

## ARCELLITES STELLATUS NEW SPECIES, A NEW MEGASPORE FROM THE LOWER CRETACEOUS OF MARYLAND, USA

MICHAEL D. NOWAK<sup>1</sup> AND RICHARD LUPIA<sup>2</sup>

<sup>1</sup>Department of Botany and Microbiology, 770 Van Vleet Oval, University of Oklahoma, Norman 73019, <mdnowak@ou.edu> and

<sup>2</sup>Sam Noble Oklahoma Museum of Natural History and School of Geology and Geophysics, University of Oklahoma, Norman 73072, <rlupia@ou.edu>

### INTRODUCTION

DISPERSED MEGASPORES with affinities to aquatic heterosporous ferns are relatively common in mesofossil assemblages from the Early Cretaceous to the Recent. Extant heterosporous ferns are free floating or shallow rooted freshwater plants, with a dominantly tropical to warm-temperate distribution (Tryon and Lugardon, 1991). Their heterosporous life cycle (including both megaspores and microspores) is likely to be an adaptation to their aquatic habit (Collinson, 1991; Hemsley et al., 1999; Kar and Dilcher, 2002). Thus the abundance of heterosporous fern megaspores, or the presence of heterosporous fern macrofossils, within a stratigraphic interval may be indicative of a shallow, calm, freshwater depositional environment (Hall, 1963; Batten et al., 1996; Rich et al., 2001).

Recent investigations using molecular and morphological data have linked the Salviniaceae Lestiboudois, 1826 and Marsileaceae Mirbel in Lamarck and Mirbel, 1803 in a monophyletic clade (Salviniales Britton, 1901) within the larger leptosporangiate fern clade (Rothwell and Stockey, 1994; Pryer et al., 1995; Pryer, 1999; Pryer et al., 2001). Regardless of their close evolutionary relationship, megaspores of the Salviniaceae and Marsileaceae are very different morphologically. A character that may unite the group is possession of an acrolamella. An acrolamella is used herein for a modification of the perine above the laesura that does not incorporate the exine (Tschudy, 1966; Hall, 1975; Schneider and Pryer, 2002). *Azolla* Lamarck, 1783 (Salviniaceae) megaspores have a densely fibrous perispore, with numerous floats attached to a small tripartite acrolamella ('gula' in Kempf, 1969; Hall, 1974), and *Salvinia* Séguier, 1754 (Salviniaceae) megaspores have a vacuolate perispore and a weakly developed tripartite acrolamella ('gula' in Kempf, 1971; Tryon and Lugardon, 1991). Modern Marsileaceae megaspores have an inner columellate and outer gelatinous perispore and a strongly reduced (or absent, cf. *Marsilea* Linnaeus, 1753), typically hexapartite acrolamella (Schneider and Pryer, 2002). Likewise, there is a considerable morphological gap between the Salviniales and their hypothesized sister group (tree ferns plus polypodiaceous ferns; Pryer et al., 2001). Therefore, improved sampling and a better understanding of the morphology of fossils with affinities to these families are necessary to understand the origin and evolution of the heterosporous fern clade. In this contribution, we illustrate and describe a new megaspore species assignable to the genus *Arcellites* Miner, 1935 emend. Ellis and Tschudy, 1964.

### MATERIAL AND METHODS

Fossil megaspores were recovered from the lower 30 cm of a dark grey, carbonaceous silt exposed from approximately 1.3 to 3 m above base of section in a drainage ditch on the west side of Maryland route 242, north of North East Plaza in North East, Cecil County, Maryland (North East Quadrangle, 39°36'42"N latitude, 75°56'51"W longitude). Silts from the North East Plaza locality contain a palynoflora referable to Zone I of the Potomac Group pollen zonation (Aptian; G. A. Upchurch, personal commun., 2002). Lower Potomac Group sediments were formed as

overbank/floodplain and backswamp deposits (Glaser, 1967; Conant, 1990). Mesofossils were isolated by sieving the matrix through a fine mesh (125 µm aperture), washing the organic residue with hydrochloric and hydrofluoric acids, rinsing with water and allowing the residue to air dry. Megaspores from the residue were picked under a dissection microscope at low magnification. The complete megaspore flora is described in Lupia (in press) and the palynoflora is currently under study.

