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MARSILEACEAE SPORO CARPS AND SPORES FROM THE LATE CRETACEOUS OF GEORGIA, U.S.A.

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A new species provisionally assigned to the extant genus *Regnellidium* Lindm. (*Regnellidium upatoiensis* sp. nov.) is established for isolated sporocarps assignable to the heterosporous water fern family Marsileaceae. Three sporocarps and hundreds of dispersed megaspores were recovered from unconsolidated clays and silts of the Eutaw Formation (Santonian, Late Cretaceous) along Upatoi Creek, Georgia, U.S.A. The sporocarps are ellipsoidal and flattened, contain both megasporangia and microsporangia, and possess a two-layered wall—an outer sclerenchymatous layer and an inner parenchymatous layer. *In situ* megaspores are spheroidal, with two distinct wall layers—an exine, differentiated into two layers, and an outer ornamented perine also differentiated into two layers. The megaspores also possess an acrolamella consisting of six (five to seven) triangular lobes that are twisted. *In situ* microspores are trilete and spheroidal, with a strongly rugulate perine, and show modification of the perine over the laesura to form an acrolamella. Comparison of the fossil sporocarps with those of four extant species of Marsileaceae reveal marked similarity with *Regnellidium diphyllum* Lindm., particularly in megaspore and microspore morphology. If found dispersed, the *in situ* megaspores would be assigned to *Molaspora lobata* (Dijkstra) Hall and the microspores to *Crybelosporites* Dettmann based on their size, shape, and ornamentation. *Regnellidium upatoiensis* sp. nov. extends the stratigraphic range of the genus back to the Santonian, nearly contemporaneous with the first evidence of *Marsilea*, and implies that the diversification of the Marsileaceae into its extant lineages occurred in the mid-Cretaceous.

Keywords: Cretaceous, heterospory, Marsileaceae, mesofossil, paleobotany, *Regnellidium*.

Introduction

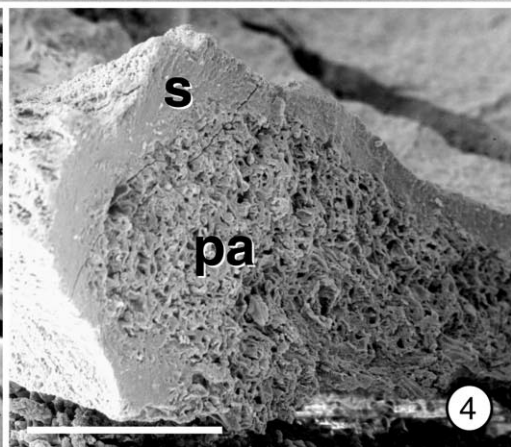
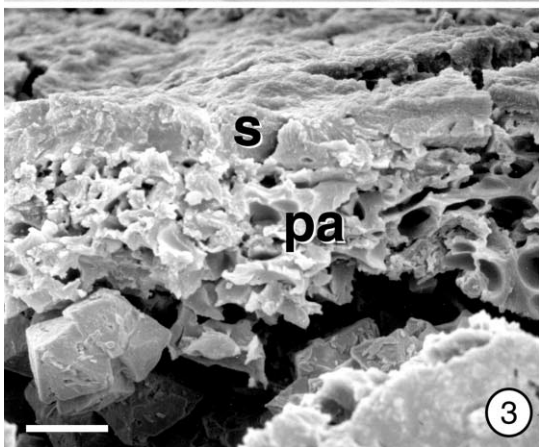
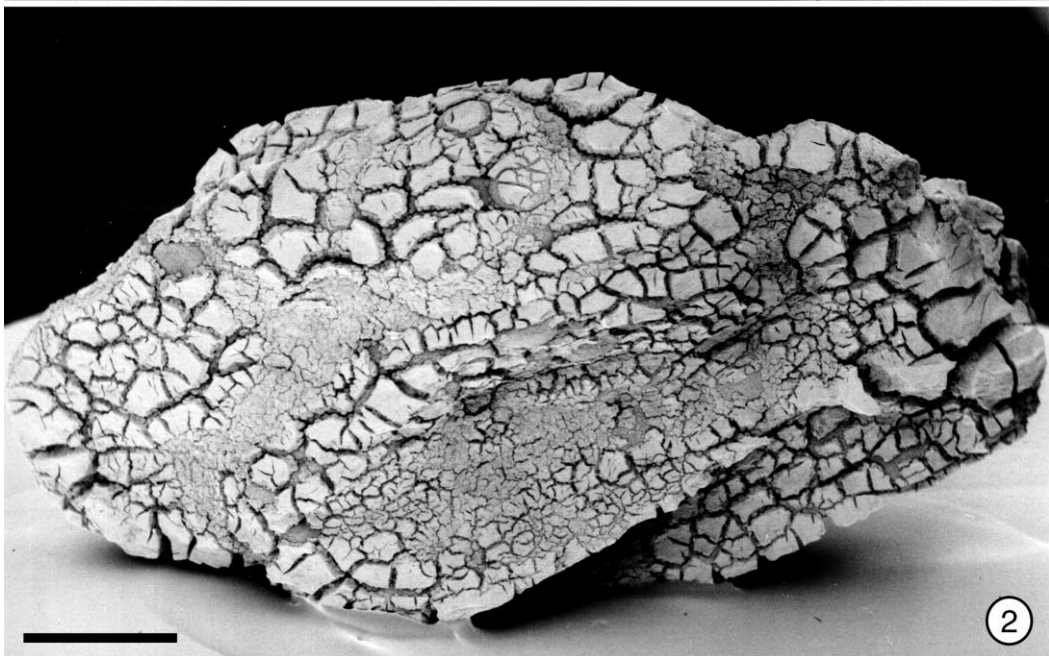
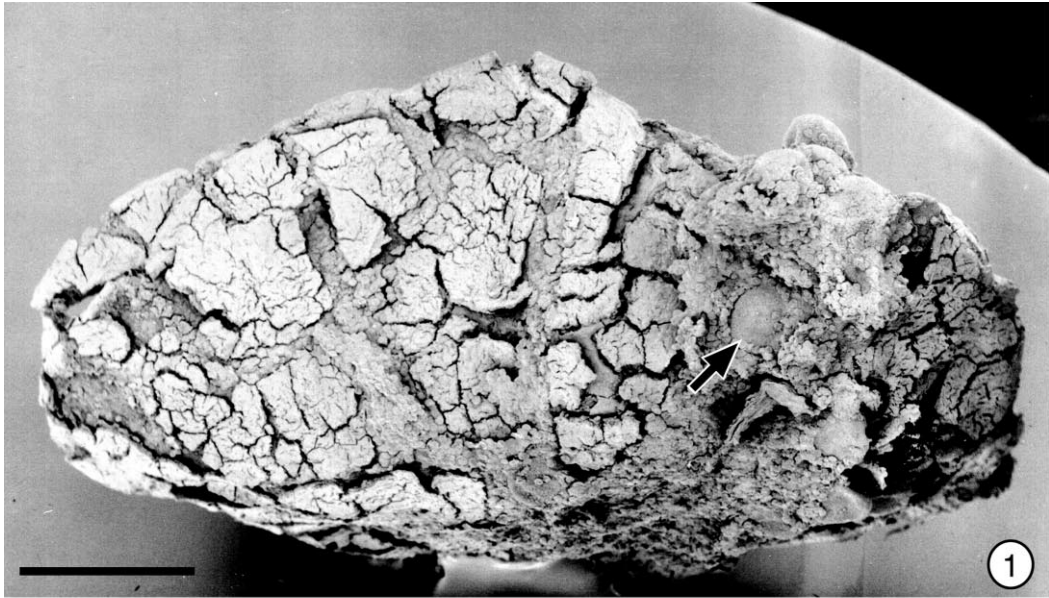
Heterospory has been labeled “the most iterative key innovation” in plant evolution (Bateman and DiMichele 1994, p. 345). The results of recent phylogenetic analyses strongly support the monophyly of extant heterosporous ferns (Marsileaceae and Salviniaceae) within the larger clade of leptosporangiate ferns (Rothwell and Stockey 1994; Hasebe et al. 1995; Pryer et al. 1995; Pryer 1999; Rothwell 1999).² As such, heterosporous ferns offer an opportunity to investigate another, relatively recent, origin of heterospory, if the history of evolutionary transitions within and among lineages can be reconstructed accurately. In this article, we describe new fossil material assignable to Marsileaceae and specifically to the ge-

nus *Regnellidium* Lindm. based on comparisons of morphological features of sporocarps, megaspores, and microspores. This material greatly extends the stratigraphic first appearance of *Regnellidium* from the Eocene to the Santonian (Late Cretaceous).

