper 361.
- KEATING, R. C. 2002. *Anatomy of the Monocotyledons*, vol. IX, Acoraceae and Araceae. Clarendon Press, Oxford, UK.
- KEIRAN, M. 1999. Discoveries in palaeontology: *Ornithomimus*, pursuing the bird-mimic dinosaur. Raincoast Books, Vancouver, British Columbia, Canada.
- KNOWLTON, F. H. 1900. Flora of the Montana Group. *U. S. Geological Survey Bulletin* 163: 1–118 + 19 plates.
- KNOWLTON, F. H. 1917. Flora of the Fruitland and Kirtland formations. *U. S. Geological Survey Professional Paper* 98S: 327–355.
- KRÄUSEL, R. 1929. Fossile Pflanzen aus dem Tertiär von Süd-Sumatra. *Verhandelingen van het geologisch mijnbouwkundig Genootschap voor Nederland en kolniën (geologische Serie)*. Den Haag 9: 335–378.
- KVAČEK, Z. 1995. *Limnobiophyllum* Krassilov—a fossil link between the Araceae and the Lemnaceae. *Aquatic Botany* 50: 49–61.
- KVAČEK, J., AND A. B. HERMAN. 2004. Monocotyledons from the early Campanian (Cretaceous) of Grünbach, Lower Austria. *Review of Palaeobotany and Palynology* 128: 323–353.
- LANDOLT, E. 1986. Biosystematic investigations in the family of duckweeds (Lemnaceae), vol. 2, The family of Lemnaceae—a monographic study. *Veröffentlichungen des Geobotanischen Institutes der ETH, Stiftung Rübel, Zürich* 71: 1–566.
- LEAF ARCHITECTURE WORKING GROUP. 1999. Manual of leaf architecture. Morphological description and characterization of dicotyledonous and net-veined monocotyledonous angiosperms. Smithsonian Institution, Washington, D.C., USA.
- LEMON, G. D., AND U. POSLUSZNY. 2000. Shoot development and evolution in *Pistia stratiotes* (Araceae). *International Journal of Plant Sciences* 161: 721–732.
- LESQUEREUX, L. 1876. On the Tertiary flora of the North American Lignitic, considered as evidence of the age of the formation. In F. V. Hayden [ed.], *U.S. Geological and Geographical Survey of the Territories, embracing Colorado and parts of adjacent territories; being a report of the exploration for the year 1874*, 275–315. Annual Report of U. S. Geological and Geographical Survey of the Territories No. 8.
- LESQUEREUX, L. 1878. The fossil flora of the Western Territories, part 2, The Tertiary flora. U. S. Geological Survey of the Territories Report 7.
- MARTÍN-CLOSAS, C. 2003. The fossil record and evolution of freshwater plants: a review. *Geologica Acta* 1: 315–338.
- MAYO, S. J., J. BOGNER, AND P. C. BOYCE. 1997. *The Genera of Araceae*. Royal Botanic Gardens, Kew, UK.
- MCIVER, E. E., AND J. F. BASINGER. 1993. Flora of the Ravenscrag Formation (Paleocene), southwestern Saskatchewan, Canada. *Palae-*

- ontographica Canadiana* Canadian Society of Petroleum Geologists/ Geological Association of Canada. 10: 1–167.
- OBRADOVICH, J. D., AND W. A. COBBAN. 1975. A time-scale for the Late Cretaceous of the Western Interior of North America. In W. G. E. Caldwell [ed.], *The Cretaceous System in the Western Interior of North America*, 31–54. Geological Association of Canada Special Paper 13.
- PIGG, K. B. 2001. Isoetalean lycopsid evolution: from the Devonian to the present. *American Fern Journal* 91: 99–114.
- RENNER, S. S., AND A. WEERASOORIYA. 2002. Phylogeny of *Pistia* and its 16 closest generic relatives among Aroideae. In *Botany 2002: annual meeting of the Botanical Society of America*, Madison, Wisconsin, 661: 168 (abstract). Available at <http://www.botany2002.org/viewer.shtml>.
- RENNER, S. S., AND L.-B. ZHANG. 2004. Biogeography of the *Pistia* clade (Araceae): based on chloroplast and mitochondrial DNA sequences and Bayesian divergence time inference. *Systematic Biology* 53: 422–432.