Once isolated, megaspores were mounted on aluminum scanning electron microscopy (SEM) stubs with nail polish and coated with gold-palladium for examination using LEO 1430VP or 1450VP SEMs. Other megaspore specimens were stained with osmium tetroxide, dehydrated with ethanol, followed by acetone, embedded in Embed 812/Araldite resin, and allowed to polymerize in an oven at 80 degrees Celsius for 12 hours. Ultrathin sections were mounted on formvar-coated slot grids for transmission electron microscopy (TEM) using a Zeiss 10A TEM. Specimens were prepared for transmitted light microscopy with a dilute bleach (Clorox<sup>®</sup>) for two to three hours and mounted on glass slides with glycerin jelly. Reflected light micrographs were captured with a Nikon Coolpix 5000 digital camera. Measurements of *Arcellites stellatus* n. sp. were taken on a dissecting microscope. Randomly selected intact megaspores were measured and size ranges are reported with means in parentheses.

### SYSTEMATIC PALEONTOLOGY

Order SALVINIALES Britton, 1901

Family INCERTAE SEDIS

Genus ARCELLITES Miner, 1935 emend.

Ellis and Tschudy, 1964

*Arcellites* MINER, 1935, p. 600.

*Triletes* SECT. *Lagenicula* (PARS) DIJKSTRA, 1951, p. 14.

(NON *Lagenicula* BENNIE AND KIDSTON, 1886 EMEND. POTONIÉ AND KREMP, 1954).

*Pyrobolospira* HUGHES, 1955, p. 204.

*Arcellites* MINER, 1935 EMEND. POTTER, 1963, p. 227–228.

*Diagnosis*.—On reexamination of Miner's type slides, Ellis and Tschudy (1964) emended the diagnosis of *Arcellites* as follows: "Megaspore with a nearly spherical spore body and a well-developed neck consisting of (usually) six leaf-like folded appendages. Spore body with or without body appendages. Spore coat of three layers: a two-layered exoexine and intexine; exoexine smooth or variously ornamented with pits, granules, or verrucae. A triradiate scar is present on the floor of the neck."

*Occurrence*.—Global distribution in Cretaceous sediments, primarily Berriasian to Santonian, with questionable Jurassic and Paleocene records (Batten and Kovach, 1990).

*Discussion*.—Overlooking Miner's original assignment, Dijkstra (1951) assigned these megaspores to the general sporomorph genus *Triletes* Reinsch, 1881 ex Bartlett, 1929 emend. Schopf, 1938. Also overlooking Miner's work, Hughes (1955) in turn transferred these taxa to the more restrictive genus *Pyrobolospira*. Potter's (1963) emendation was the first to recognize Miner's assignment of *Arcellites*, although there were some issues left

unresolved (see Ellis and Tschudy, 1964, p. 74–75). Ellis and Tschudy (1964) improved upon Potter's (1963) emendation of the genus by emphasizing the size and folding of the neck, or acrolamella, and by correctly determining the three-layered nature of the spore wall. We follow Schneider and Pryer (2002) in their use of the terms exine (for the inner layer) and perine (for the outer two layers) of the megaspore wall. *Arcellites* is quite diverse with over 16 described species (Kovach and Batten, 1989; Batten and Kovach, 1990), although individual species commonly are restricted to specific geographic regions or stratigraphic intervals (Ellis and Tschudy, 1964; Batten et al., 1996).

ARCELLITES STELLATUS new species

Figures 1, 2.1–2.3, 2.6–2.8

**Diagnosis.**—Trilete megaspore; body spherical, bearing numerous hollow appendages; appendages perforate, long, tapered, bluntly terminated or slightly swollen; acrolamella granulate, perforate, generally shorter than diameter of spore body, widest at base, loosely joined or tightly bound at apex; ridges of acrolamella poorly formed to strongly invaginated, but neither twisted nor separated into individual leaves along their length; spore wall three-layered, outer surface of spore body ornamented with small dimpled elements.