Marsileaceae are composed of three extant genera, *Marsilea* (ca. 70 spp.; cosmopolitan), *Regnellidium* (1 sp.; Brazil and Argentina), and *Pilularia* (ca. 6 spp.; cosmopolitan). All are rooted semiaquatic plants, but the family is poorly represented in the fossil record. *Marsilea* is the oldest of the three genera, with whole plants and individual leaflets (assigned to *Marsilea johnhallii* Skog and Dilcher) known from the Dakota Formation (early Cenomanian) of Kansas (Skog and Dilcher 1992, 1994). *Pilularia* and *Regnellidium* are known only from Eocene or younger sediments (Collinson 1991). Several genera of dispersed fossil megaspores and microspores have been assigned to, or allied with, the Marsileaceae. *Molaspora* Schemel, emend. Hall, consists of five species of megaspores that are essentially restricted to the Cretaceous (Batten and Kovach 1990). *Arcellites* Miner, emend. Ellis and Tschudy, contains ca. 18 species of megaspores that are also primarily Cretaceous in age. Both are considered to be related to Marsileaceae. Microspores assignable to *Crybelosporites* Dettmann have been

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² In this article, the term “heterosporous ferns” is used exclusively for the lineage comprising two living fern families, Marsileaceae and Salviniaceae, and their extinct relatives. The terrestrial, incipient heterosporous fern genus *Platyzoma* is not closely related to this lineage (Hasebe et al. 1995; Pryer et al. 1995). We also exclude explicitly the enigmatic Carboniferous group Stauropteridales.



found attached to some *Arcellites* species and are morphologically similar to microspores of extant *Regnellidium* and *Pilularia*.

Rodeites dakshini Sahni, emend. Chitaley and Paradkar, from the Deccan Intertrappean Series (latest Maastrichtian?–early Paleocene) of India, is presently the only fossil sporocarp with *in situ* spores that is attributed to Marsileaceae (Chitaley and Paradkar 1972). Chitaley and Paradkar (1972) argued that this sporocarp most closely resembles *Marsilea* because of its bilateral symmetry and the attachment of the sori. *Rodeites* contains megaspores identical to *Molaspora lobata* (Dijkstra) Hall, which is distinguished by its baculate perine and acrolamella (Dijkstra 1949; Kovach and Dilcher 1988).³ *Rodeites* also contains trilete and spheroidal, baculate to spiny microspores that resemble those of extant *Marsilea*. Currently, there are no illustrations of microspores attached to dispersed *M. lobata* specimens, although Hall (1967) stated that he had one specimen of *Molaspora* associated with *Crybelosporites* microspores.

Material and Methods

Bulk samples were collected from unconsolidated carbonaceous clays and silts exposed along the south shore of Upatoi Creek on the Fort Benning Military Reservation, Chattahoochee County, Georgia, U.S.A. (lat. 32°24'N, long. 84°50'W). Exposures are poor and the details of stratigraphy remain to be established, but examination of dispersed palynomorphs from these samples has yielded an assemblage equivalent to the upper part of the *Sohlipollis* Taxon Range Zone (Santonian; Christopher et al. 1999; R. A. Christopher, personal communication, 1999). Biostratigraphic correlation places these outcrops in the Eutaw Formation or its nonmarine equivalent on the Gulf Coastal Plain (R. A. Christopher, personal communication, 1999). Preliminary analysis of the exposures and palynological results suggest deposition in a nonmarine environment perhaps in close proximity to marine conditions (R. A. Christopher, personal communication, 1999; R. Lupia, unpublished data).

Samples were soaked in detergent solution to disaggregate the matrix, rinsed, and washed with water through a 125- μ m

sieve. Remaining clay matrix was then removed by immersing the material in HCl and HF acids. Organic material was then rinsed in water and air dried. The fossils, preserved as charcoalified and lignified material, were sorted using a dissecting microscope at $\times 10$ – 20 magnification. Two complete sporocarps, one incomplete sporocarp, and eight dispersed megaspores were selected for detailed examination with scanning electron microscopy (SEM). Specimens were mounted on stubs using clear nail polish, gold coated, and photographed using an Amray 1810 SEM. The incomplete sporocarp specimen (PP45950) was dissected further by detaching a portion of the specimen from the stub. The remaining fragment was recoated with gold and reexamined. The detached portion of the sporocarp was soaked in water and macerated. Macerated material was mounted on microscope slides in glycerin jelly, examined, and photographed using a compound microscope (Zeiss Axiophot). Twelve dispersed megaspores were also mounted on microscope slides. Four were mounted without treatment, four were bleached for 1 h, and four were bleached for 2 h using Clorox bleach. This material also was photographed using a compound microscope. All fossil material is housed in the paleobotanical collections of the Field Museum, Chicago (PP).

Modern material used in this study was obtained from the pteridophyte collection of the Field Museum (F). Four modern sporocarps were removed from the following herbarium specimens: *Regnellidium diphyllum* Lindm. (*Bloom s.n.*, Brazil, F1709990), *Pilularia americana* A. Br. (*Hill 8654*, U.S.A., F186631), *Pilularia globulifera* L. (*Chevallier s.n.*, France, F802279), and *Marsilea vestita* Hook. & Grev. (*Palmer 13465*, U.S.A., F741964). Sporocarps from all four species were softened in 10% KOH and hand sectioned with razor blades. Megaspores and microspores of modern species were extracted from the sporocarps with a dissecting needle and cleaned using a modified acetolysis procedure for comparison with fossil material. Spores were treated with concentrated sulfuric acid for 2–3 min, dehydrated using a EtOH series (50%, 75%, 90%, 95%, 100%), and critical point dried. All modern material was mounted on stubs, gold coated, and examined using the SEM.

Systematics

Family—Marsileaceae

Genus—*Regnellidium* Lindm.

Species—*Regnellidium upatoiensis*—Lupia, Schneider, and Moeser, sp. nov. (Figs. 1.1–2.11)

Specific diagnosis (including *in situ* and dispersed megaspores and microspores). Sporocarp ellipsoidal, 5.5–6.9 mm long, 3.1–3.7 mm wide, ca. 1–2 mm thick. Sporocarp wall 25–95 μ m thick, consisting of two layers: an outer scleren-

³ In this article, we follow Tschudy (1966) and Hall (1975) and use “acrolamella” for a strong modification of the perine (not including the exine) above the proximal pole of megaspores or microspores. In Marsileaceae, an acrolamella is characterized generally by multiple perine lobes. In *Marsilea*, it is reduced to a small structure of a circular outline, “hilum,” distinctly delimited from the rest of the perine by reduction of ornament and/or thickness. The structure we refer to as “acrolamella” previously has been called “leaf-like appendage” by Ellis and Tschudy (1964); “aspis” by Chitaley and Paradkar (1972); “cone-shaped neck” by Batten (1988); and “papilla-like” by Tryon and Luggard (1991).

Fig. 1 *Regnellidium upatoiensis* sp. nov., Marsileaceae. Fig. 1.1, Sporocarp in lateral view showing fractured sporocarp wall and *in situ* megaspore (arrow) (PP45948, holotype). Scale bar = 1 mm. Fig. 1.2, Sporocarp in lateral view (PP45949). Scale bar = 1 mm. Figs. 1.3, 1.4, Detail of sporocarp wall illustrating parenchymatous inner layer (*pa*) and outer sclerenchymatous layer (*s*). Fig. 1.3, Detail of specimen in fig. 1.1 (PP45948, holotype). Scale bar = 10 μ m. Fig. 1.4, Detail of specimen in fig. 1.2 (PP45949). Scale bar = 100 μ m.

