

Cretaceous flowers of Nymphaeaceae and implications for complex insect entrapment pollination mechanisms in early Angiosperms

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Based on recent molecular systematics studies, the water lily lineage (Nymphaeales) provides an important key to understanding ancestral angiosperm morphology and is of considerable interest in the context of angiosperm origins. Therefore, the fossil record of Nymphaeales potentially provides evidence on both the timing and nature of diversification of one of the earliest clades of flowering plants. Recent fossil evidence of Turonian age (≈ 90 million years B.P.) includes fossil flowers with characters that, upon rigorous analysis, firmly place them within Nymphaeaceae. Unequivocally the oldest floral record of the Nymphaeales, these fossils are closely related to the modern Nymphaealean genera *Victoria* (the giant Amazon water lily) and *Euryale*. Although the fossils are much smaller than their modern relatives, the precise and dramatic correspondence between the fossil floral morphology and that of modern *Victoria* flowers suggests that beetle entrapment pollination was present in the earliest part of the Late Cretaceous.

The angiosperm order Nymphaeales has been most commonly treated as comprising one or two families of entirely aquatic plants, Nymphaeaceae *sensu stricto* (water lilies), including the genera *Nymphaea*, *Nuphar*, *Barclaya*, *Victoria*, *Euryale*, and *Ondinea*, and the less widely known Cabombaceae, including the genera *Cabomba* and *Brasenia* (1, 2). The nonaquatic woody group Illiciales (*Illicium* and *Schisandraceae*) have been placed as a sister group of the core Nymphaeales based on some, but not all, recent molecular analyses. The overall phylogenetic position of the broad Nymphaeales (with or without *Illicium* and *Schisandraceae*) varies depending on the analysis and particular data set used, but all recent molecular studies place Nymphaeales, *Amborella*, or *Amborella* plus Nymphaeales as a sister group to the remainder of extant angiosperms (e.g., refs. 3 and 4). Thus, Nymphaeales provide an important key to understanding ancestral angiosperm morphology and are of considerable interest in the context of angiosperm origins (4). This putative basal or near-basal position within angiosperms of the Nymphaeales and *Amborella* has revived interest in these taxa among biologists, although the “debate over the phylogenetic position of the Nymphaeales *sensu lato* is at least a century old” (5). The question of whether the earliest angiosperms were aquatic has been brought to the forefront by recent discovery of an Early Cretaceous aquatic angiosperm (*Archaeofructus*) from China (6). Based on cladistic analysis of a combined matrix of morphology and molecular data, *Archaeofructus* was placed as a sister taxon to extant angiosperms (6). However, a recent reanalysis with modifications of the original matrix resulted in additional trees in which *Archaeofructus* was also placed within Nymphaeales, next to *Cabomba* (which was added to the original matrix), although the position as sister taxon to extant angiosperms was equally parsimonious (7). However, other than an aquatic habit, *Archaeofructus* is dramatically different from any extant Nymphaeales. We interpret its placement within Nymphaeales (7) as spurious, influenced by the interpretation of the leaves of *Cabomba*, which were incorrectly coded as only dichotomously divided, when in fact *Cabomba* also bears floating leaves with anastomosing veins

(8). When *Cabomba* is accurately coded for leaf form/venation, the phylogenetic position returns to the one found in the original publication and is never within Nymphaeales, even when all other modified character codings from the reanalysis are retained (8). Because of their key phylogenetic position, the fossil record of Nymphaeales is extremely important to understanding angiosperm origins, potentially providing evidence of both the timing and nature of one of the earliest clades of flowering plants. In this context, the occurrence of early nymphaeaceous fossils can be an important source of evidence to evaluate and interpret the results of molecular analyses of extant taxa. As with most angiosperm families, the fossil record for the Nymphaeales has been primarily based on fossil leaves and pollen. The oldest leaves, petioles, and stems known with nymphaeoid characters come from the Kurnub Group (Upper Aptian, Uppermost Albian, 97–124 million years B.P., Early Cretaceous) of Jordan (D. W. Taylor, personal communication), whereas the oldest record of pollen assignable to Nymphaeaceae is of Maastrichtian, Upper Cretaceous age (9). The Albian–Aptian records place the group among the oldest known angiosperm fossils. Recently, Friis *et al.* (10) described another Early Cretaceous (100–125 million years B.P.) Portuguese fossil flower with associated pollen grains as a member of the Nymphaeaceae. However, the features of this fossil taxon are equally compatible with Illiciaceae as well as other angiosperm families, and the fossil cannot be unequivocally assigned to Nymphaeales *sensu stricto* as defined by Les *et al.* (2).

