Scutifolium jordanicum gen. et sp. nov. (Cabombaceae), an aquatic fossil plant from the Lower Cretaceous of Jordan, and the relationships of related leaf fossils to living genera

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A new species of aquatic plant, Scutifolium jordanicum gen. et sp. nov., Taylor, Brenner & Basha, is described from the Albian of Jordan. The leaves are microphyllous with a symmetrical, elliptical to suborbiculate shape, convex to rounded apex and base, and actinodromous to palinactinodromous primary venation. The petiole, centrally attached petiololes are narrow, elongate, and alternately arranged on similarly sized stems. The leaves appear to be thick and have aerenchyma. Comparisons to plants with centrally peltate leaves and palmate venation and to aquatic plants with floating leaves suggest that S. jordanicum belongs to the Cabombaceae lineage within the Nymphaeales. Cladistic analysis including the fossil and living members of the Nymphaeales shows that the S. jordanicum is basal to the living members of the family and has unique characters not found in any living genera. This is the oldest evidence of the Cabombaceae from the Old World. Inclusion of two other Early Cretaceous peltate leaf fossils in the phylogenetic analysis indicates their affinities to Cabombaceae and that some of the shared derived characters for the living members are progressively acquired in the fossils. These data show the Cabombaceae were widespread in Gondwana and Laurasia by the mid-Cretaceous.

Key words: Cabombaceae; fossil leaves; Lower Cretaceous; Nymphaeaceae; Nymphaeales; paleoherbs; phylogenetic relationships; water lilies.

The Nymphaeales is composed of approximately 70 extant aquatic plant species with worldwide distribution (Schneider and Williamson, 1993; Williamson and Schneider, 1993) that are classified in two families (APG, 2003) and eight genera (Williamson and Schneider, 1993). Scientific interest in the Nymphaeales is spurred by the realization that this monophyletic clade (Chase et al., 1993; Zanis et al., 2002; Borsch et al., 2003; Löhne and Borsch, 2005) is one of the most basally placed among living angiosperms (Zimmer et al., 1989; Qiu et al., 1999; Soltis et al., 1999, 2000; Barkman et al., 2000; Zanis et al., 2002). Much recent work has elucidated the morphology, biology, and phylogeny of this interesting order, including evidence of relationships within Nymphaeales (Les et al., 1999; Padgett et al., 1999; Borsch et al., 2003, 2007; Löhne and Borsch, 2005; Taylor, in press).

Phylogenetic analyses of morphological and molecular characters now yield congruent results indicating that the Nymphaeales can be divided into two major clades: Cabombaceae and Nymphaeaceae. Within Cabombaceae, the genera Brasenia and Cabomba are monophyletic. Within the Nymphaeaceae, the six genera are arranged as follows from the base. First is Nuphar followed by Barclaya, Ondinea, the subclade Euryale-Victoria and Nymphaea. Recent analyses including multiple species suggest the genera are monophyletic, except that the results from the trnT-trnF data set suggest Ondinea may be embedded within Nymphaea (Borsch et al., 2007).

There is a rich Tertiary record of Nymphaeales (e.g., Collinson, 1980; Muller, 1981, 1984; Cevallos-Ferriz and Stockey, 1989; Mai and Walther, 1991; Taylor, 1991; Mai, 1995; Gee and Mörs, 2001, Taylor et al., 2006), yet well-described Cretaceous fossils, and in particular Early Cretaceous fossils, are rare (Mohr and Friis, 2000; Friis et al., 2001; Gandolfo et al., 2004; Wang and Dilcher, 2006; Mohr et al., in press a). This is unfortunate as molecular analyses have suggested that the two clades diverged in the Eocene (46 Ma; Yoo et al., 2005) and the living taxa attained their current distribution through dispersal rather than by vicariance (Yoo et al., 2005). Both of these hypotheses can be tested with well-dated and well-described fossils with phylogenetically secure relationships. A new fossil species is described with peltate, elliptical, palmately veined leaves and attached stems from the Albian (100 Ma) of Jordan. The taxon is significant because it is well preserved, is from a well-dated locality, is compared morphologically to living taxa with peltate leaves and palmate venation including aquatic plants with floating leaves, and has well-supported affinities based on a phylogenetic analysis of leaf and vegetative characters. The fossil’s relationship to Cabombaceae within the Nymphaeales provides unequivocal evidence of the family during the Early Cretaceous, the oldest evidence of the family in the Old World, and illuminates the evolution of morphological vegetative characters within the clade.

MATERIALS AND METHODS

Fossils were found at the Mahis locality in north-central Jordan (Fig. 1) at N 31°59′34.7′, E 035°45′29.2′. Jordan is tectonically part of the Arabian Shelf (Beydoun et al., 1994; Qummou et al., 1997), and during the Cretaceous, it was attached to the northeastern part of the African plate and had a paleolatitude around 10° to 15° N (Scotese, 2001; Skelton et al., 2003; Ogg et al., 2004).
Climate was considered to be mild, wet tropical at the beginning of the Cretaceous, but by the beginning of the late Cretaceous, the northward movement of the African plate had moved the area into a more arid zone (Scotese, 2001).