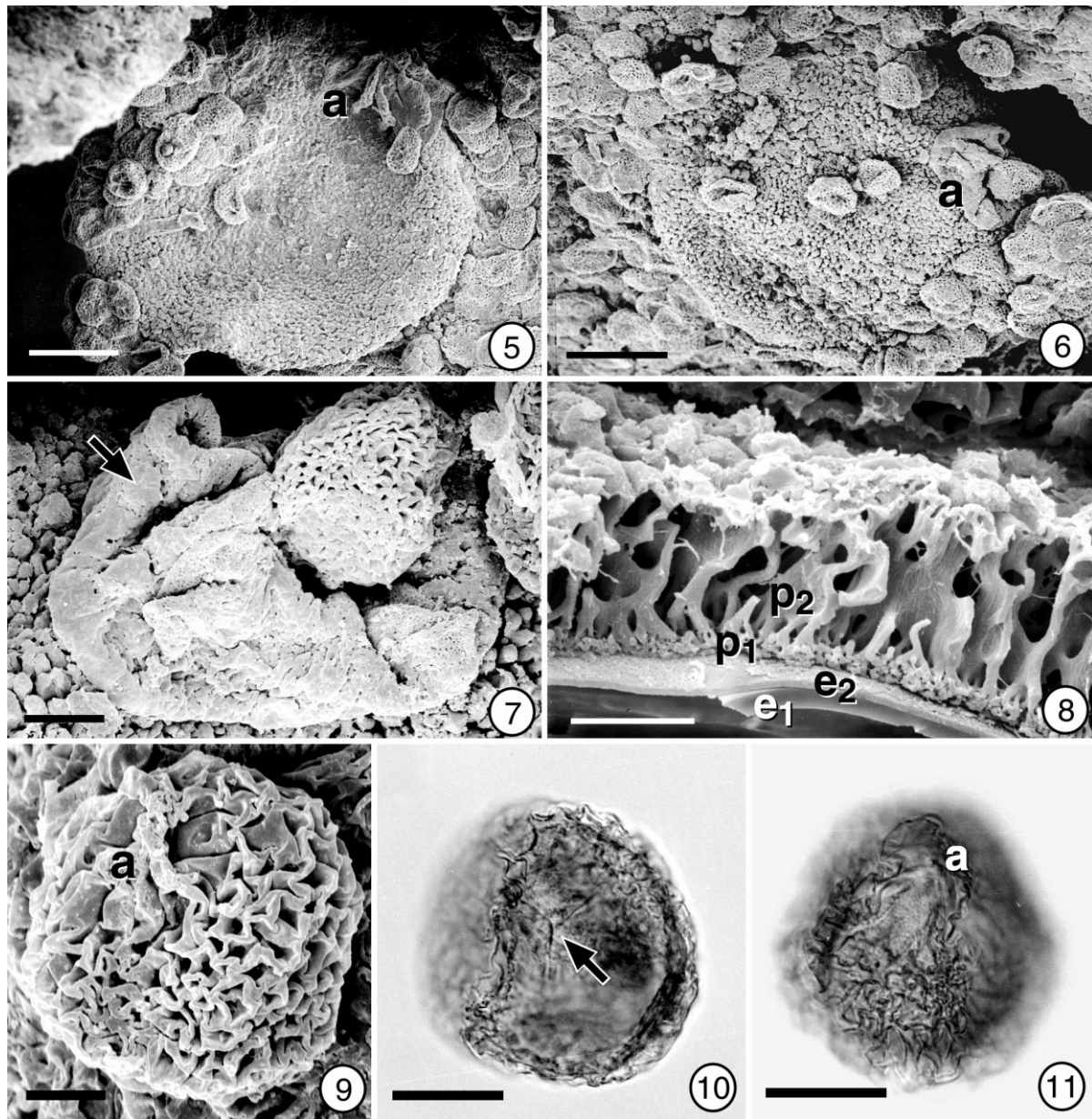


Fig. 2 Megaspores and microspores from fossil sporocarps of *Regnellidium upatoiensis* sp. nov., Marsileaceae. Figs. 2.5–2.7, Megaspores from sporocarp in fig. 1.1. Fig. 2.5, Megaspore with adherent microspores and acrolamella (*a*) at top right (PP45948, holotype). Scale bar = 100 μ m. Fig. 2.6, Megaspore with baculate surface sculpture and acrolamella (*a*) (PP45948, holotype). Scale bar = 100 μ m. Fig. 2.7, Detail of acrolamella in fig. 2.6 showing triangular lobes (arrow) and adhering rugulate/reticulate microspore (PP45948, holotype). Scale bar = 20 μ m. Fig. 2.8, Cross section through megaspore wall illustrating thin two-layered exine (*e*₁ and *e*₂) and thick two-layered perine. The perine is differentiated into an inner thin granular layer (*p*₁) and an outer, thick, alveolate layer (*p*₂) (PP45950). Scale bar = 10 μ m. Fig. 2.9, *In situ* microspore with rugulate/reticulate perine and a smoother region of perine forming an acrolamella (*a*) (PP45948, holotype). Scale bar = 10 μ m. Figs. 2.10, 2.11, Light micrographs of two microspores macerated from sporocarp (PP45950). Fig. 2.10, Middle focus revealing trilete mark at arrow (PP45950). Scale bar = 20 μ m. Fig. 2.11, High focus on different spore than in fig. 2.10, showing rugulate/reticulate sculpture and modification of perine to form an acrolamella (*a*) (PP45950). Scale bar = 20 μ m.

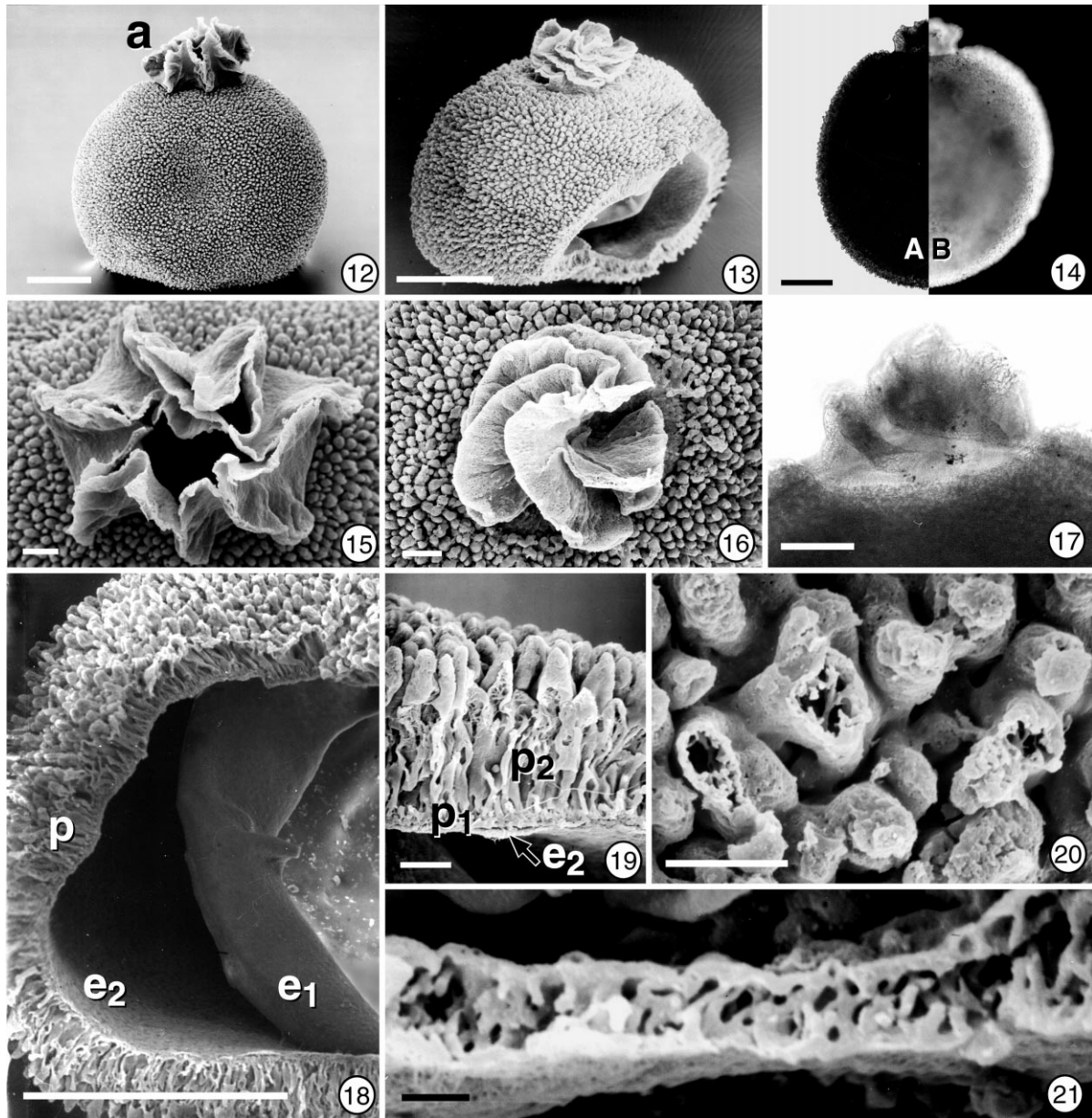


Fig. 3 Dispersed megaspores of *Molaspora lobata* (Dijkstra) Hall. Fig. 3.12, Complete megaspore showing baculate surface sculpture and distinct triangular lobes of acrolamella (*a*) (PP45951). Scale bar = 100 μ m. Fig. 3.13, Broken megaspore illustrating smooth inner surface of megaspore wall and acrolamella (PP45952). Scale bar = 100 μ m. Fig. 3.14, Light micrographs of megaspore: middle focus (PP45956). Scale bar = 100 μ m. *A*, Brightfield showing baculae extending at margin; *B*, darkfield showing baculate surface sculpture. Fig. 3.15, Detail of acrolamella in fig. 3.12 with seven lobes and showing aperture in center (PP45951). Scale bar = 20 μ m. Fig. 3.16, Detail of acrolamella illustrating spiral twisting of lobes, uniform size of baculae, and absence of baculae around the immediate base of the acrolamella (PP45953). Scale bar = 20 μ m. Fig. 3.17, Light micrograph of acrolamella showing the absence of baculae around its immediate base (PP45957). High focus. Scale bar = 50 μ m. Fig. 3.18, Detail of broken megaspore wall in fig. 3.13 showing perine (*p*), smooth inner surface of outer exine (*e*₂), and separated smooth inner exine (*e*₁) (PP45952). Scale bar = 100 μ m. Fig. 3.19, Detail of broken megaspore wall in fig. 3.18 showing thin exine layer (*e*₂) and outer perine differentiated into thin granular zone (*p*₁) and outer loosely alveolate zone (*p*₂). Note that outer alveolate zone grades into separate hollow baculate elements. Scale bar = 10 μ m. Fig. 3.20, Top view of hollow baculate elements of perine showing internal alveolate structure and confluent bases. Scale bar = 10 μ m. Fig. 3.21, Cross section through one lobe of acrolamella illustrating dense alveolate internal structure. Scale bar = 2 μ m.