Thus, although molecular evidence indicates that the Nymphaeales clade was represented among the earliest radiations of the angiosperms, reports of the oldest fossil “nymphaealeans” are equivocal because of incomplete preservation (7). Herein we report newly discovered fossil flowers that are exquisitely preserved, providing complete and detailed structures that have a complement of characters unique to the extant nymphaeaceous genus *Victoria* (the extant and spectacular giant Amazon water lily), allowing a precise placement of the flowers within the Nymphaeaceae *sensu stricto*. These new fossil flowers, preserved by a process of charcoalification, were collected from sediments of the Raritan Formation exposed in the Old Crossman Clay Pit in New Jersey, United States.

Materials and Methods

Fossil Collection and Preparation. The fossil flowers were collected at the Old Crossman Clay locality of the Raritan Formation (Turonian, ≈ 90 million years B.P., earliest Upper Cretaceous) in Sayreville, NJ (11–13). The paleoenvironment is described as fluvial with levee/back levee and swamp conditions and the paleoclimate as subtropical to tropical. The associated paleoflora previously described is also consistent with such a climate. The Nymphaeaceae flowers are associated with other angiosperm flowers and fruits, representing at least 100 separate taxa

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(14–27), various leaves and strobili of gymnosperms (17, 28), ferns (29, 30), and mosses (17). The fossils were prepared following Nixon and Crepet (25) with the modifications suggested by Gandolfo *et al.* (29). Fossils were mounted on stubs and sputter-coated with gold/palladium for studying with a Hitachi 4500 scanning electron microscope. Fossilization is by charcoalification, leaving the floral morphology perfectly preserved. This, combined with the exquisite retention of cell-by-cell anatomical details, allows observation of key characters in these flowers. Specimens are housed in the L. H. Bailey Hortorium Paleobotanical Collection, Department of Plant Biology, Cornell University (CUPC 1475–1481).

Cladistic Analyses. This new fossil taxon was included in a combined matrix produced by fusion of two matrixes, one molecular (rbcL, matK, and 18S rDNA data) and one morphological (31 vegetative and habit characters and 37 reproductive features), both of which were originally published by Les *et al.* (ref. 2; see original work for discussion of characters). The two matrixes were fused by using standard matching (data concatenation by taxon) with the program WINCLADA (www.cladistics.com). The resulting combined matrix includes all eight recognized genera of the Nymphaeales (*Cabomba*, *Brasenia*, *Nuphar*, *Barclaya*, *Ondinea*, *Nymphaea*, *Euryale*, and *Victoria*) and the fossil taxon *Microvictoria*. We added one morphological character to the matrix, “Paracarpels” (presence = 0, absence = 1), which is present in the fossil and modern *Victoria*. The following characters were coded for the fossil taxon: Perianth insertion perigynous/epigynous (Char. 33), Number of sepals greater than 4 (Char. 34), Number of petals greater than 5 (Char. 37), Corolla tube absent (Char. 38), Petal nectaries absent (Char. 39), Stamen insertion spiral (Char. 40), Number of stamens greater than 50 (Char. 41), Stamen attachment free (Char. 42), Staminodes present (Char. 43), Filament laminar (Char. 46), Gynoecium syncarpous (Char. 52), Floral apex process projecting (Char. 54), Carpillary appendages present (Char. 55), and Stigmatic surface continuous (Char. 56). Parsimony analyses were performed with the program NONA (www.cladistics.com). For the analysis, extensive tree searches were conducted by using thousands of random starting points and TBR swapping holding 20 trees, followed by TBR swapping of shortest trees holding up to 50,000 trees (mult* and max* commands of NONA). A bootstrap analysis was also performed by using WINCLADA and NONA. This is a conservative bootstrap, which utilizes the strict consensus of each replicate.