The fossil species is from the Jarash Formation of the Early Cretaceous Kurnub Group. Amireh (1997, 2000) divided the Kurnub Group in northern and central Jordan into three formations: the Ramel, Jarash, and Bir Fa‘as. The Ramel Formation is divided into two subunits: a lower transgressive unit (FR1) from the upper Jarash Formation (Amireh and Abed, 1999) and a glauconitic sandstone that is part of the Bir Fa‘as Formation. Because the Bir Fa‘as Formation is considered Albian in age (Amireh et al., 1998; G. J. Brenner, S. H. Basha and D. W. Taylor, unpublished data on palynology of several localities), the new fossil was collected from the Meandering River facies of the upper Jarash Formation, below the glauconitic sandstone that is part of the Bir Fa‘as Formation. The age of the Kurnub Group is Late Neocomian/early Barremian (130 Ma) to Albian (100 Ma) of the Early Cretaceous (Amireh, 1997, 2000; Amireh and Abed, 1999) based on several lines of evidence. The lower age is constrained by Kurnub Group’s position above the Middle to Late Jurassic Carbonates (Basha, 1983; Amireh and Abed, 1999). The Neocomian age is based on the foraminifera Weichselia reticulata (Edwards, 1926), and a palynomorphic study of the lower Kurnub Group (Al-Said and Mustafa, 1994). Based on pollen zonation (Brenner, 1976, 1996), Brenner and Bickoff (1992) proposed a late Barremian age for the basal part of the Kurnub Group in Israel. The upper age constraint is based on the position of the Kurnub Group’s position below the Cenomanian Nodular Limestone Member of the Na‘ur Formation of the Ajlun Group. The upper Albian age is based upon the ammonite Kuenemierzus and a glauconite marker bed in the Bir Fa‘as Formation at the top of the Kurnub Group (Amireh, 1997; Amireh et al., 1998) dated at 96.1 ± 1.1 Ma (million years ago) (Amireh et al., 1998). Carbonaceous layers from the Upper Jarash Formation also contain Albian palynomorphs (G. J. Brenner, S. H. Basha and D. W. Taylor, unpublished data on palynology of several localities). The fossil was collected from Meandering River facies of the upper Jarash Formation, below the glauconitic sandstone that is part of the Bir Fa‘as Formation. The age for the basal part of the Kurnub Group in Israel is late Neocomian/early Barremian (130 Ma) to Albian (100 Ma) of the Early Cretaceous (Amireh, 1997, 2000; Amireh and Abed, 1999).

RESULTS
Systematics—
Order: Nymphaeales
Family: Cabombaceae
Genus: Scutifolium gen. nov. Taylor, Brenner & Basha
Type species: Scutifolium jordanicum
Diagnosis of genus—Leaves microphyllous, symmetrical with petiole having centrally peltate attachment. Lamina elliptical to suborbiculate, with convex to rounded apex and base, and entire margin. Primary venation actinodromous to palinactinodromous with 4–7 primaries. Lateral primaries branching mostly dichotomously to form festoon brochidodromous architecture with inner loops radially elongate and outer polygonal. Secondaries from medial primary with decreasing spacing toward base. Third order venation random reticulate to alternate percurrent near center to random reticulate toward margin. Highest order venation with polygonal reticulate arrangement. Petioles average 1.5 mm wide and 20 mm long, and attached alternately to similar sized stems. Branching appears sympodial with largest continuing axis next to leaf petiole and smaller axis opposite petiole.

Etymology of genus—Scutifolium is derived from scutum from the Latin for shield, folium from the Latin for leaf.

Discussion of genus—The new genus was established for the leaves and stems that are distinct from any other living or fossil genus in the family. The diagnostic characters are the symmetrical, elliptical to suborbiculate shape; actinodromous to palinactinodromous primary venation with 4–7 veins; festoon brochidodromous secondary venation; and petioles about 20 mm long and 1.5 mm wide attached to similar sized branches with sympodial branching.

Type species—Name: S. jordanicum sp. nov. Taylor, Brenner & Basha (Figs. 2–20)

Diagnosis: Same as for genus.

Holotype: 99–2B-Na,b Yale Peabody Museum (YPM); (part and counterpart, Figs. 2, 3)

Paratype: 99–2B-Ga,b (part and counterpart, Figs. 14, 15)

Etymology of species: jordanicum meaning from Jordan.

Locality: Mahis, northwest Jordan (N 31°59′29.2″, E 035°45′42.9″)

Stratigraphic occurrence: Jarash Formation, Kurnub Group

Age: Albian, Lower Cretaceous

Description—The description is based on dispersed leaves with similar size, venation, and structure, four axes with attached leaves, plus dozens of axes with similar morphology. The microphyllous, elliptical, symmetrical leaves (Figs. 2–9) range from 22 to 51 mm long and 19–37 mm wide with the average length 40 mm (N = 10) and width 27 mm (N = 9). The average length to width (L/W) ratio is 1.5, and the ratio of the distance from the central attachment of the petiole to the distal end vs. to the proximal end is 1.1. This attachment frequently creates a small funnel-shaped indentation (Fig. 2). Both the apex and the base have the same obtuse angle and same convex to round shape (Figs. 2, 3, 7, 8). The margins are entire, and the venation is looped and does not extend completely to the leaf edge (Figs. 2, 5, 7).

The leaves have an actinodromous (Figs. 2, 3) to palinactinodromous (Figs. 6, 9, 10) primary architecture of radiating veins in which some laterals are fused briefly after leaving the petiole attachment (Figs. 9, 10). There is a medial primary, two pairs of lateral primaries that may be fused at the base and one (Figs. 6, 9) or two (Figs. 2, 3) primaries directed away from the apex into the petiole base. Thus the number of primary veins can range from four to seven. The lateral primaries and secondaries branch dichotomously, either evenly or less frequently unevenly to form loops making a festoon brochidodromous architecture (Figs. 2, 3, 7, 8). Near the petiole attachment the brochidodromous loops are radially elongate, while those near the margin are polygonal (Figs. 2, 3, 7, 8). The medial primary may be slightly thicker than the other primaries and does have a series of secondaries decreasingly spaced toward the base, a uniform vein angle, and a straight or slightly apical course (Figs. 2, 3, 5, 6). Third order venation is mostly random reticulate, although some alternate percurrently arranged veins closer to the petiole attachment have a straight, sinuous and occasionally chevron course (Figs. 2, 3, 7). The angle of the secondaries to the medial primary is obtuse, but in general the angle to the higher rank veins is inconsistent. The last, fourth, order has a polygonal reticulate arrangement.