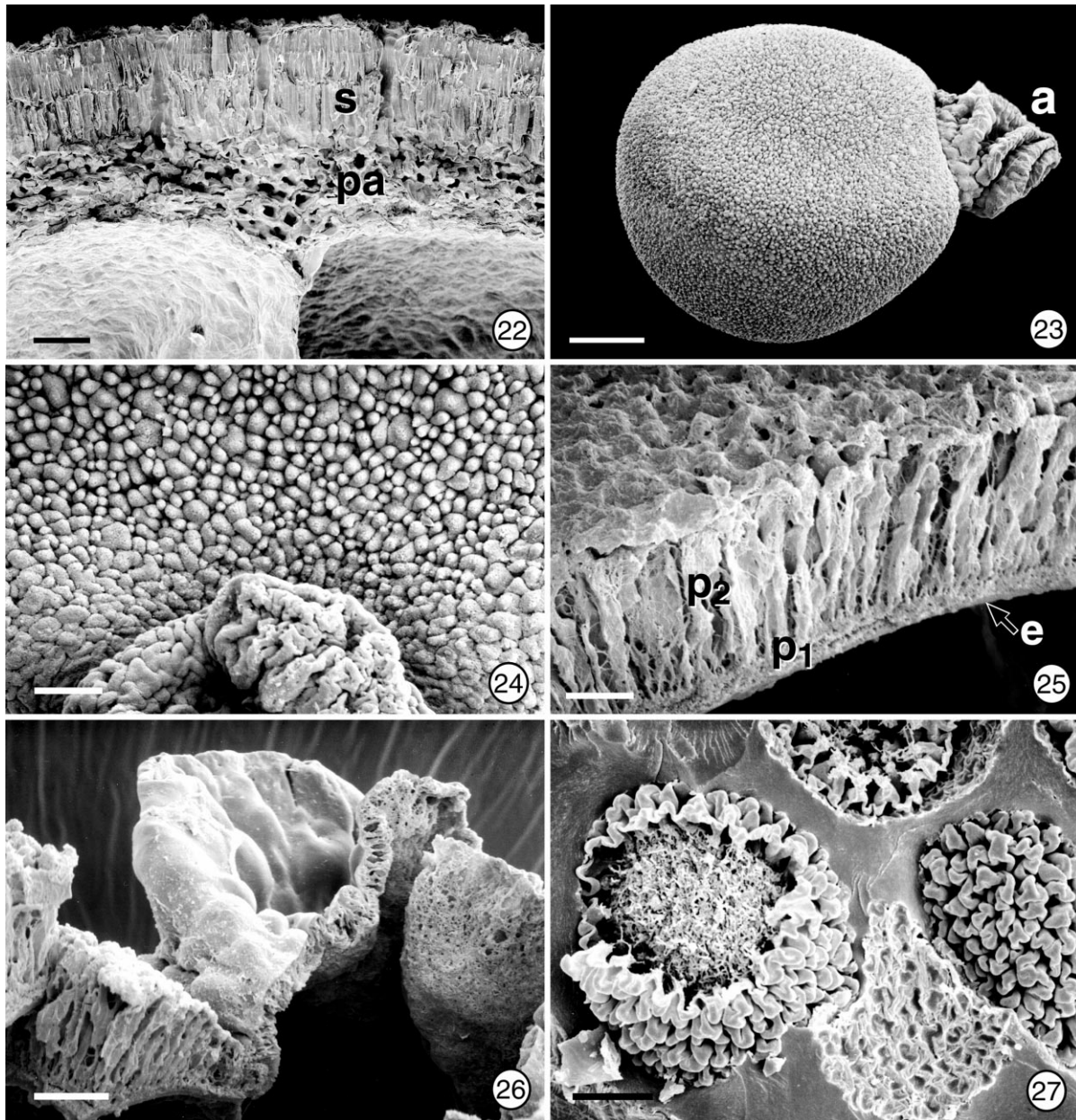


Fig. 4 Extant *Regnellidium diphyllum* Lindm. Fig. 4.22, Cross section of sporocarp wall showing parenchymatous inner layer with more than three cell layers (*pa*) and sclerenchymatous outer layer (*s*) that is two cell layers thick. Scale bar = 100 μ m. Fig. 4.23, Megaspore showing verrucate surface and acrolamella (*a*). Scale bar = 100 μ m. Fig. 4.24, Closeup of proximal face of megaspore illustrating different sizes of verrucae on surface. Scale bar = 20 μ m. Fig. 4.25, Cross section of megaspore wall showing that verrucate surface results from the tips of baculae. Three layers of the megaspore wall are visible in this image—exine layer (*e*) and granular inner perine (*p*₁) and loosely alveolate outer perine (*p*₂) that grades outward into baculae. Note also that megaspore surface retains a thin covering of perine. Scale bar = 10 μ m. Fig. 4.26, Cross section showing gradual thinning of outer perine to form acrolamella and internal reticulate structure of the lobes of acrolamella. Scale bar = 20 μ m. Fig. 4.27, Microspores showing rugulate surface sculpture. Scale bar = 10 μ m.

chymatous wall layer 5–25 μ m thick and an inner parenchymatous wall layer 20–70 μ m thick. Sporocarp containing both megasporangia and microsporangia. Megaspores spheroidal, 396–533 μ m in diameter, prominent acrolamella 60–125 μ m high and 95–175 μ m wide with six (rarely five or seven) tri-

angular lobes. Megaspore wall 18–33 μ m thick, consisting of an inner exine and outer perine. Exine psilate, ca. 2.5 μ m thick; perine prominent, 16–30 μ m thick, consisting of two layers: the inner layer granular and the outer layer alveolate grading into hollow baculae. Microspores spheroidal, 27–58 μ m in

diameter, trilete, with acrolamella. Microspore wall 6–8 μm thick, strongly rugulate.

Holotype. PP45948 (figs. 1.1, 1.3; figs. 2.5–2.7, 2.9).

Paratypes. PP45949 (figs. 1.2, 1.4); PP45950 (figs. 2.8, 2.10, 2.11).

Dispersed megaspores. PP45951 (figs. 3.12, 3.15), PP45952 (figs. 3.13, 3.18, 3.19), PP45953 (fig. 3.16), PP45954 (fig. 3.20), PP45955 (fig. 3.21), PP45956 (fig. 3.14), PP45957 (fig. 3.17).

Etymology. The name is derived from the river, Upatoi Creek, along which the locality was discovered.

Type locality. Upatoi Creek, Chattahoochee County, Georgia, U.S.A.

Stratigraphy. Eutaw Formation.

Age. Santonian, Late Cretaceous.

Description and Remarks on the Material

Sporocarp

Sporocarps are flattened, ellipsoidal in shape (figs. 1.1, 1.2), ca. 5.5–6.9 mm in length and 3.1–3.7 mm wide ($n = 2$ complete specimens). The sporocarp wall is 25–95 μm thick ($n = 3$) with two distinct wall layers (figs. 1.3, 1.4). The outer wall layer is compact, lacks obvious cell lumina (=sclerenchymatous), and is 5–25 μm thick. We are unable to determine whether the compact exterior layer is a result of preservation or is characteristic of this sporocarp. The inner wall layer is composed of cells with thin to slightly thickened walls (=parenchymatous) and is 20–70 μm thick.

All three sporocarps contain both megaspores and microspores, but they are not obviously spatially segregated. *In situ* megaspores are spheroidal with a diameter of 396–460 μm ($n = 2$); they exhibit baculate ornamentation on their surfaces (figs. 2.5, 2.6). We were unable to observe a trilete mark, but it is likely to be hidden beneath the acrolamella (fig. 2.7). The acrolamella consists of six (rarely five or seven) triangular lobes that are twisted and is 60–100 μm high and 114–143 μm wide (fig. 2.7). The megaspore wall is 18.5 μm thick ($n = 1$) and consists of an inner exine and outer perine (fig. 2.8). The exine is psilate, two layered, and ca. 2.5 μm thick (fig. 2.8). The two layers of the exine are typical of the blechnoid construction seen in spores of extant Marsileaceae (Tryon and Lugardon 1991, pp. 4 and 564). The perine is ca. 16 μm thick and also is divided into two layers. The inner layer is ca. 2 μm thick and composed of dense interwoven strands that result in a granular structure in cross section. The outer perine layer is 14 μm thick and composed of longer, less dense strands that form a baculate structure; the baculae are hollow with closed apices (fig. 2.8).