Taxonomic Treatment. Family. Nymphaeaceae R. A. Salisbury.

Genus. *Microvictoria*, Nixon, Gandolfo, and Crepet, gen. nov.

Type species. *Microvictoria svitkoana* Nixon, Gandolfo, and Crepet, sp. nov.

Generic diagnosis. Minute, actinomorphic hermaphrodite, epigynous flower; all floral parts numerous and helically arranged, perianth formed by tepals, floral receptacle clothed with imbricate spirally arranged tepals. Tepals either sepaloid, covering the floral cup from the pedicel to the cup rim, or petaloid, attached around the rim of the cup. Androecium with outer staminodes and inner stamens. Stamens free, laminar, not differentiated into filament and anther; pollen grains unknown. Staminodes free, flattened, and tongue-shaped. Stamens and staminodes are S-shaped in lateral view. Gynoecium formed by paracarpels covering the stigmatic area, several rows of carpillary appendages surrounding the rim of the stigmatic cup followed by numerous rows of carpels; stigmatic cup surrounding a central column; ovary inferior; number of locules and ovules unknown.

Species. *Microvictoria svitkoana* Nixon, Gandolfo, and Crepet, sp. nov.

Specific diagnosis. As for the genus.

Etymology. The generic name *Microvictoria* reflects the similarities between the extant genus *Victoria* and the fossil. The epithet *svitkoana* honors Jennifer L. Svitko.

Holotype. L. H. Bailey Hortorium Paleobotanical Collection CUPC 1475.

Paratypes. L. H. Bailey Hortorium Paleobotanical Collection CUPC 1476–1481.

Repository. Cornell University Paleobotany Collection, L. H. Bailey Hortorium, Department of Plant Biology, Cornell University, Ithaca, NY.

Type locality. Old Crossman Clay Pit, Sayreville, NJ.

Stratigraphic position. South Amboy Fire Clay, Raritan Formation.

Age. Turonian, Late Cretaceous.