**Description.**—Megaspore 320–(510)–700  $\mu\text{m}$  long and 220–(451)–700  $\mu\text{m}$  wide ( $n = 32$ ) in equatorial view. Megaspore body spherical or nearly so, 160–(258)–360  $\mu\text{m}$  long and 200–(289)–380  $\mu\text{m}$  wide ( $n = 32$ ) in equatorial view. Megaspore body covered with 15–(21)–34 hollow appendages ( $n = 32$ ; Figs. 1.1, 1.2, 1.8, 2.6, 2.7) that are 20–(106)–200  $\mu\text{m}$  long ( $n = 32$ ), narrow distally, and terminate bluntly or only very slightly swollen (Fig. 1.7). Acrolamella 100–(166)–240  $\mu\text{m}$  long ( $n = 32$ ), formed as an extension of the outer perine layer, with 5–(6.3)–9 ridges ( $n = 10$ ) poorly formed (Figs. 1.1, 1.2, 2.7) to strongly invaginated (Figs. 1.5, 2.6), but never twisted. Acrolamella open to tightly bound at apex (Fig. 1.5, 1.6). Ratio of acrolamella height to body diameter, exclusive of appendages, 0.33–(0.67)–1.11 ( $n = 32$ ). Trilete laesura positioned in the spore body beneath the acrolamella (Figs. 1.6, 2.8). Megaspore body surface covered in small (~2–5  $\mu\text{m}$ ) dimpled sculptural elements of the outermost perine layer (Fig. 1.3). Appendages and acrolamella irregularly granulate and perforate (Fig. 1.4), lacking dimpled sculptural elements distally (Fig. 1.7). No microspores were found adherent to any *A. stellatus* megaspores.

Spore body wall approximately 31  $\mu\text{m}$  thick and three-layered (Fig. 2.1–2.3). Composed of an inner exine layer (~4  $\mu\text{m}$ ; e in Fig. 2.1, 2.3) within two perine layers (p1 and p2 in Fig. 2.1, 2.3). Inner exine layer dense, and composed of three sublayers; a middle sublayer with branching channels between two solid sublayers (Fig. 2.3). Inner perine layer fibrous (~14  $\mu\text{m}$ ; p1 in Fig. 2.1, 2.3) with two discrete zones of density, the inner zone closer to the exine being more densely fibrous than the outer zone. Outer perine layer granular (~13  $\mu\text{m}$ ; p2 in Fig. 2.1, 2.3), granules coalescing to form a thin, homogenous surface layer. Homogenous surface layer irregularly crumpled, appearing as small, dimpled sculptural elements (Figs. 1.3, 2.2, dse in Fig. 2.1). Wall measurements based on TEM section of one specimen.

**Etymology.**—Latin, *stellatus*, starry, shaped like a star; with

reference to the assemblage of triangular appendages on the spore body.

**Types.**—Holotype herein designated: FMNH PP46718 (Fig. 1.1, 1.3, 1.4, 1.7); paratypes: FMNH PP46716 (Fig. 1.8), PP46717 (Fig. 1.2), PP46720 (Fig. 1.6), PP46721 (Fig. 1.5), PP46722 (Fig. 2.2), PP46723 (Fig. 2.6), PP46724 (Fig. 2.7, 2.8), and PP46725 (Fig. 2.1, 2.3), plus 32 measured megaspores. Type megaspore specimens are mounted on aluminum SEM stubs with nail polish, on microscope slide in glycerin jelly or free in micromount. Over 250 additional specimens are stored in separate micromounts.