These fossil megaspores fall within the circumscription of the dispersed megaspore species *Molaspora lobata* (Dijkstra) Hall, which is distinguished mainly by wall morphology and the presence of a twisted acrolamella. Only this species of *Molaspora* has spore walls that are characterized by baculate ornamentation (Kovach and Dilcher 1988; cf. figs. 2.5, 2.6). *Molaspora lobata* is also characterized by an acrolamella composed of six triangular lobes that are twisted, which is evident in the *in situ* megaspores described here (fig. 2.7).

In situ microspores are spherical in shape and 27–58 μm in

diameter ($n = 96$ specimens; figs. 2.9–2.11) and display a trilete mark with light microscopy. Laesurae extend ca. one-half of the radius of the spore (fig. 2.10). The microspore wall is composed of two layers. The perine is thick, making the exine difficult to distinguish with light microscopy (figs. 2.10, 2.11). The perine is rugulate, with the folds often anastomosing to form a loose reticulum. The perine forms an acrolamella that obscures the trilete mark when viewed with the SEM (fig. 2.9). There are many similarities between these fossil microspores and *Crybelosporites* Dettmann. *Crybelosporites* has a “proximally cavate, sculptured sculptine [=perine] which has a reticulate to foveolate surface pattern” (Dettmann 1963, p. 80). If found dispersed, the *in situ* microspores described here would be assigned to *Crybelosporites pannuceus* (Brenner) Srivastava on the basis of their size, anastomosing rugulate perine sculpture, and presence of an acrolamella.

Associated Dispersed Megaspores

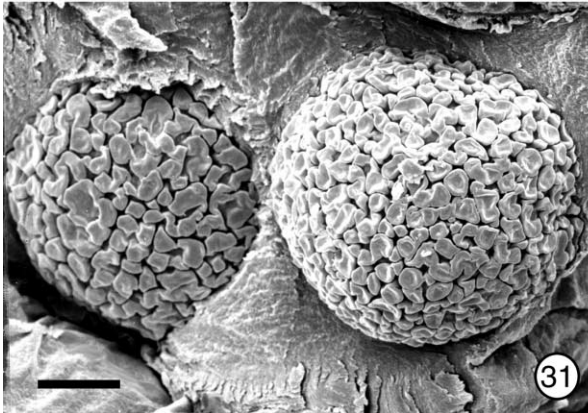
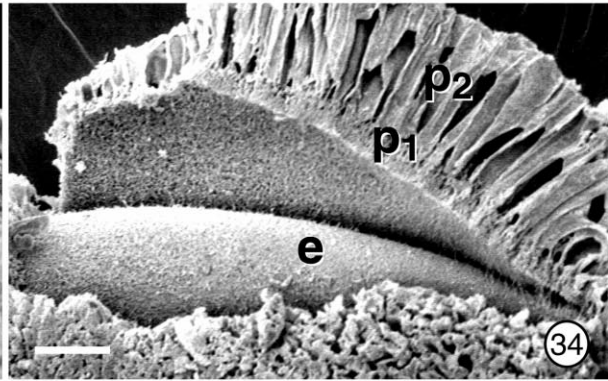
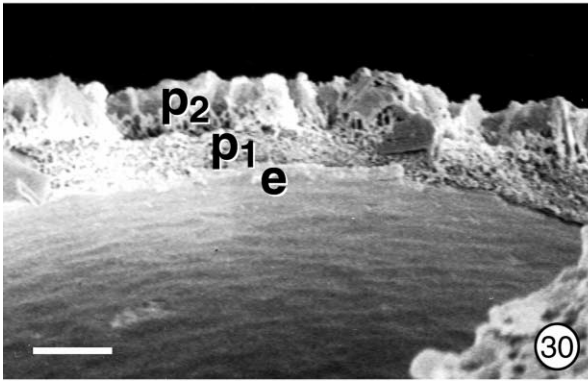
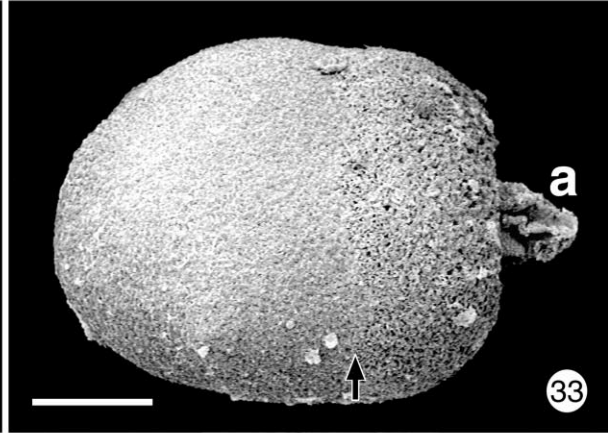
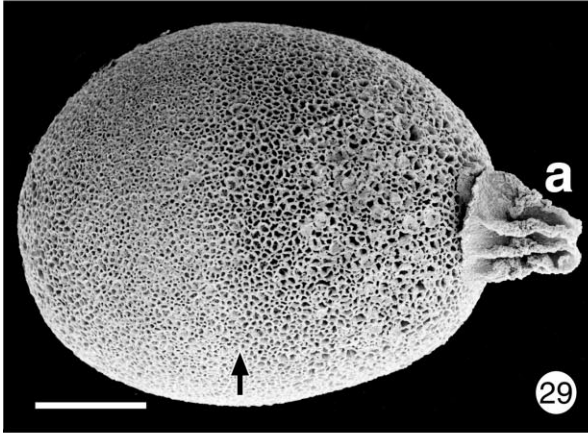
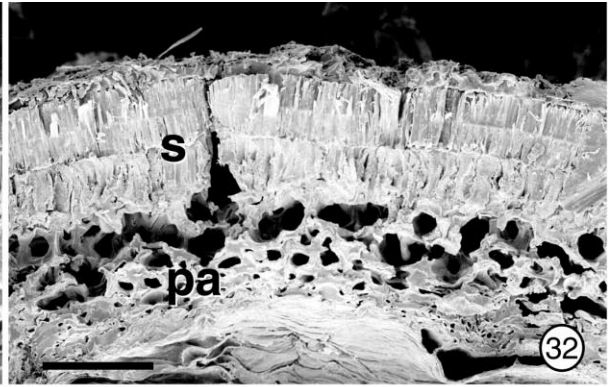
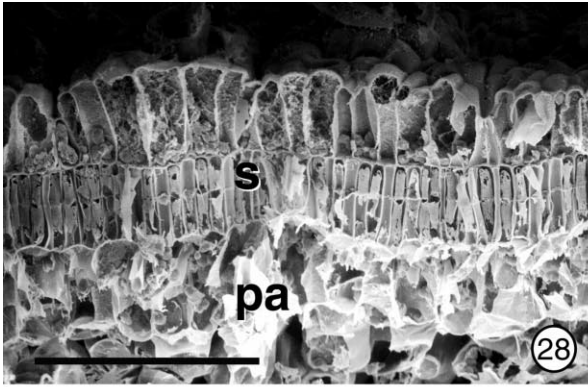
Many dispersed megaspores identical to the *in situ* megaspores and matching the circumscription of *M. lobata* were also found in the same samples from Upatoi Creek. Dispersed megaspores are spheroidal in shape, 412–533 μm in diameter ($n = 12$ specimens; figs. 3.12–3.14). Viewed from the outside, the trilete mark is apparently hidden by the acrolamella. The acrolamella is 60–125 μm high and 95–175 μm wide and bears six (rarely five or seven) triangular lobes that are twisted (figs. 3.15–3.17). The megaspore wall is 22–33 μm thick and composed of two layers (fig. 3.18). The exine is thin and psilate and, like the *in situ* megaspore wall, possesses two layers (fig. 3.18). The perine is thick and ornamented and consists of two layers (fig. 3.19). Broken megaspores reveal the structure of the perine ($n = 3$). The inner layer is composed of dense strands forming a granular structure and is ca. 2 μm thick (fig. 3.19). Most of the perine is composed of the outer layer (18–28 μm thick), which possesses radially disposed, less dense strands that create the hollow baculae on the megaspore surface (figs. 3.19, 3.20). In cross section, the lobes composing the acrolamella are 2–4 μm thick and perforate and have a granular inner structure (fig. 3.21). On the basis of the similarities between the *in situ* fossil megaspores and the dispersed fossil megaspores found in the same assemblage, we conclude that the dispersed megaspores belong to *Regnellidium upatoiensis*.

Discussion

The fossils described herein possess several morphological characters that indicate their relationship to Marsileaceae and specifically, to the extant genus *Regnellidium* Lindm. Morphological features of the fossil sporocarps and spores and those of four extant species within Marsileaceae—*Regnellidium diphyllum* (figs. 4.22–4.27), *Pilularia americana* (figs. 4.28–4.31), *Pilularia globulifera* (figs. 5.32–5.35), and *Marsilea vestita* (figs. 6.36–6.39)—are presented in table 1 for comparison.