Description and remarks. Flowers of *Microvictoria* are minute, actinomorphic, hermaphrodite, and epigynous and pedicellate (2.3–3.4 mm long and 1.2–1.6 mm in diameter) (Fig. 1 *a–c*). The pedicel is stout (0.4–1.8 mm long) (Fig. 1 *a* and *b*). All of the floral parts are numerous and are attached in helical arrangement (Fig. 1 *c–e* and *i*). The deep floral receptacle bears imbricate spirally arranged appendages (Fig. 1 *a–c*). Because of their position on the floral cup, we interpret them as tepals. The tepals are either sepaloid or petaloid. The sepaloid tepals cover the floral cup from the pedicel to the rim of the cup and are thick and have the aspect of bracts (Fig. 1*a*). The petaloid tepals are attached around the rim of the cup, are very thin and broad, and are of different sizes, with the larger ones outermost and the smaller ones innermost (Fig. 1 *c, d*, and *f*). A chamber is defined by an appendage-free expanse of the receptacle between the androecium and gynoecium; the chamber is 0.9–1.3 mm in height (Fig. 1*b*). The androecium is composed of two zones: an outer zone of numerous stamens closer to the rim of the receptacle, and a lower inner zone of staminodes (Fig. 1 *e* and *f*). The stamens are flattened, not differentiated into filament and anther, have cuspidate tips, and are S-shaped in lateral view (360–570 μm long and 63–143 μm wide) (Fig. 1 *e–g*). The staminodes are also flattened but tongue-shaped, with incurved and triangular tips, and are 490–800 μm long and 125–150 μm wide (Fig. 1 *e, f*, and *h*). The staminodes delimit a central pore that we interpret as a pollinator entry portal (Fig. 1*e*). The gynoecium is composed of numerous paracarpels, styler processes, or carpillary appendages, a stigmatic cup, and a central column. The paracarpels are situated in a closely packed helix outside and overarching the stigmatic area but do not cover the sterile tip of the central column, are oblong in shape, and are 220–360 μm long and 118–164 μm wide (Fig. 1 *i* and *j*). The paracarpels are followed by rows of filiform styler processes or carpillary appendages that are spirally arranged around the rim of the stigmatic cup; they are 300–340 μm long (Fig. 1 *j* and *k*). The carpillary processes are continuous with the stigmatic cup (Fig. 1 *j* and *k*). The stigmatic cup surrounds a central sterile column. The central column is basally swollen and 318–320 μm in height. It narrows distally, culminates in a hexagonal tip 133–135 μm in diameter (Fig. 1 *i* and *j*), and has separate empty chambers, although the chambers may be due to mode of preservation (Fig. 1 *j* and *k*). This column appears to be the prolongation of the floral axis. A stigmatic cup is formed by the space between the paracarpels and the sterile column. Although we have detected no locules, the ovary is clearly inferior based on the position of the sessile stigmatic cup in relationship with the rest of the organs. Receptacular vascular bundles include xylem conductive elements with helical thickenings (Fig. 1*l*). The lack of preserved ovary locules is consistent with the missing pollen in suggesting that these flowers were buds preserved at relatively early developmental stages.

Results of the Cladistic Analyses. Parsimony analyses of the combined morphological and molecular analyses resulted in two most parsimonious trees, with *Microvictoria* placed as a sister