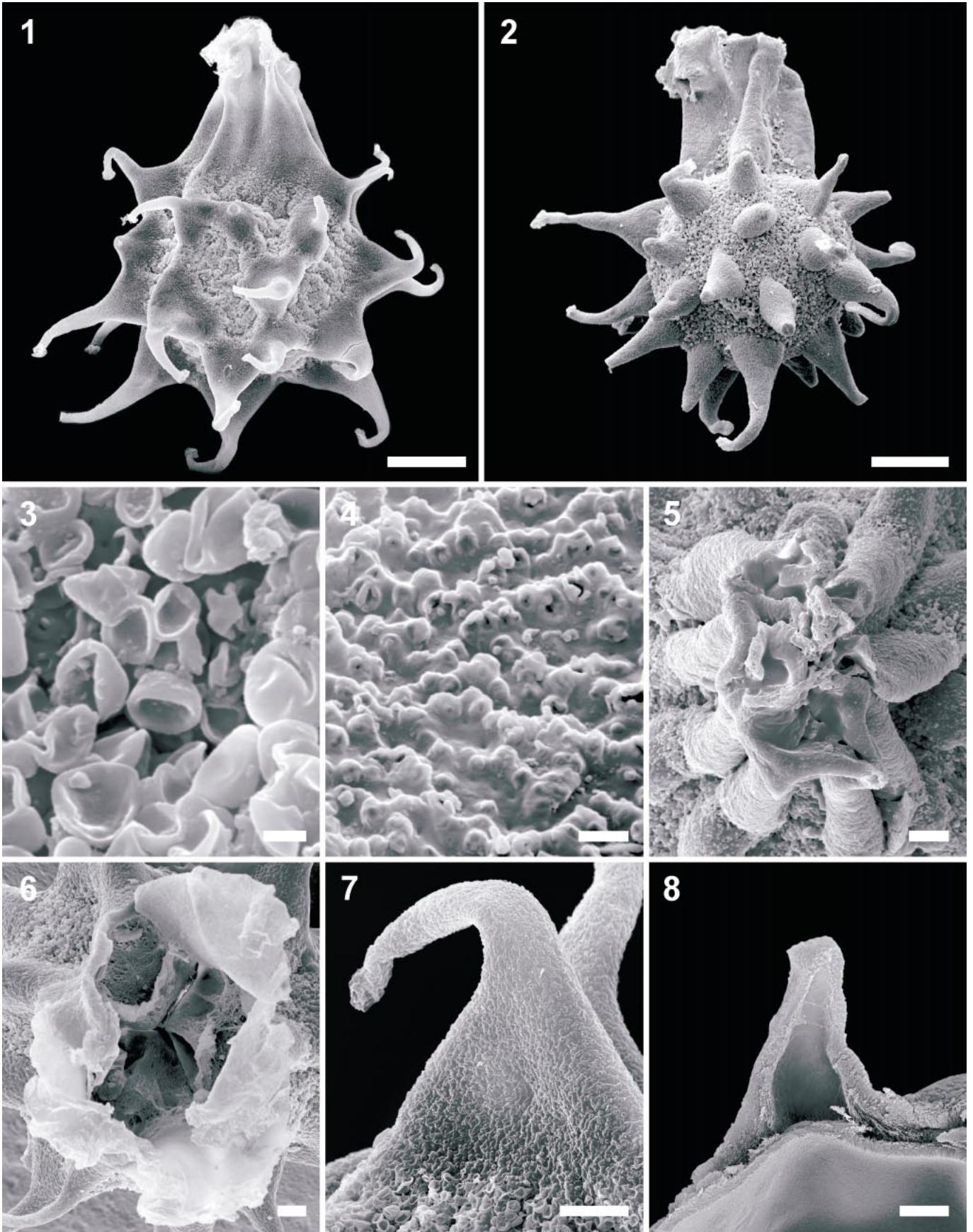
**Occurrence.**—Known only from a mesofossil locality within Zone I of the Early Cretaceous Potomac Group pollen zonation (Aptian; G. A. Upchurch, personal commun., 2002), mapped as Potomac Group undifferentiated by Higgins and Conant (1986). The locality is a carbonaceous silt exposed on the west side of Maryland Route 242, north of North East Plaza in North East, Cecil County, Maryland (North East Quadrangle, 39°36'42"N latitude, 75°56'51"W longitude).