The higher order venation is difficult to discern. Occasionally there appear to be fifth order veins or freely ending veinlets (FEVs), but this preservation pattern also could be a result of the preserved airspaces (aerenchyma) that in fossils can give the appearance of a fine net vein pattern. In some cases, the break between the part and counterpart leaves evidence of a regular pattern (Fig. 11). In these cases, the size appears similar to the aerenchyma observed and documented for living members of Nymphaeales (Wang and Dilcher, 2006). Based on the regular pattern of lateral primaries and of the secondaries off the medial primary, the leaves are given a lower second leaf rank (Leaf Architecture Working Group, 1999). Vein counts off the medial primary (Hickey and Taylor, 1991) are seven to eight deutrals (lateral primaries and secondaries) and no opadials (intersecondaries) and about 5–6 trinals (third order veins).

Additional characters can be discerned by examining the preservation of the leaves and axes. The leaves have variable preservation with some having only the veins preserved (with [Fig. 6] or without oxidized color [Figs. 2, 3]) to others that are dark with the venation obscure (Figs. 4, 8, 13). Based on the evidence from individual fossil leaves that have multiple preservation types (Figs. 6, 9) and an understanding of extant aquatic leaves (Kaul, 1976; Wang and Dilcher, 2006), it is possible to interpret the variation. In living leaves (including Nymphaeales), the adaxial portion of the leaf is composed of a thick palisade layer(s), and the abaxial portion has aerenchyma surrounding the veins. If the leaf is preserved before much diagenesis, the preservation may be dark and the thick leaf may seem to split within the aerenchyma. As a result, the adaxial part may or may not have preserved venation, while the abaxial counterpart may possess well-preserved venation. The upper surface was determined by the indentation created at the point of petiolar attachment, with the funnel pointing toward the bottom surface of the leaf. This type of preservation can be seen on a part and counterpart, where the venation in the adaxial part (Fig. 4) in the upper portion of the specimen is less well preserved than in the counterpart (Fig. 5). The same can be seen in another leaf, contrasting the well-preserved abaxial part (Fig. 7) and the less well-preserved adaxial part (Fig. 8). In some fossils, the veins of the abaxial counterpart may be well preserved, with an oxidized coloring from the remains of the organic carbon that appears to disappear under a film of rock sediments (Fig. 9, light sediment to left). These veins have no evidence of carbon, and are three dimensionally preserved. In these cases, the split seems to go from within the aerenchyma (between the palisade parenchyma and the lower epidermis) to between the outside of the epidermis and the sediment. That it does not split next to the parenchyma suggests that the sediment is adhering
to the epidermis, as would be expected if hairs or mucilage were found. The only evidence for hairs or mucilage is an impression that seems to have a central cell surrounded by subsidiary cells (Fig. 12) that are the same size and shape as a mucilage hair cell or hydropote complex found in living Nymphaeales (Carpenter, 2006). Finally, leaves that have the basic venation lightly preserved in both the part and counterpart (Figs. 2, 3) are interpreted to be the result of more decayed leaves that are missing the parenchyma.

The broken axes have a maximum length of 90 mm, and the width ranges from 1.5 mm to 4.5 mm (Figs. 13–20). The preservation ranges from impressions with no details (Figs. 14, 15), to darkened axes (Figs. 16, 19, 20) that can have a dark medial strand composing up to 40% of the width (Fig. 16), but no cellular or cuticular remains were observed. The internodes range from at least 75 mm to 33 mm in length with an average of 53 mm (N = 6). The nodes may have a single organ (Figs. 16 at N, 19, 20) or two organs (Figs. 13–15, 17, 18). The attached organs could be petioles, stems (presumably auxiliary shoots), and possibly peduncles, although no flowers were found. The petioles attached to leaves have similar morphology (at P, Figs. 2, 3, 4, 14–16, 20, 21), and have a maximum length of 29 mm and average width of 1.5 mm (N = 6). The four that are attached to stems have an average length of 20 mm. Because of the similarities between the shoots, lateral shoots and petioles, the axes without attached leaves frequently appear as dichotomies (Fig. 16), or pseudotrichotomies (Figs. 17, 18). Those with leaves show that the pseudotrichotomies (Figs. 13–15) have the axis nearest the leaf (A2) larger than the continuing axes (A1), suggesting a modified sympodial growth. An example of a pseudotrichotomy can be seen best in Fig. 14. The petiole and leaf (P) are on the right, and in the center the axillary branch (A2) continues on at a slight angle, while the continuing stem (A1) becomes smaller and branches again at N. The leaf arrangement is alternate (Figs. 16, 19, 20). Similar structure is found in living members of the Cabombaceae (Cronquist, 1981).

Identification of fossil to family based on morphology—
The definitive fossil characters (Table 1 excluding inferred characters) were entered in the two open access keys, resulting in 22 families from the key of Hansen and Rahn (1969, 1972, 1979) and seven families from Watson and Dallwitz (1992). Several additional characters are inferred to be likely. First is the herbaceous habit. The fact that the axes are of similar size to the leaf petiole suggests that the plant did not produce large herbaceous stems. The fact that the axes are of similar size to the plant did not produce large herbaceous stems. Second is whether the plant was aquatic on water (Sculthorpe, 1967; Kaul, 2006). Finally, leaves that have the basic venation lightly preserved in both the part and counterpart (Figs. 2, 3) are interpreted to be the result of more decayed leaves that are missing the parenchyma.