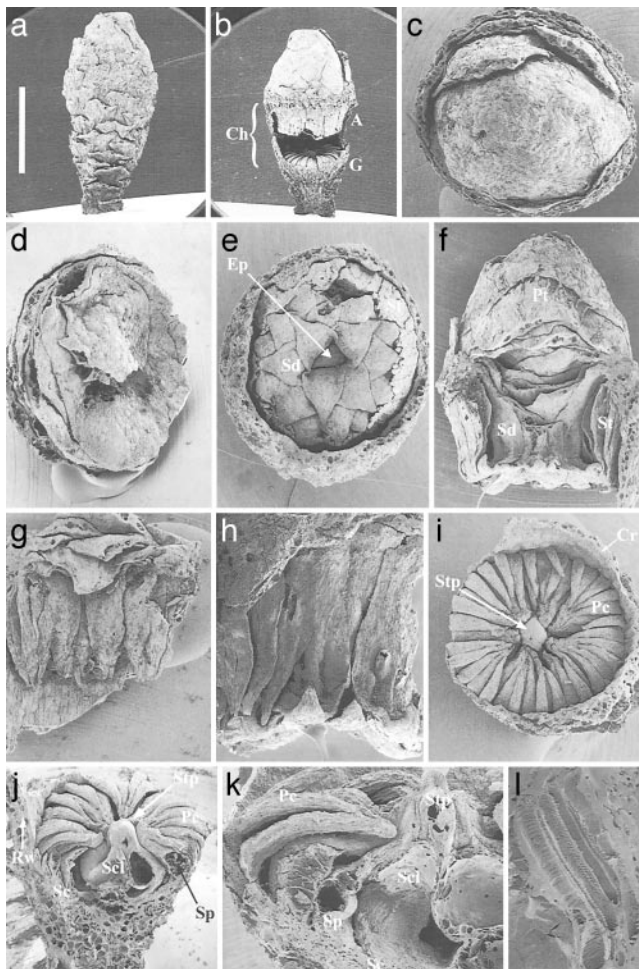


Fig. 1. Scanning electron micrographs of *Microvictoria svitkoana* Nixon, Gandolfo, and Crepet, gen and sp. nov. CUPC 1475. (a) Depicted is a lateral view of the flower showing the perianth formed by sepaloid and petaloid tepals, stout pedicel, and overall shape of the flower bud. Note the spiral placement of the sepaloid tepals covering the floral cup. (Bar, 1.2 mm.) (b) Lateral view of the flower bud after removing part of the perianth to expose the androecium (A) and gynoecium (G). Note the chamber (Ch) between the androecium and gynoecium. (Bar, 1.2 mm.) (c) Top view of the flower, showing the spirally arranged petaloid tepals. (Bar, 500 μ m.) (d) Adaxial view of the petaloid tepals. Note the different sizes. (Bar, 430 μ m.) (e) Abaxial view of the androecium showing spirally arranged stamens (St) and staminodes (Sd). See also the entry portal (Ep). (Bar, 500 μ m.) (f) Side view of the petaloid tepals (Pt) and androecium formed by one cycle of stamens (St) and one cycle of staminodes (Sd). (Bar, 500 μ m.) (g) Lax S-shaped, laminar stamens with acute tip, and the receptacle wall. (Bar, 430 μ m.) (h) Tongue-shaped, laminar staminodes showing the incurved and triangular tips. (Bar, 300 μ m.) (i) Top view of the flower receptacle after removing the androecium. Note the cup rim (Cr) and numerous spirally arranged paracarpels (Pc) leaving visible the sterile tip (Stp). (Bar, 430 μ m.) (j) Longitudinal section of the receptacle cup showing the receptacle wall (Rw), paracarpels (Pc), stylar processes (Sp), stigmatic cup (Sc), and sterile column (Scl) and tip (Stp). (Bar, 430 μ m.) (k) Detail of the paracarpels (Pc), stylar processes (Sp), stigmatic cup (Sc), and sterile column (Scl) and tip (Stp). (Bar, 150 μ m.) (l) Detail of tracheids of vascular bundles that supply the receptacle cup. (Bar, 33 μ m.)

taxon to *Victoria* in one, and as a sister taxon to the *Victoria*–*Euryale* clade in the other. The strict consensus of these two trees is identical to the majority rule consensus of 100 replicates, as presented in Fig. 2. Because we did not include an outgroup, the trees were rooted Cabombaceae (*Brasenia* and *Cabomba*) and Nymphaeaceae, both of which are widely considered to be monophyletic based on multiple lines of

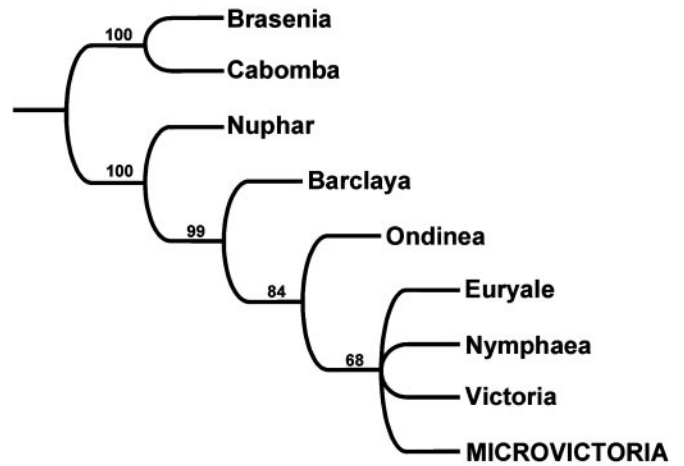


Fig. 2. Majority rule consensus of 100 replicates. This tree is identical to the strict consensus of the two equally most parsimonious trees obtained in the analysis.

evidence. The overall topology of the trees without the fossil was identical to the trees obtained by Les *et al.* (2) and to our separate analyses of the matrices. The placement of the fossil, considering the limited number of characters available, is relatively strongly supported (68% bootstrap value, very high for a clade including a fossil with missing data) as a member of the *Nymphaea*–*Victoria*–*Euryale* clade. These results confirm the placement of *Microvictoria* within Nymphaeaceae, as a close relative of *Victoria* or the broader clade that includes both *Victoria* and *Euryale*. The implications of this placement are discussed below.