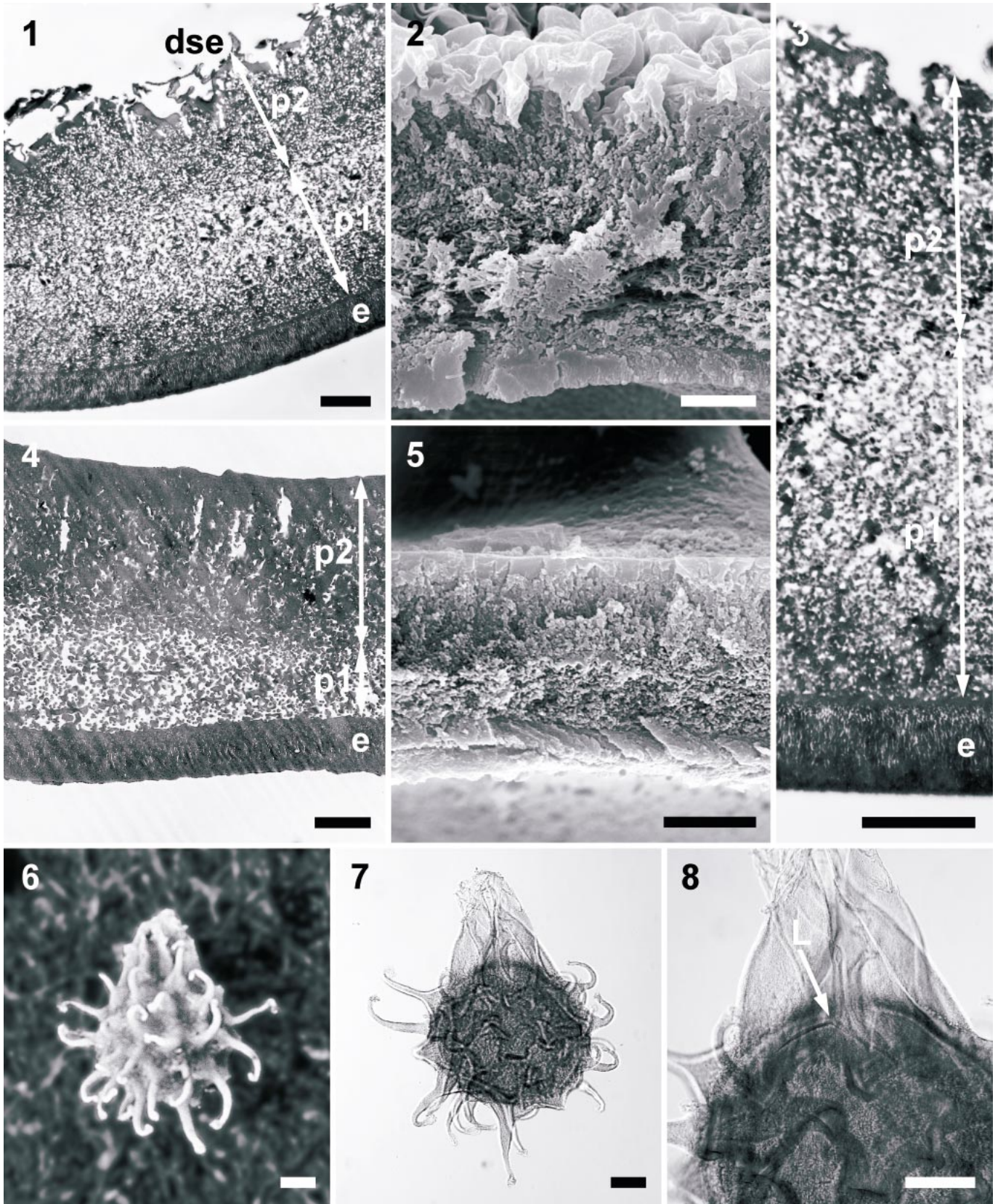
**Discussion.**—Gross morphology: The acrolamellae of *Arcellites stellatus* and *A. medusus* (Dijkstra, 1951) Potter, 1963 are similar to each other and different from all other *Arcellites* species (e.g., Cookson and Dettmann, 1958; Li and Batten, 1986; Batten et al., 1996) in that they are not separated into individual leaves that are either free, or fused along margin/crenulations, as seen in *Arcellites hexapartitus* (Dijkstra, 1951) Potter, 1963 (Fig. 3.1). *A. stellatus* and *A. medusus* are further distinguished from other *Arcellites* species in possessing acrolamellae that are not twisted into a spiral. The acrolamella of *Arcellites stellatus* is also shorter, on average, than the diameter of the spore body compared to most other *Arcellites* species (e.g., *A. hexapartitus*, Fig. 3.1) in which the acrolamella is taller than the spore body. The acrolamella of *A. stellatus* is found both open and tightly sealed at its apex. In modern Marsileaceae this opening acts as the passage to the "sperm lake" where fertilization of the megaspore is initiated (Schneider and Pryer, 2002). Thus the extent which the acrolamella is open might indicate either preservational state or the maturational stage of the megaspore.