These three characters were added to those already selected from the key in Hansen and Rahn (1969) resulting in a total of 11 characters (Table 1). Only 11 families (considering Nelumbo as in a separate family from Nymphaeaceae) have these characters: Nymphaeaceae, Cabombaceae, Ranunculaceae, Haloragidaceae including Gunneraceae, Euphorbiaceae, Papilionaceae (Fabaceae), Lentibulariaceae, Umbelliferae (Apiaceae), Menyanthaceae, Compositae (Asteraceae), and Nelumbonaceae.

Finally, four other characters from the character list of Watson and Dallwitz (1992) also appear likely. These include being autotrophic based on broad, typical leaves, spiral arrangement based on leaf attachment, nonmarine based on depositional environment, and orbicular shape based on leaf shape and character state choices. The use of all 20 characters in Watson and Dallwitz (1992) resulted in three families: Araliaceae, Cabombaceae, and Tropaeolaceae. The use of the peltate and palmate venation characters excludes all the monocots because they are either not peltate or they have parallel (acrodromous) venation based on these keys.

In addition, a key for aquatic plants by Cook (1996) had sufficient leaf characters to restrict the Scutifolium to Cabombaceae, Nelumbonaceae, Nymphaeaceae, Urticulacia (Umbellulacaeae), or Hydrocotyle (Apiaceae). These results completely overlap with the results from Hansen and Rahn (1969). Nevertheless, the fossil was compared to all the families identified by the keys through the definitive characters (Table 1) because there has not been a detailed leaf architectural comparison of fossils with centrally peltate, aquatic leaves with similar terrestrial and aquatic leaves of living plants.

The centrally peltate character of the fossil is absent from many of the peltate or aquatic families noted, occurring in only four terrestrial families (Begoniaceae, Berberidaceae, Piperaceae, Tropaeolaceae), terrestrial members of two families with aquatic members (Apiaceae, Lentibulariaceae), and three aquatic families (Nymphaeaceae, Cabombaceae, Nelumbonaceae). Begoniaceae leaves have an asymmetrical shape, sharp apex, and cladodromous secondary architecture without much evenly dichotomous branching. Berberidaceae leaves have some combination of lobing, marginal teeth, elongate narrow apices, and craspedodromous to semicraspedodromous architecture. Leaves of Piperaceae have a combination of agrophic veins, lack of even branching of the lateral primaries and secondaries, and a rough texture. Although nearly circular in outline, leaves of Tropaeolaceae have nonentire margins (usually), craspedodromous architecture, and do not have even dichotomies of the lateral primaries and the secondaries. Scutifolium differs by having leaves that are elliptical, symmetrical on both ends, entire margined, and enervated with radiating veins that commonly dichotomize evenly to form a festoon brochidodromous secondary architecture.

Apiaceae leaves are mostly compound and frequently have teeth, although they can occasionally be reduced to simple leaves or have entire margins. The leaves most similar to Scutifolium are from two unusual aquatic genera Centrella and
Specimens of *Scutifolium jordanicum*. In Figs. 2–4, 6–10, leaf apices are directed to the left. 2, 3. Part, counterpart of holotype showing typical leaf shape and venation. Small, laterally compressed specimen with peltate attachment preserved at P. 99–2B-Na,b YPM. 4, 5. Part with stem, petiole (P) and leaf; counterpart with part of the leaf. The basal portion of leaf missing and distal portion with venation. 99–2B-Wa,b YPM. 6. Leaf with multiple preservation types. To right, compression with veins preserved as oxidized remains; to left, veins preserved as molds and sediment attached. Detail of radiating veins in Fig. 11. 99–2B-M YPM. 7, 8. Part and counterpart of leaf with sector still covered showing differential darkness and preservation of the venation. 99–2B-Na,c YPM. 9. Leaf with dark preservation and with sediment attached to left. Possible aerenchyma and epidermal remains preserved at arrowhead (Figs. 11, 12). 99–2B-Y YPM. 10. Detail of Fig. 6 showing differential preservation and palenactinodromous branching of some lateral primaries. 99–2B-M YPM. 11. Detail of Fig. 9 showing regular pattern of raised sediment separated by fissures similar in size and shape to aerenchyma. 99–2B-Y YPM. 12. Detail of Fig. 9 showing possible epidermal cell impressions with a central cell and surrounding cells similar to a trichome complex. 99–2B-Y YPM. 13. Specimen with a pseudotrichotomous node having two attached axes (A1, A2) and a petiole (P) attached to a poorly preserved leaf lamina with typical venation. 99–2B-Y YPM. Scale bar = 1 cm Figs. 2–10, 13; = 1 mm Figs. 11, 12.
Figs. 14–20. Specimens of *Scutifolium jordanicum*. 14, 15. Part and counterpart with axes (A1, A2), petiole (P), and portion of leaf. Axes form pseudotrichotomy with a petiole (P) attached to an incompletely preserved leaf in the upper corner, a larger central axis (A2) that diverges from the course of the original axis, and a last axis (A1) that is thinner and has a second node (N) with two axes. 99–2B-Ga,b YPM. 16. Block showing long narrow axis with stele preserved in places and two nodes (N) having only two axes. 99–2B-FF YPM. 17, 18. Part and counterpart with node having three axes (A1, A2, A3). Axes form a pseudotrichotomy with the central axis (A2) continuing at a divergent angle, and two smaller axes, one of which has a sinuous course (A1). 99–2B-GGa,b YPM. 19, 20. Part and counterpart with main stem with attached axis (A) and petiole (P) terminating in the leaf. Stele preserved in some parts and petiole at second node centrally attached to poorly preserved leaf. 99–2B-GGc,d YPM. Scale bar = 1 cm.
Table 1. Characteristics of Scutifolium used in the open access keys of Hansen and Rahn (1969) and INKEY (Watson and Dallwitz, 1992). Numbers are characters for each key, respectively. Those labeled “inferred” assumed based on the morphology and paleoecology of the fossil (see text for justification). NA, not applicable.