Discussion

The family Nymphaeaceae as defined by Les *et al.* (2) encompasses six genera and \approx 66 species with tropical and subtropical distribution (31). Flowers of Nymphaeaceae are complex in that there are usually several zones of appendages, including sterile appendages that are variously interpreted based on position as either staminodes or pistillodes (paracarpels) (32–34).

Flowers of *Microvictoria* exhibit a host of features that solely and in combination indicate a close relationship to modern Nymphaeaceae, and in particular with the *Victoria*–*Euryale* clade, and within it, unquestionable similarities to those of the modern genus *Victoria*. Both genera, the fossil *Microvictoria* and the modern *Victoria*, are actinomorphic (plesiomorphic), perfect, epigynous, and composed of numerous floral parts. But most remarkably, there is a one-to-one structural and positional correspondence between the floral organs of the fossil and those of the modern genus *Victoria*. This correspondence includes (locants refer to Fig. 1), moving from the outside of the flower toward its center, tepals gradually increasing in size (a); numerous spirally arranged petaloid tepals (the innermost presumed petaloid based on thin delicate texture and shape in fossil) (b); incurved staminodes with triangular tips, positioned around and forming an entry portal (c); fertile incurved stamens (d); paracarpels overarched the stigmatic cup (e); stylar processes on margin of stigmatic cup (f); discoid sessile stigmatic cup (g); and sterile central projection (h).

There is also morphological congruence among the different classes of floral organs. The perianths of both genera are comparable. Both have “sepaloid” tepals covering the receptacle (Fig. 1a) and “petaloid” tepals (Fig. 1b–d). In modern *Victoria*, there is additionally an outer cycle of four tepals that might be

called sepals. These are somewhat keeled and petaloid (33). Because of preservation in the fossil, we are uncertain of the existence of such a cycle but cannot rule it out.

The androecia are also similar. Moseley (35) and Schneider (33) described the androecium of extant *Victoria* as composed of an indefinite number of flattened stamens and numerous subulate to lanceolate staminodes; both are arched in an S shape and are spirally arranged. *Microvictoria* displays this pattern as well (Fig. 1 e–g). Its stamens and staminodes are helically arranged in two zones; they are numerous and show the general lax S-shape morphology. Another feature present in stamens and staminodes of both genera is their sterile distal tips (Fig. 1 e–h) (35).

The gynoecia of both the fossil and extant genera have the same number, relative positions, and morphology of component organs (see above). Modern *Victoria* has syncarpous carpels that are enclosed by and fused dorsally to a continuous cup-like sheath of tissue (probably receptacular). This unique whorl of carpels surrounds the base of the floral apex that is free from the carpels. The carpels are extended distally, forming the carpellary appendages or stylar processes, which are separated one from another and horseshoe-shaped (33). In *Victoria*, there is an additional zone of numerous sterile appendages between the androecium and the gynoecium. These appendages are called “paracarpels” or “guard cones” and are interpreted as food bodies or as nectaries (33). *Microvictoria* has a corresponding arrangement of organs: the paracarpels are attached around the rim of the cup and are closely packed in a spiral over the stigmatic region, leaving exposed the tip of the central sterile column (Fig. 1 i and j). The paracarpels are followed directly by the set of stylar processes (Fig. 1 j and k). The stylar processes, as in modern *Victoria*, are horseshoe-shaped and continuous with the stigmatic cup.