*Arcellites stellatus* is distinguished from *A. medusus*, to which it is otherwise most similar, and *A. santacrucensis* Baldoni (1987) by possession of more numerous, but shorter appendages. *Arcellites stellatus* is distinguished from *A. disciformis* Miner, 1935 emend. Ellis and Tschudy, 1964, *A. hexapartitus*, and *A. yiminen-sis* Li and Batten, 1986 in possessing triangular appendages that narrow distally rather than spatulate or triangular appendages that are markedly expanded distally. The external dimpled sculptural elements on the *A. stellatus* spore body are unique to this species (Fig. 1.3) and serve to distinguish *A. stellatus* from all other *Arcellites* species.

**Ultrastructure:** The spore wall of *A. stellatus* is slightly thicker (~31  $\mu\text{m}$ ) than that of *A. hexapartitus* (~28  $\mu\text{m}$ ) (Fig. 2) and most other species of *Arcellites* (e.g., Cookson and Dettmann, 1958; Li and Batten, 1986; Batten et al., 1996). Differences in wall thickness seem to be the result of variability in the perine layer. Perine thickness is also somewhat variable within a single species of *Arcellites*, as can be seen in *A. hexapartitus* (compare Fig. 2.4 and 2.5), probably due to position of the section relative

FIGURE 1—SEM micrographs of *Arcellites stellatus* n. sp. 1, Megaspore, holotype, FMNH PP46718, scale bar 100  $\mu\text{m}$ ; 2, megaspore with markedly spherical body, FMNH PP46717, scale bar 100  $\mu\text{m}$ ; 3, close-up of dimpled sculptural elements on spore body, holotype, FMNH PP46718, scale bar 2  $\mu\text{m}$ ; 4, close-up of outer surface of an appendage showing perforate granules, holotype, FMNH PP46718, scale bar 2  $\mu\text{m}$ ; 5, polar view of acrolamella, FMNH PP46721, scale bar 20  $\mu\text{m}$ ; 6, polar view looking into acrolamella showing trilete laesura in spore body at base, FMNH PP46720, scale bar 20  $\mu\text{m}$ ; 7, close-up of appendage, holotype, FMNH PP46718, scale bar 20  $\mu\text{m}$ ; 8, section through appendage showing hollow interior, FMNH PP46716, scale bar 20  $\mu\text{m}$ .