<table>
<thead>
<tr>
<th>Character</th>
<th>Hansen and Rahn</th>
<th>INKEY</th>
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<tbody>
<tr>
<td>Habit: herb, inferred</td>
<td>2</td>
<td>5</td>
</tr>
<tr>
<td>Leaves: well developed</td>
<td>NA</td>
<td>12</td>
</tr>
<tr>
<td>Plants: autotrophic, inferred</td>
<td>NA</td>
<td>15</td>
</tr>
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<td>Ecological type:</td>
<td></td>
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</tr>
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<td>hydrophytic, inferred</td>
<td>3</td>
<td>30</td>
</tr>
<tr>
<td>Hydrophytic habit:</td>
<td>NA</td>
<td>31</td>
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<tr>
<td>nonmarine, inferred</td>
<td></td>
<td></td>
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<tr>
<td>Leaves: floating, inferred</td>
<td>3</td>
<td>33</td>
</tr>
<tr>
<td>Leaves: small</td>
<td>NA</td>
<td>36</td>
</tr>
<tr>
<td>Leaves: alternate</td>
<td>22</td>
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<td>Leaves: spiral</td>
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<td>Leaves: flat, inferred</td>
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<tr>
<td>Leaves: petiolate</td>
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<td>Leaves: nonsheathing</td>
<td>41</td>
<td>45</td>
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<tr>
<td>Leaves: simple</td>
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<tr>
<td>Leaves: peltate</td>
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<td>52</td>
</tr>
<tr>
<td>Leaves: entire</td>
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<td>57</td>
</tr>
<tr>
<td>Lamina: orbicular, inferred</td>
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<td>59</td>
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<tr>
<td>Lamina: palmately veined</td>
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<td>61</td>
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<tr>
<td>Lamina: cross venulate</td>
<td>NA</td>
<td>62</td>
</tr>
<tr>
<td>Leaves: extipulate</td>
<td>41</td>
<td>65</td>
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<tr>
<td>Lamina margins: entire</td>
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<td>73</td>
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Hydrocotyle, although their leaves normally do not float. Centrella asiatica is the only aquatic member of the genus and the leaves are cordate/peltate with a long petiole, and plicate, with teeth, a low L/W ratio, and a blunt apex. The leaves have agrophic veins and are festoon semicircapodromous with dichotomizing lateral primaries and secondaries. Some terrestrial members of Centrella are similar, while others are lobed and are not cordate. The six species of Hydrocotyle vary from cordate/peltate (e.g., H. leucocephala) to centrally peltate in H. vulgaris. In all cases, the margins are toothed. In most, there is the evidence of a cordate base and lobing (most obvious in H. ranunculoides), and the radiating primaries frequently have a pair of closely paired secondaries that make the branching appear to be trichotomous. The thick leaves have a low L/W ratio, long petioles, craspedemodromous architecture with few dichotomies that are not even, and agrophic veins (weak in more peltate members). The nonaquatic members are quite similar although some have trichomes. Of all the species in the Lentibulariaceae, the terrestrial species Utricularia nelumbifolia is most similar to the fossil, and the thin leaves have a round outline, an entire margin, an elongate centrally placed, funnel-shaped attachment of the petiole, and a central medial primary with about 6–8 radiating veins. The medial primary has good secondaries, of which the distal pair do not dichotomize, and the proximal and the lateral primaries dichotomize to form an actinodromous, festoon brochiodromous architecture. Scutifolium leaves are dissimilar by having thickened, ovate leaves with 4–5 primary veins forming an actinodromous-palinaclinic architecture that branch in even dichotomies, no agrophic veins, and entire margins.

The fossil shares aquatic characters with members of Nelumboaceae, Nymphaeaceae, and Cabombaceae. Nelumboaceae have many pairs of veins radiating from the petiole and a nearly round shape, frequently with notches at the apex and base (Upchurch and Wolfe, 2005). The venation has a medial primary without secondaries and has tertiary veins between the lateral primaries that change from alternate to opposite percurrent. In contrast, Scutifolium has many fewer radiating veins some of which can be palinactinodromous, an elliptical outline, secondaries off the medial primary, the veins between the lateral primaries that are random and a festoon brochiodromous secondary architecture.

Nymphaeaceae have rhizomes buried below the soil that are much larger than the petioles, and only a few species have centrally peltate leaves. The two genera with such leaves are Victoria and Euryale and have large leaves, a symmetrical, nearly circular shape (with a basal cordate notch), few radiating veins forming a palinactinodromous, weakly festoon brochiodromous architecture, and large hairs that may form teeth on the margins (Taylor, in press). In contrast, Scutifolium elliptical leaves have no cordate base, no large or marginal teeth, actinodromous to palinactinodromous primary architecture with a moderate number of radiating veins, festoon brochiodromous secondary venation, and stems and petioles of similar size.