In contrast to *Victoria*, the *Microvictoria* stigmatic cup is not immediately obvious because of the juxtaposition of the stylar processes and the central column, a probable correlate of the immature stage of development at the time of preservation (Fig. 1j). In *Victoria*, the stigmatic tissue covers the distal section of the gynoecium and is extended from the floral axis to the stylar processes (33). Another difference between the taxa is the nature of the central sterile column. In the fossil, the central sterile projection is lobed, but centrally fused, and chambered. We interpret this as the sterile floral tip. In modern Nymphaeaceae, this sterile tip is less complicated in structure. Although we have not detected locules in these immature fossil buds, the ovary in *Microvictoria* is clearly inferior. This interpretation is consistent with the presence of the sessile stigmatic cup. In modern taxa, the carpels develop immediately below or somewhat lateral to the stigmatic cup, embedded in the tissue of the receptacle. There is no likely alternative position for the ovary in the fossil taxon, and we interpret it as fully inferior. In modern Nymphaeaceae, the carpel locules form at late stage in floral development (33, 36, 37), supporting our interpretations. The fossil differs from modern *Victoria* mostly in the more deeply developed floral cup, resulting in a chamber that separates the stamens and staminodes above from the paracarpels and stigmatic cup in the bottom of the cup (Fig. 1b).

Although we were not able to distinguish particular vascular bundles, we found two vascular strands in the receptacle. We interpret these as part of the gynoecial vascular network

because of their position in the receptacle very near the stylar processes, which is similar to the gynoecial vascular system of *Victoria* (33). The xylary vascular bundles are formed by tracheids with annular and helical thickenings; again, similar to the types of tracheids found in corresponding bundles in modern Nymphaeaceae (5, 38).

The precise correspondence and unique nature of the reproductive parts of fossil *Microvictoria* and modern *Victoria* supports the interpretation that pollination mechanisms, and pollinators, were similar in the two taxa. We have observed precise structural correspondences in pollinator adaptations between flowers of other Turonian taxa and closely related living ones (15); however, as in this instance, there is always a discrepancy in size with the fossil taxon being considerably smaller than its modern counterpart. In view of the corresponding complexity of the structures associated with particular types of insect pollination, it seems unlikely that different mechanisms were involved in fossil pollination (such complex and apparently specific modes of adaptation do not make sense at the scale observed in the tiny flowers where the complexities could not exclude or otherwise accommodate much larger pollinators). This finding suggests the possibility that shrinkage associated with this particular mode of preservation may have been even more dramatic than the $\approx 50\%$ that has been observed experimentally (39). If, as suggested by complex and congruent floral morphology, the mode of insect pollination was essentially similar to that of modern *Victoria*, then the pollinators of *Microvictoria* were small beetles (Coleoptera) and the complex floral chamber effected a trap and release mechanism as in modern *Victoria* (40). It is likely that, in the first phase of pollination, as in modern *Victoria*, beetles entered the floral chamber through the apical pore formed by the infolded staminodes, presumably attracted to an odor produced by flower. Candidate structures for the source of such an odor are the carpellary appendages or stylar processes (or perhaps the chambered sterile tip). In the phase of the partially opened flower, the staminodes would still be in place and the stamens would be shielded from contact with insect visitors by the paracarpels. Any beetles trapped in the chamber would have been likely to eat the carpellary processes as in modern *Victoria*. Later, when the flower might have been completely open (as in the second night in *Victoria*), the staminodes would have unfolded upward to reveal the stamens, allowing the beetles to leave the flowers and, in doing so, become dusted with pollen from the open, inward-facing anthers around the exit pore.

The fossil taxon *Microvictoria* is notable for its remarkable structural congruence with flowers of the modern genus *Victoria* and for the order of magnitude difference in size between the modern and fossil taxa. Although the morphology of the fossil suggests a mode of pollination similar to that of modern *Victoria*, the tiny size of the fossils suggests that the pollinators were correspondingly smaller than those of modern Nymphaeaceae. The occurrence of a precise floral morphology suggesting beetle entrapment pollination in the earliest part of the Late Cretaceous supports other data (15, 19) suggesting that many modern insect–plant associations were already established by this time.

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