- ROBERTS, L. N. R., AND M. A. KIRSCHBAUM. 1995. Paleogeography of the Late Cretaceous of the Western Interior of middle North America—coal distribution and sediment accumulation. *U. S. Geological Survey Professional Paper* 1561.
- ROEHLER, H. W. 1990. Stratigraphy of the Mesaverde Group in the central and eastern greater Green River Basin, Wyoming, Colorado, and Utah. *U. S. Geological Survey Professional Paper* 1508.
- ROTHWELL, G. W., AND R. A. STOCKEY. 1994. The role of *Hydropteris pinnata* gen. et sp. nov. in reconstructing the phylogeny of heterosporous ferns. *American Journal of Botany* 81: 479–492.
- ROTHWELL, G. W., M. VANATTA, H. E. BALLARD, AND R. A. STOCKEY. 2003. Molecular phylogenetic relationships among Lemnaceae and Araceae using the chloroplast *trnL-trnF* intergenic spacer. *Molecular Phylogenetics and Evolution* 30: 378–385.
- SCHECKLER, S. E. 1986. Geology, floristics, and paleoecology of Late Devonian coal swamps from Appalachian Laurentia (USA). *Annales de la Société Géologique de Belgique* 109: 209–222.
- SCULTHORPE, C. D. 1967. *The biology of aquatic vascular plants*. Edward Arnold (Publishers), London, UK.
- STEWART, W. N., AND G. W. ROTHWELL. 1993. *Paleobotany and the evolution of plants*, 2nd ed. Cambridge University Press, Cambridge, UK.
- STOCKEY, R. A. 2006. The fossil record of basal monocots. *Monocots III/Grasses IV*. Rancho Santa Ana Botanical Garden. *Aliso* 22: 89–104.
- STOCKEY, R. A., G. L. HOFFMAN, AND G. W. ROTHWELL. 1997. The fossil monocot *Limnobiophyllum scutatatum*: resolving the phylogeny of Lemnaceae. *American Journal of Botany* 84: 355–368.
- STOCKEY, R. A., AND G. W. ROTHWELL. 1997. The aquatic angiosperm *Trapago angulata* from the Upper Cretaceous (Maastrichtian) St. Mary River Formation of southern Alberta. *International Journal of Plant Sciences* 158: 83–94.
- SUN, G., M. AKHMETIEV, Z. M. DONG, A. R. ASHRAF, Y. W. SUN, E. BUGDAEVA, D. L. DILCHER, L. GOLOVNEVA, I. HARDING, K. JOHNSON, T. KEZINA, T. KODRUL, J. S. LU, V. MARKEVICH, H. NISHIDA, H. OKADA, S. O. PARK, C. L. SUN, X. Z. XIONG, Y. L. XING, AND Z. L. ZHOU. 2002. In search of the Cretaceous-Tertiary boundary in Heilongjiang River area of China. *Journal of Geoscience Research NE Asia* 5(2): 105–113.
- SWEET, A. R. 1986. The Cretaceous-Tertiary boundary in the central Alberta Foothills. II. Miospore and pollen taxonomy. *Canadian Journal of Earth Science* 23: 1375–1388.
- WANG, H., AND D. L. DILCHER. 2006. Aquatic angiosperms from the Dakota Formation (Albian, Lower Cretaceous), Hoisington III Locality, Kansas, USA. *International Journal of Plant Sciences* 167: 385–401.
- WILDE, V., Z. KVAČEK, AND J. BOGNER. 2005. Fossil leaves of the Araceae from the European Eocene and notes on other aroid fossils. *International Journal of Plant Sciences* 166: 157–183.
- WING, S. L., L. J. HICKEY, AND C. C. SWISHER. 1993. Implications of an exceptional fossil flora for Late Cretaceous vegetation. *Nature* 363: 342–344.
- YAMADA, T., AND M. KATO. 2002. *Regnellites nagashimae* gen. et sp. nov., the oldest macrofossil of Marsileaceae, from the Upper Jurassic to Lower Cretaceous of western Japan. *International Journal of Plant Sciences* 163: 715–723.



Appendix. *Cobbania corrugata* gen. et comb. nov., a floating aquatic aroid, being inspected by an *Ornithomimus* dinosaur. The *Cobbania* quarry from Dinosaur Provincial Park, Alberta, Canada produced numerous whole plants and the most complete skeleton of this dinosaur ever recovered. (Currently on display at the Tyrrell Museum of Palaeontology, Drumheller, Alberta). Image by Marjorie Leggitt.