Finally, Cabombaceae have stems in the water column that are similar in size to the petioles of the leaves and the peduncles of the flowers (Cronquist, 1981). The nodes may have a leaf petiole, or a leaf petiole and a peduncle or stem, and because of the similar size, they appear as dichotomous or pseudotrachotomous branching (although they are in fact sympodial). The leaves of Cabombaceae are elliptical, symmetrical with no cordate base (except in the tiny transitional aquatic leaves of Cabomba), actinodromous to occasionally palinactinodromous with a variable number of radiating veins, and a weak brochiodromous to campylodromous (in small leaves) secondary architecture (Taylor, in press). Lastly, the leaves have large air spaces (Kaul, 1976), as do most aquatics. Scutifolium stems and leaves share all these characters, although they have fewer radiating veins and more festoon brochiodromous venation than do Brasenia and large-leaved species of Cabomba.

Due to the relationship to the Nymphaeales, the fossil characters are placed in the data matrix of vegetative and leaf architectural characters of Taylor (in press) and a cladistic analysis of the relationship performed. The resulting topology did not change from the original analysis, and Scutifolium is placed as a basal member of the Cabombaceae clade (Fig. 21). The synapomorphies supporting Nymphaeales, Cabombaceae, and Nymphaeaceae are also nearly identical. The synapomorphies for Nymphaeales are aquatic stems not above the soil, peltate leaves, wide obutse base angle, obtuse apex angle, convex apex shape, centrally peltate, entire margin, actinodromous, primaries or secondaries radiating from the base, 6–11 radiating veins, uniformly spaced secondaries, and secretory canals.

The synapomorphies of the Cabombaceae (including the fossil) are stems aquatic in the water column, less than mesophyll leaf size, primaries of similar size, no intersecondaries, and variable tertiary angle. Weak brochiodromous venation, quaternaries absent, and major veins dichotomous are synapomorphies for the living Cabombaceae clade. In the original analysis, these were all synapomorphies for Cabombaceae. The derived states for the Nymphaeaceae remained the same: very eccentric peltate attachment, cordate base with a shallow sinus, curved sides and rounded tips, and nonagrophic veins. The fossil is nested within Nymphaeales, is most parsimoniously placed at the base of the Cabombaceae, and has some of the synapomorphies for the living genera.
Comparisons to similar Cretaceous fossil leaves—The new species was compared to similar centrally peltate, palmately veined leaf fossils from the Cretaceous of the Middle East and Africa and from the Lower Cretaceous elsewhere. Such leaves are of the “Nymphaeaphyll” morphotype and have been placed in a variety of form genera (Crabtree, 1987) including Nelumbites and Nymphaeites. Nelumbites is a leaf-form genus for leaves that are nearly circular, are centrally peltate, and have a high number of radiating primaries (Upchurch et al., 1994; Krassilov et al., 2005; Wang and Dilcher, 2006). Upchurch et al. (1994) also pointed out that fossil early Tertiary Nelumbo leaves that are very similar to living species should be called Nelumbago (also McIver and Basinger, 1993). Nymphaeites was originally a form genus for rhizomes that were similar to those found in the Nymphaeaceae, but was expanded (probably incorrectly, see Krassilov et al., 2005) to including nymphaeaceous leaves when such leaves were found in association (see Heer 1870; Hollick, 1930; Duarte and Silva Santos, 1993). Usually, these are leaves with a cordate base and from the Tertiary (e.g., N. nevadensis [Knowlton] Brown), but some specimens are centrally peltate (Álvarez-Ramis, et al., 2004), and probably belong in Nelumbites. None of the fossils from these genera can be assumed to be members of Nymphaeales, although some of the Tertiary reports probably are. Those correctly assigned to Nelumbites and Nelumbago are likely members of the Nelumboaceae lineage (Upchurch and Wolfe, 2005).

In the Middle East and Africa, similar leaf fossils have only been described from the Upper Cretaceous. These either have cordate bases such as Nymphaea mesozonica (Dobruskina, 1997; Krassilov et al., 2005) or are centrally peltate with high numbers of radiating veins such as Nelumbites (Lejal-Nicol and Dominik, 1990; Dobruskina, 1997; Schrank and Rüffle, 2003; Krassilov et al., 2005) and related to Nelumbo. Elliptical, eccentric peltate leaves are described from the Cretaceous of Sudan (Hassan, 1973). These are not well preserved, but appear to have seven radiating primaries that rarely branch dichotomously and to be more similar to living terrestrial species. Scutifolium clearly differs from all these species by having a small size, an elliptical shape with central placement and no more than seven radiating veins.
Peltate leaves and presumed aquatic leaves have been extensively described in the literature from the Lower Cretaceous around the world. *Nymphaeites choffati* from the Lower Cretaceous of Brazil is based on nearly round, cordate leaves that have a dentate margin with many veins extending to the margins in what appears to be a semicraspedodromous architecture (Duarte and Silva Santos, 1993). This was proposed to be an aquatic but has been recently redescribed by Mohr et al. (in press a) and is likely to be a monocot herb. Two possible water lilies were described by Mohr and Friis (2000). The first has a rosette with attached stems, roots and leaves, which are orbicular, cordate, and eccentrically peltate, and have 7–9 radiating primaries that branch dichotomously and form brochidodromous loops. The other, *Pluricarpellatia*, has small (3 cm or less) elliptical, eccentrically to centrally peltate leaves (Mohr and Friis, 2000; Mohr et al., in press b). Unfortunately, the venation is obscure, but there appear to be up to four veins on one-half of the lamina suggesting a total over eight. The leaves are attached to rhizomes with filiform structures that the authors suggest might be adventitious roots (although some dichotomize in a pattern similar to submerged leaves), and the rhizomes are of nearly the same diameter as the petioles and peduncles. These leaves are most similar to those of the Cabombaceae in shape, size, and the number of veins. *Scutifolium* is similar to this taxon, including the elliptical, symmetrical, centrally peltate leaves, and lack of distinction on the size of the petioles and stems. *Scutifolium* differs by the larger lamina size, fewer radiating veins, and the pseudotrichotomous branching of the axes.