Systematic Assignment

The fossils described in this article are assigned to the Marsileaceae on the basis of the shared possession of (1) sporocarps containing megasporangia and microsporangia, with walls



composed of two layers (inner parenchymatous; outer sclerenchymatous); (2) complex structure of the perine consisting of two layers (inner granular, outer alveolate); and (3) modification of the perine at proximal pole of spores to form a lobate acrolamella (see Pettitt 1966; Collinson 1991; Tryon and Lugardon 1991). The fossils are excluded from the other group of leptosporangiate ferns to exhibit heterospory (Salviniaceae) by the morphology of their sporocarp and megaspore walls, which differ markedly from those of Marsileaceae (see Collinson 1991; H. Schneider, unpublished data).

Among extant Marsileaceae, the fossil is more similar to *Regnellidium* and *Pilularia* than to *Marsilea*. In the sporocarp, spongy parenchymatous tissue with more than three cell layers is found below the outer sclerenchymatous layer in the fossil (figs. 1.3, 1.4) as well as in *Regnellidium* (fig. 4.22) and *Pilularia* (figs. 5.28, 5.32). This tissue is restricted to the area above the sorophore in *M. vestita*. Elsewhere, the walls of the sporocarp of *M. vestita* consist of parenchymatous tissue that is only one cell layer thick with cells of an hourglass shape (*pa* in fig. 6.36). Preliminary examination of additional species of *Marsilea* found the same organization of the inner layer of the sporocarp wall (H. Schneider, unpublished data). Microspores of *M. vestita* (and *Marsilea quadrifolia* and *Marsilea strigosa* based on illustrations in Stafford 1995) are characterized by the possession of baculate perine sculpture (fig. 6.39), whereas the fossil (fig. 2.9), *Regnellidium* (fig. 4.27), and *Pilularia* (figs. 5.31, 5.35) each have a dominantly rugulate perine sculpture.

The most obvious differences between *Marsilea* and the other taxa are found in the structure of the megaspore. The acrolamella of *Marsilea* is reduced to form a hilum (see note 3; fig. 6.37; Stafford 1995, pls. 12, 13). In contrast, the fossil (figs. 2.7, 3.15), *Regnellidium* (fig. 4.23), and *Pilularia* (figs. 5.29, 5.33) have a strongly developed acrolamella. In addition, the outer perine layer of *M. vestita* (and *M. quadrifolia* and *M. strigosa* based on illustrations in Stafford 1995) forms a uniform open reticulum composed of nearly complete walls that are microperforate (fig. 6.38). The outer perine of the fossil (figs. 2.8, 3.19) is baculate, and even if the tops of the baculae were removed, the fossil would not show a regular reticulum beneath (figs. 2.8, 3.20).

Like *Regnellidium*, the fossil is similar to *Pilularia* in possessing megaspores with an acrolamella and also in producing trilete microspores with rugulate perines and acrolamellae. The outer perine of *P. americana* and *P. globulifera* megaspores is characterized by nonuniform reticula with lumina that are gra-

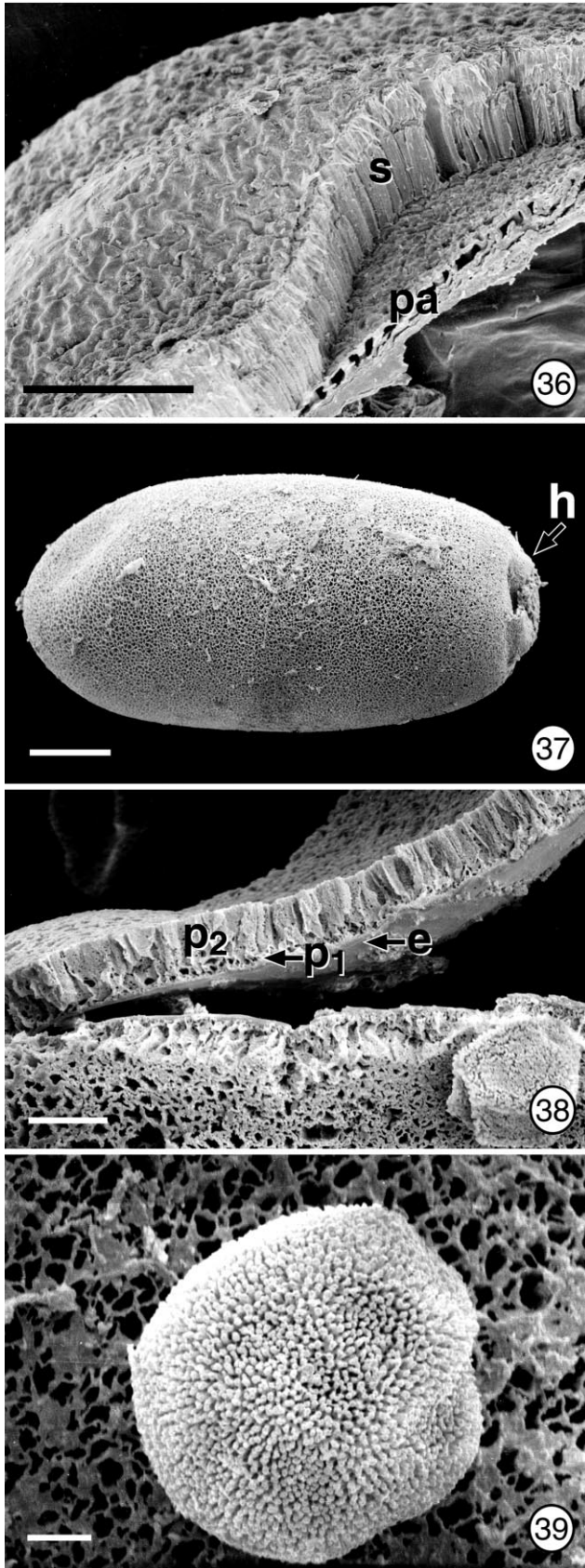
dational in size (*P. americana*; fig. 5.29) or in degree of closure/covering (*P. globulifera*; fig. 5.33). In contrast, the fossil (figs. 2.8, 2.12, 2.19, 2.20) and *Regnellidium* (figs. 4.24, 4.25) do not possess either a reticulate surface sculpture or any open/uncovered perine. It is worth noting that the gradational nature of the reticulum in *Pilularia*—open to closed—probably results from a difference in resistance of the perine to acetolysis (Stafford 1995), but it is consistent in its location on the megaspore, particularly in *P. globulifera* where the transition occurs at a subequatorial furrow (cf. fig. 5.33 with Stafford 1995, pl. 14). In addition, *P. americana* (fig. 5.30) and *P. globulifera* are both characterized by an inner perine layer that is relatively thick compared to the outer perine and markedly more granular than either the fossil (figs. 2.8, 3.19) or *Regnellidium* (fig. 4.25). Finally, the lobes of the acrolamella of *P. americana* and *P. globulifera* are straight (figs. 5.29, 5.33), rather than being twisted as in most dispersed specimens of the fossil (figs. 3.13, 3.16, 3.17; but not fig. 3.15, which is open). An acrolamella with straight lobes is also apparent in illustrations of *P. globulifera* by Stafford (1995, plates 14, 15).

Among extant Marsileaceae, the fossil is clearly most similar to *R. diphyllum* but can be distinguished from it by two features of the perine. In the fossil, the perine is characteristically thinner than in *R. diphyllum* (16–30 μm vs. 36–38 μm ; table 1), and the baculae formed by the outer perine layer are nearly uniform in diameter across the surface of the fossil (figs. 3.12, 3.13, 3.15, 3.16). In contrast, in *R. diphyllum*, the baculae are differentiated, with large-diameter baculae dispersed among small-diameter baculae (figs. 4.23, 4.24). In all preserved features of the sporocarp, megaspore, and microspore, the fossil is very similar to *R. diphyllum* and is distinguished easily from other extant genera of Marsileaceae. On the basis of these similarities, and recognizing that vegetative characters are currently unknown, we provisionally assign the fossil to the genus *Regnellidium* as a new species: *Regnellidium upatoiensis*.

Cretaceous Fossil Record of Marsileaceae and Evolutionary Implications

The sporocarps of *R. upatoiensis* contain megaspores that conform to the description of the dispersed form-genus *Molaspora*. *Molaspora lobata* is one of five species in this genus recognized by Kovach and Batten (1989). The genus is globally distributed with four of the five species restricted to the Cretaceous; only *M. lobata* extends into the Paleocene (fig. 7). All of the species of *Molaspora* have an acrolamella (Hall 1963).