Similar Early Cretaceous leaves have been described from the east coast of the United States (Doyle and Hickey, 1976; Hickey and Doyle, 1977; Upchurch et al., 1994 and references therein), although most of the species are not centrally peltate. The peltate leaves have been assigned to *Nelumbites* (some formerly members of *Menispermites*). The type species *N. virginensis* (Fontaine) Berry is peltate with about seven radiating veins, but the type specimen is not complete, so the shape and base type are unknown. One well-described species is *N. exstenuinervis* (Upchurch et al., 1994), which has centrally peltate

![Majority rule consensus tree of 11043 trees based on a parsimony analysis including Scutifolium jordanicum, Basenites kansense, and Pluricarpellatia peltata in the data set of Taylor (in press). Tree length = 159, CI = 0.484, RI = 0.771, RC = 0.373. Numbers above the branches are the percentage of trees in which each given clade appears based on a majority rule consensus analysis, and numbers below the branches are bootstrap support values; only values over 50% are shown.](image)
leaves that are orbicular, with 8–10 radiating veins that are dichotomous at the margins and form brochidodromous loops, and a medial primary with a few secondaries. In addition to those from the Potomac, leaves of “Nelumbo” weymouthi are described from the Aptian of Wyoming (Brown, 1933) with centrally peltate attachment of ~12 radiating veins that may form loops, but more often are connected by percurrent third order veins. All of these are similar to Nelumbo, while Scutifolium differs in shape, size, venation, number of primary veins, or similar tertiary architecture.

Brasenites kansense has been described from the now Albian Dakota Formation (Wang and Dilcher, 2006). These leaves are centrally peltate, orbicular with 10 primaries, festooned brochidodromous venation and have evidence of aerenchyma. The species is suggested to be a member of the Cabombaceae, which appears likely. Scutifolium leaves are similar but have a lower number of radiating veins that have more festooned brochidodromous loops, and the leaves are attached to similarly sized axes.

Finally, there have been reports of similar fossils from the Lower Cretaceous of Europe. Brasenopsis was created for leaves similar to members of the Cabombaceae and species described from Portugal (Saporta, 1894), although it is also similar to Menispermites (Teixeira, 1948). Unfortunately, the figures are drawings, so the following description cannot be confirmed. The leaves appear small (maximum 4.5 cm long and 4 cm wide), elliptical-ovate, centrally peltate, a strong medial primary, and few to no radiating lateral primaries. The secondaries form festoon brochidodromous loops to the entire margin. As drawn and described, the fossil genus is unlike any living or fossil group and should be reinvestigated. Scutifolium has radiating primaries, and the number of loops is not as great. Other species are Nymphaeites choaffati, now considered a monocotyledonous herb (Mohr et al., 2007), and Nymphaeites rhizostigma, that is based on rhizomes remains.

Based on this survey, the only Cretaceous reports of the family are from the Aptian of Brazil and the Albian of North America described earlier. For further understanding the relationships of these taxa with Scutifolium and justifying it as a new genus and species, all three taxa were added to the data set of leaf and vegetative characters of the Nymphaeales (Taylor, in press). The results of phylogenetic analysis show that the generic topology did not change, but there was a slight change in the specific relationships in Nymphaea (Fig. 22, compared to 21). In the strict consensus, the three fossil species form a polytomy at the base of the order, yet the majority rule consensus shows that the three fossils form an unresolved trichotomy at the base of the Cabombaceae in 77% of the trees (Fig. 22) with weak bootstrap support (51%). If each fossil genus is added separately, Scutifolium and Pluricarpelatia were always at the base of Cabombaceae, while Brasenites was at the base of the Nymphaeaceae in 54% of the trees.

Among the shortest trees (Fig. 22), most often the fossils form a pectinate pattern with Brasenites at the base, followed sequentially by Pluricarpelatia, Scutifolium, Brasenia, and the Cabomba species. The synapomorphies supporting the Nymphaeales, Cabombaceae, and Nymphaeaceae clades were also nearly identical to the tree of living taxa. In the trees with the fossils, synapomorphies for Nymphaeales are aquatic stems not above the soil, centrally peltate leaves, wide obtuse base angle, obtuse apex angle, convex apex shape, entire margin, actinomorphic primary architecture with the medial primary slightly thicker than lateral primaries, 6–11 primaries or secondaries radiating from the base, uniformly spaced secondaries, secondaries absent, and secretory canals.

The synapomorphies of the Cabombaceae clade (including the fossils) are stems aquatic in the water column, less than mesophyll leaf size, variable tertiary angle and course. At the node above Brasenites, the synapomorphy is primaries of similar size, above Pluricarpelatia the clade is defined by quaternaries absent and major veins dichotomous, and finally the living Cabombaceae synapomorphy (above Scutifolium) is weak brochidodromous secondary venation. All these were synapomorphies for Cabombaceae in the original analysis with the only state excluded being no intersecondaries that became a synapomorphy for Nymphaeales. The derived states for the Nymphaeaceae stayed the same as the previous analyses. Scutifolium does not consistently become a sister taxon to any living or described fossil species or genus of Nymphaeales and appears best placed as a new species among the Cabombaceae clade.

DISCUSSION

Discoveries of fossils with relationships to Cabombaceae are important for understanding the evolution of the Nymphaeales. There is strong evidence that Scutifolium is a member of Nymphaeales and related to living genera of Cabombaceae where it has a basal position within the family (Fig. 21). Important synapomorphies with living Cabombaceae include small leaves, centrally peltate leaves, and actinomorphic architecture with a low number of radiating veins of similar size, yet the fossil is clearly transitional, lacking synapomorphies for the living genera such as weak brochidodromous venation. Two other Early Cretaceous fossils also appear to have affinities to the family (Fig. 22). One of these, Pluricarpelatia, also appears to be strongly placed at the base. Although Brasenities has great similarities to Nymphaeaeae (in particular, the larger size, more orbicular shape, and more strongly expressed medial primary vein), it is more similar to living genera of Cabombaceae with their higher degree of excurrent branching of the lateral primaries. The inconsistency in Brasenities placement raises the possibility it could be a member of a third extinct lineage and perhaps part of a primary radiation of the order (Mohr et al., in press b).

The analysis also shows the importance of transitional fossils. If Brasenities is added alone, it would be thought to be a basal member of Nymphaeaeae; yet with the addition of the other two fossils, it appears more often as a member of the Cabombaceae clade. The phylogenies including the fossils (Figs. 21, 22) are congruent with those based on DNA sequence and morphological data (Les et al., 1999; Borsch et al., 2003, 2007; Löhne and Borsch, 2005; Taylor, in press), although the support for relationships among the species of the Ondinea, Eurale-Victoria clade and Nymphaea is weak.

Based on the phylogeny including the fossils, the ancestors to Nymphaeales had centrally peltate leaves, had only rhizomatous stems, and were aquatic with the related aquatic adaptations, while coriaceous leaves are derived in Nymphaeales and aquatic stems above the soil are derived in living Cabombaceae. Having a central peltate attachment and only rhizomatous stems as ancestral states is most parsimonious, but it would be helpful to have additional evidence to support this conclusion. These fossils confirm that the actinomorphic leaves with festoon brochidodromous secondary architecture are ancestral in both families (even though these are lacking in living Cabombaceae).
The fossils allow us to understand the evolutionary acquisition of characters found in extant Cabombaceae leaves. First, small leaves with less organized tertiaries evolved. This stage was followed by reduction of the medial primary to the same strength as the lateral primaries and by the loss of higher levels of venation. Finally, there was reorganization with increased excurrent branching of the secondaries and lateral primaries, resulting in weak brochidodromous venation. Thus the fossils can be considered transitional forms, with different mosaics of ancestral and derived characters, between the common ancestor with Nymphaeaceae and the two living genera of Cabombaceae.

The presence of the Cabombaceae lineage during the Lower Cretaceous and of the Nymphaeaceae during the middle Cretaceous (Gandolfo et al., 2004), and possibly the Lower Cretaceous (a possible dispersed nymphaeaceous flower has been described by Friis et al. [2001] although diagnostic synapomorphies appear to be missing [Gandolfo et al., 2004; Yoo et al., 2005]) is in conflict with divergence predictions from molecular clock analyses (Yoo et al., 2005). Clock data suggest that the two families split no later than the Eocene, 46 Ma, less than half the age of any of these fossils. Our data suggest the fossils are members of the stem lineage, while the living species of Cabombaceae are in the crown group. The Cretaceous age of the Cabombaceae fossils is supported by the fossil floral evidence of the order (Gandolfo et al., 2004), suggesting that there may be a lack of understanding of the molecular evolution of the clade. It should be noted that the discord between the fossil data and the molecular clock divergence time of the living species (Soltis et al., 2002) is also found for Chloranthaceae (Zhang and Renner, 2003), a group with a robust fossil record (e.g., Eklund et al., 2004 and references therein). There is growing evidence of duplication and evolution of floral genes (Irish and Litt, 2005), raising the possibility that early in the evolution of angiosperms, there was a major reorganization of the genome. This might have resulted in a major change in the rates of molecular change throughout the genome to a degree that is not reconciled with current methods for estimating divergence time.

The living members of Nymphaeales currently have a worldwide distribution from the tropics to temperate areas (Schneider and Williamson, 1993; Williamson and Schneider, 1993). Based on the high diversity of Tertiary specimens and the divergence times based on molecular data, it has been suggested that the current biogeographic distribution pattern is due to dispersal and extinction (Yoo et al., 2005). The new evidence presented here does not directly address these hypotheses, but does strongly suggest Cabombaceae was present in tropical South America, subtropical northern Africa, and temperate North America during the Early Cretaceous. These fossils would suggest an initially tropical distribution along the Tethys Seaway with later diversification after the continents became separated by water gaps (Taylor, 1988, 1990, 1991, 1995).

The identification of the morphologically diverse ANITA grade as the basalmost living angiosperms has created problems in interpreting the morphology and habit of the early angiosperms. One question has been when early angiosperms invaded the aquatic realm (Taylor and Hickey, 1996; Feild and Arens, 2005). There is strong evidence that the cabombaceous fossils were indeed aquatic and that these fossils have the morphologic traits found in living floating aquatic leaves, including aerenchyma. In addition, all three fossil localities are considered to be freshwater depositional environments. Thus the Nymphaeales were aquatic at least by the end of the Early Cretaceous. These fossils are not the only evidence of aquatic fossil angiosperms. It seems likely that Archaeofructus was also an aquatic plant (Sun et al., 1998, 2002; Friis et al., 2003; Ji et al., 2004). Yet the shoot morphology of both Scutifolium and Pluricarpellata suggest that the leaf petioles were of moderate length and that the fossil species either floated or lived in relatively shallow water. Thus the elongated petioles currently found in the Nymphaeales may be derived.

LITERATURE CITED