Fig. 5 Two species of extant *Pilularia* L. Figs. 5.28–5.31, *Pilularia americana* A.Br. 28. Cross section of sporocarp wall showing parenchymatous inner layer with more than three cell layers (*pa*) and sclerenchymatous outer layer (*s*) that is two cells thick. Scale bar = 100 μm . Fig. 5.29, Megaspore showing open reticulate surface sculpture of perine and decrease (near arrow) in lumen diameter from proximal to distal faces. Acrolamella (*a*) is characterized by lobes that are straight rather than twisted. Scale bar = 100 μm . Fig. 5.30, Cross section of megaspore wall illustrating smooth surface of the exine (*e*), relatively thick inner perine (*p*₁) that is densely granular, and relatively thin outer perine (*p*₂) that forms the walls of the reticulum. Scale bar = 10 μm . Fig. 5.31, Microspore showing rugulate perine sculpture. Scale bar = 10 μm . Figs. 5.32–5.35, *Pilularia globulifera* L. Fig. 5.32, Cross section of sporocarp wall showing parenchymatous inner layer with more than three cell layers (*pa*) and sclerenchymatous outer layer (*s*) that is three cells thick. Scale bar = 100 μm . Fig. 5.33, Megaspore showing perine sculpture that is open and irregularly reticulate proximally, but becomes closed and verrucate abruptly at equatorial furrow (arrow). Acrolamella (*a*) has lobes that are straight rather than twisted. Scale bar = 100 μm . Fig. 5.34, Cross section of megaspore wall illustrating exine (*e*), inner perine (*p*₁) that is densely granular, and the thick outer perine (*p*₂) that forms the walls of the reticulum but lacks perforations or alveolae. Scale bar = 10 μm . Fig. 5.35, Microspores showing tightly rugulate perine sculpture. Scale bar = 10 μm .



Molaspora [*Triletes*] *lobata* was considered by Dijkstra (1959) to be related to Marsileaceae and specifically to *Regnellidium*. Dijkstra (1959) also considered the sporocarp *Rodeites* to be closely related to *Regnellidium*. Subsequent work has suggested that although *in situ* megaspores conform to *M. lobata*, *Rodeites* shares several features with *Marsilea* and is perhaps closer to that genus (Chitale and Paradkar 1972).

Hall (1967) mentioned that he found *Crybelosporites* microspores associated with *Molaspora* but did not state with which species and did not illustrate the spores. Collinson (1991) reported that no microspores were known to be associated with dispersed *M. lobata*. The only microspores previously associated with *M. lobata* were those contained in the *Rodeites* sporocarp (Chitale and Paradkar 1972). According to Chitale and Paradkar (1972), *Rodeites* microspores are trilete and spheroidal, with baculate to spiny ornamentation, and without an acrolamella. Thus, the microspores of *Rodeites* are more similar to those of *Marsilea* than to *Regnellidium* or *Pilularia* (table 1). Microspores of *R. upatoiensis* differ from those of *Rodeites* but are similar to those of *Regnellidium* and *Pilularia*. If found dispersed, such microspores would be assigned to the form-genus *Crybelosporites*. *Crybelosporites* was established by Dettmann (1963) for microspores with a "proximally cavate, sculptured sculptine [= perine], which has a reticulate to foveolate surface pattern" (Dettmann 1963, p. 80). At least 10 species of *Crybelosporites*, or species potentially assignable to it (e.g., *Perotrilites convolutus*), have been documented around the world (see appendix). The stratigraphic range of *Crybelosporites* extends from the Late Jurassic to the Maastrichtian (fig. 7; appendix). The microspores associated with the fossil described herein extend the range of *Crybelosporites pannuceus* to sediments as young as the Santonian.

A full review of *Arcellites* is beyond the scope of this article, but there is also evidence this genus is associated with the fossil record of Marsileaceae. Miner (1935) established *Arcellites* for "rotund" megaspores that bear "tube-like appendages." Miner (1935) did not include possession of an acrolamella with six lobes in his original description, but on reexamination, Ellis and Tschudy (1964) emended the description to include an acrolamella. *Arcellites* contains ca. 18 species and is distributed throughout the world in Cretaceous sediments, with only questionable records in the Jurassic and Paleocene (Kovach and Batten 1989; Batten and Kovach 1990). Unlike *Molaspora*, microspores have been found attached to the acrolamella of dispersed *Arcellites* megaspores. These microspores are morphologically identical to *Crybelosporites striatus* (e.g., see

Fig. 6 Extant *Marsilea vestita* Hook. & Grev. Fig. 6.36, Cross section of sporocarp wall showing parenchymatous inner layer (*pa*) composed of one cell layer with hourglass-shaped cells and sclerenchymatous outer layer (*s*) composed of two cell layers that differ markedly in thickness. Scale bar = 100 μ m. Fig. 6.37, Megaspore showing uniformly reticulate perine sculpture and hilum (*h*) on proximal face. Scale bar = 100 μ m. Fig. 6.38, Cross section of megaspore wall illustrating smooth exine (*e*), granular inner perine layer (*p*₁), and the perforated walls of the outer perine (*p*₂) that form the reticulum. Scale bar = 20 μ m. Fig. 6.39, Microspore showing uniform baculate perine sculpture. Scale bar = 10 μ m.

Table 1
Comparison of Morphological Characters between *Regnellidium upatoiensis* and Selected Species of Marsileaceae

	<i>Regnellidium upatoiensis</i> sp. nov.	<i>Regnellidium diphyllum</i> Lindm.	<i>Pilularia americana</i> A.Br.	<i>Pilularia globulifera</i> L.	<i>Marsilea vestita</i> Hook & Grev.	<i>Rodeites dakshini</i> Sahni emend. Chitaley & Paradkar
Sporocarp:						
Shape	Ellipsoidal	Spheroidal	Spheroidal	Spheroidal	Ellipsoidal	Spheroidal?
Number of wall layers	2	2	2	2	2	2
Outer layer	Sclerenchymatous	Sclerenchymatous	Sclerenchymatous	Sclerenchymatous	Sclerenchymatous	Sclerenchymatous
Inner layer	Parenchymatous	Parenchymatous	Parenchymatous	Parenchymatous	Parenchymatous	Parenchymatous
Megaspore:						
Shape	Spheroidal	Spheroidal	Prolate	Prolate	Prolate	Spheroidal
Dimensions (μm diam.)	396–533	425–480	290–410/ 250–300	320–410/ 270–330	450–520/ 320–400	650–850
Perine:						
Thickness (μm)	16–30	36–38	10–13	24–33	18–25	?
Surface	Baculate	Baculate	Reticulate	Undulate/reticulate	Reticulate	Baculate
Modification near aperture	Acrolamella	Acrolamella	Acrolamella	Acrolamella	Hilum	Acrolamella
Microspore:						
Laesura	Trilete	Trilete	Trilete	Trilete	?	Trilete
Shape	Spheroidal	Spheroidal	Spheroidal	Spheroidal	Spheroidal	Spheroidal
Dimensions (μm diam.)	27–58	35–55	42–58	44–62	65–80	45–70
Perine:						
Thickness (μm)	4.5–5.2	4.3 ^a	4.1 ^a	4.3 ^a	4.1 ^a	?
Surface	Rugulate	Rugulate	Rugulate	Rugulate	Baculate	Baculate to spiny
Modification near aperture	Acrolamella	Acrolamella	Acrolamella	Acrolamella	?	None(?)

Note. For megaspore dimensions, x/y measurements are polar/equatorial axes, respectively, of prolate forms. Question mark indicates unknown or uncertain morphology.

^a Single measurement.

Cookson and Dettmann 1958; Hueber 1982) and *Crybelosporites minor* (Li and Batten 1986).

The discovery of the fossil marsileaceous sporocarps from Georgia reveals character combinations in Marsileaceae not recorded previously. *Rodeites* contains megaspores referable to *M. lobata* but microspores similar to those of *Marsilea*, whereas *R. upatoiensis* contains *M. lobata* megaspores, but microspores nearly identical to those of *Regnellidium*. If *Rodeites* is most closely related to *Marsilea* than to either *Regnellidium* or *Pilularia*, as argued by Chitaley and Paradkar (1972) or is sister taxon to the crown group, it is reasonable to suggest that *M. lobata* represents the morphology of early members of the Marsileaceae, given the hypothesis of the phylogenetic relationships among extant members (fig. 7, B; Pryer 1999). In addition, some species of *Arcellites* megaspores and *M. lobata* megaspores (as documented herein) are associated with species of the microspore genus *Crybelosporites*. Therefore, the fossil record of 23 species of megaspores belonging to *Molaspora* and *Arcellites*, united by the presence of an acrolamella composed of six lobes and by similar microspore morphology, reasonably suggests that megaspores and micro-

spores bearing an acrolamella are synapomorphies for Marsileaceae. Testing the hypothesis that the possession of megaspores and microspores with an acrolamella is a synapomorphy of Marsileaceae awaits an expanded analysis of the phylogenetic relationships among marsileaceous taxa, including extant members, fossil sporocarps, and dispersed megaspores (e.g., *Arcellites* and *Molaspora*) and microspores (H. Schneider, R. Lupia, and K. M. Pryer, unpublished manuscript).

Marsilea is documented in the Cretaceous (Cenomanian) by quadripinnate fronds and presence of sporocarps (lacking *in situ* spores) as observed in compression material (Skog and Dilcher 1992). However, megaspores morphologically similar to those of extant *Marsilea* are unknown. There are many possible reasons for this apparent discrepancy, of which the most likely in our opinion is that Cretaceous fossils exhibit a different combination of features to that seen in extant taxa. Further attempts to identify sporocarp material by sorting through charcoaled and lignified mesofossils offer the exciting possibility of expanding our knowledge of the fossil record

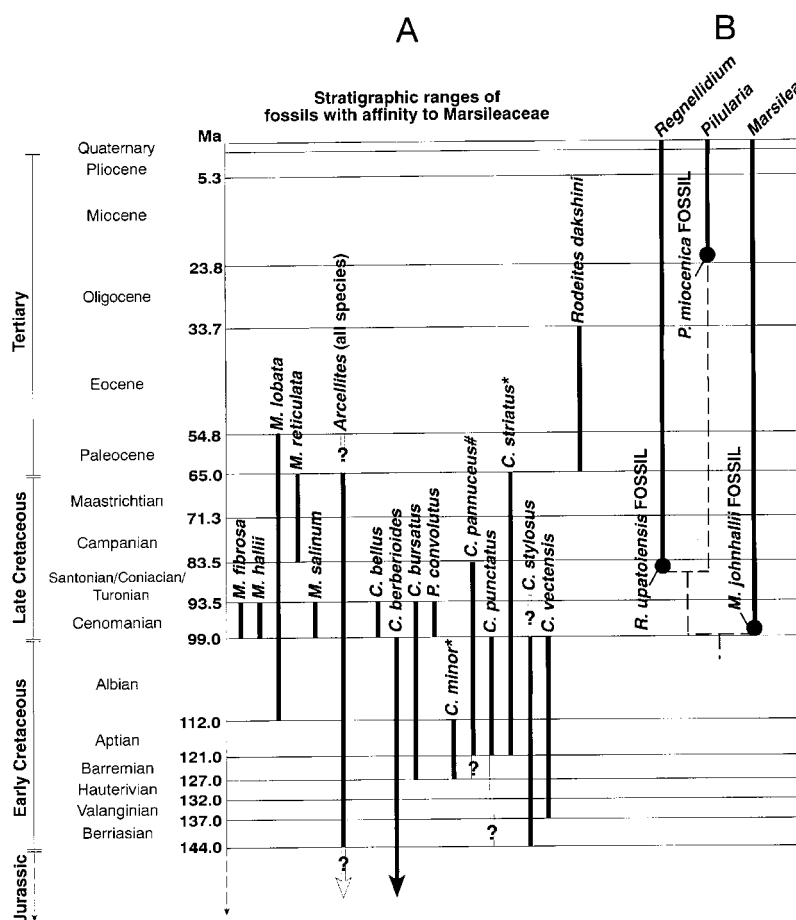


Fig. 7 Stratigraphic ranges for extant genera of, and fossils with affinity to, Marsileaceae. *A*, Age-level stratigraphic ranges of named fossil species with affinities to Marsileaceae: *Molaspora* and *Arcellites* (megaspores), *Crybelosporites* (microspores) including *Perotrilites convolutus*, and *Rodeites dakshini* (sporocarp). *Crybelosporites* species are associated with both *Molaspora* (crosshatch) and *Arcellites* (asterisk) megaspores. Solid bars indicate accepted ranges; open bars with question marks indicate possible range extensions based on uncertain identification or dating. Arrows indicate range extension into Jurassic. Megaspore and *Rodeites* range data collected from Kovach and Batten (1989) and Batten and Kovach (1990). Microspore range data collected from sources in appendix. *B*, Stratigraphic ranges of extant genera within Marsileaceae mapped onto best estimate of phylogenetic relationships among them. Filled circles indicate occurrences of earliest representative of each extant genus (*Marsilea johnhallii* [Skog and Dilcher 1992]; *Pilularia miocenica* [Dorofeev 1968]; *Regnellidium upatoiensis* [this article]). Solid bars indicate accepted ranges. Vertical dashed lines indicate minimum estimates of gaps in the fossil record inferred from sister group relationships. Diagram modified after Pryer (1999) with additional data from Batten and Kovach (1989) for *Regnellidium*. Ma = millions of years ago.

and evolution of Marsileaceae and its close relatives and understanding the transition to heterospory in this group.

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Appendix

The following is a synopsis of species of *Crybelosporites* and their stratigraphic ranges based on the literature. Batten and Kovach (1990) provides a similar survey for megaspores. Original material was not examined to confirm identifications and/or age assignments.

***Crybelosporites* Dettmann 1963**

Type species: *Crybelosporites striatus* (Cookson and Dettmann) Dettmann 1963

***Crybelosporites bellus* Singh 1983**

Reports: early-middle Cenomanian (Alberta, Canada: Singh 1983).

***Crybelosporites berberoides* Burger 1976**

Reports: Late Jurassic–Albian (Falkland Islands: Kotova 1983); Neocomian–Aptian (Australia: Burger 1976); Neocomian–early Albian (Burger 1980).

***Crybelosporites bursatus* (Hall) Ravn and Witzke 1995**

Perotriletes [sic] *striatus* auct. non. Cookson and Dettmann; Brenner 1963, pp. 66–67, pl. 19, fig. 3; pl. 20, fig. 1

Perotriletes bursatus Hall 1963.

***Crybelosporites brennerii* Playford 1971**

Reports: early Barremian–late Albian (Canada: Burden and Hills 1989); early Aptian–middle Albian (Maryland, U.S.A.: Brenner 1963); middle-early late Albian (Manitoba and Saskatchewan, Canada: Playford 1971); late Albian (Oklahoma, U.S.A.: Wingate 1980); late Albian (Wyoming, U.S.A.: Ravn 1995); Cenomanian (Iowa, U.S.A.: Hall 1964; Ravn and Witzke 1995); early-middle Cenomanian (Alberta, Canada: Singh 1983).

***Crybelosporites minor* Li and Batten 1986**

Reports: Barremian–Aptian (China: Li and Batten 1986).

***Crybelosporites pannuceus* (Brenner) Srivastava 1977**

Perotriletes [sic] *pannuceus* Brenner 1963

Crybelosporites pannuceus (Brenner) Srivastava 1977

Crybelosporites pannuceus (Brenner) Wingate 1980

Reports: late Aptian–late Albian (Maryland, U.S.A.: Brenner 1963); Albian (Louisiana, U.S.A.: Phillips and Felix 1971); early Albian (Spain: Arias and Doubinger 1980); middle-early late Albian (Manitoba and Saskatchewan, Canada: Playford 1971); Albian–Cenomanian (Peru: Brenner 1968); Albian–Cen-

omanian (Brazil: Herngreen 1973); late Albian (Oklahoma, U.S.A.: Hedlund and Norris 1968; Srivastava 1977; Wingate 1980); late Albian (Wyoming, U.S.A.: Ravn 1995); late Albian–Cenomanian (West Africa: Kotova 1978); middle Cenomanian (Alberta, Canada: Singh 1983); Santonian (Georgia, U.S.A.: this article).

***Crybelosporites punctatus* Dettmann 1963**

Reports: Berriasian?–Albian (Australia: Dettmann 1963); early-middle Albian (Burger 1980).

***Crybelosporites striatus* (Cookson and Dettmann) Dettmann 1963**

Perotriletes striatus Cookson and Dettmann 1958

Crybelosporites striatus (Cookson and Dettmann) Dettmann 1963

Reports: Aptian–Albian (Australia: Cookson and Dettmann 1958; Dettmann 1963); Aptian–early Maastrichtian (Helby et al. 1987); early-middle Aptian (Virginia, U.S.A.: Hueber 1982); Albian (Nebraska, U.S.A.: Ellis and Tschudy 1964); early Albian (Spain: Arias and Doubinger 1980); early-middle Albian (Burger 1980); late Albian–Cenomanian (Australia: Playford et al. 1975); Albian–middle Cenomanian (New Zealand: Raine et al. 1981).

***Crybelosporites stylosus* Dettmann 1963**

Reports: Berriasian–Valanginian (Australia: Dettmann 1963); Neocomian–early Albian (Burger 1980); late Albian–Turonian (Raine 1984).

***Crybelosporites vectensis* Kemp 1970**

Reports: lower to middle Valanginian (District of Mackenzie, Canada: McIntyre and Brideaux 1980); Aptian–Albian (District of Mackenzie, Canada: Brideaux and McIntyre 1975); early Aptian–early Albian (England: Kemp 1970).

This species might not belong in *Crybelosporites*.

Other

***Perotriletes convolutus* Hall 1964**

Reports: Cenomanian (Iowa, USA: Hall 1964).

This species probably belongs in *Crybelosporites* based on the illustrations published in Hall (1964). Ravn and Witzke (1995) suggest that *P. convolutus* might be conspecific with *C. pannuceus*.

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