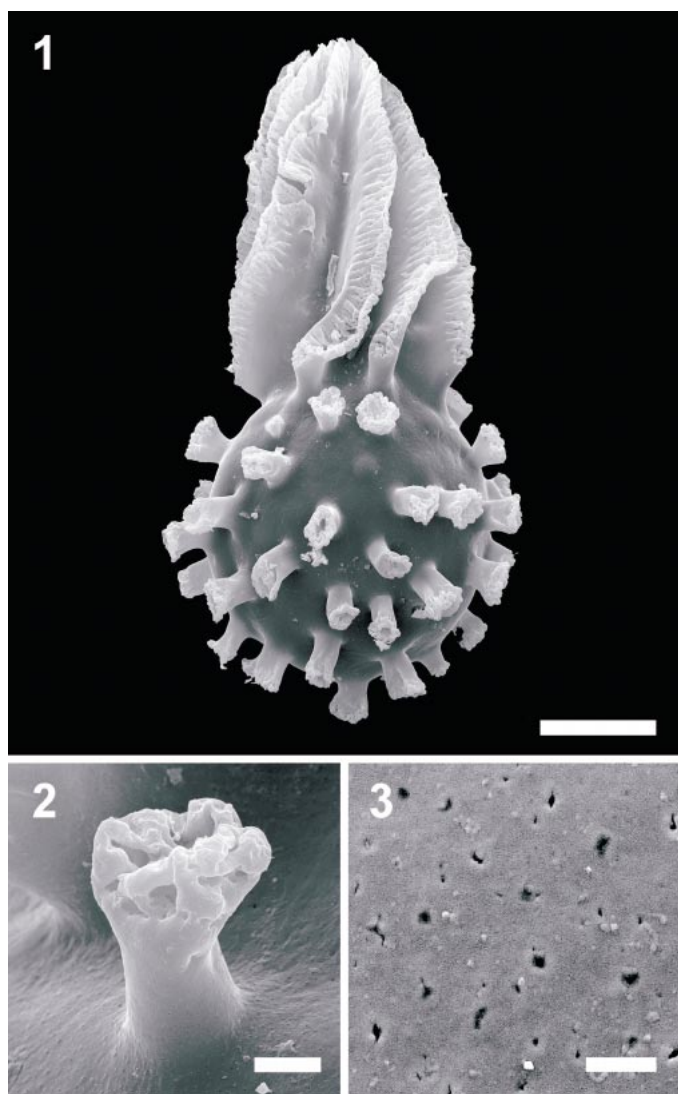


FIGURE 3—SEM micrographs of *Arcellites hexapartitus*. (Also from North East Plaza). 1, Megaspore, FMNH PP46709, scale bar 100  $\mu\text{m}$ ; 2, close-up view of appendage, FMNH PP46713, scale bar 10  $\mu\text{m}$ ; 3, close-up of outer surface of megaspore showing perforations, FMNH PP46713, scale bar 2  $\mu\text{m}$ .

to appendages (also noted by Batten et al., 1996), and to preparation method (i.e., dry for SEM, fixed for TEM). The perine of *A. stellatus* is similar to all studied *Arcellites* in that it is composed of two primary layers, but it is thicker on average ( $\sim 27 \mu\text{m}$ ) than *A. hexapartitus* ( $\sim 23 \mu\text{m}$ ) and other species of *Arcellites*. The surface of the outer perine is formed of a nearly homogenous layer giving rise to dimpled elements that are not clearly discrete

(e.g., not gemmae or clavae) when viewed with TEM (dse in Fig. 2.1) The inner perine of *A. stellatus* exhibits two distinct sublayers based on the density of the fibers; this character is not shared with *A. medusus* or other species of *Arcellites*. The exine of *A. stellatus* ( $\sim 4 \mu\text{m}$ ) is similar in thickness to *A. hexapartitus* ( $\sim 4\text{--}5 \mu\text{m}$ ), *A. reticulatus* (Cookson and Dettmann, 1958) Potter, 1963, and *A. plicatus* Li and Batten, 1986, and only slightly thicker than other *Arcellites* ( $\sim 2.5 \mu\text{m}$ ). The channeling visible in the exine of *A. stellatus* (Fig. 2.3) and *A. hexapartitus* (Fig. 2.4) is recorded from all species examined (Batten et al., 1996). Channeling is visible with SEM and in ultrathin sections with TEM, and only slightly variable in all species of *Arcellites*.

Comparison to extant genera in Salviniales: In extant Marsileaceae, *Regnellidium* Lindman, 1904 and *Pilularia* Linnaeus, 1753 each bear a small acrolamella on the proximal pole above the laesura; in *Regnellidium* it is twisted but in *Pilularia* it is not, although separate leaves are present in both. Megaspores of *Marsilea* do not bear a rigid (sporopollenin-rich) acrolamella, but the presumably homologous structure exists at hydration as a lobate gelatinous extension (Machlis and Rawitscher-Kunkel, 1967; Schneider and Pryer, 2002). Extant marsileaceous megaspores, examined after acetolysis, possess a similar dense exine and two-layered perine. In all extant taxa, the inner perine appears granulate in cross section, but fibrous in three dimensions. In contrast to *Arcellites* in general, and *A. stellatus* specifically, the outer perine of extant marsileaceous taxa exhibits a typically columellate appearance in cross section (Lupia et al., 2000). The narrow channels apparent in the exine of *Arcellites* have not been observed in any extant marsileaceous megaspore.

In *Azolla* and *Salvinia*, an acrolamella is also present, but it is trifoliate with leaves joined centrally rather than basally (e.g., Kempf, 1969, 1971, called 'gula' therein) and thus more closely resembles species of *Ariadnaesporites* Potonié, 1956 emend. Tschudy, 1966, *Capulisporites* Potonié, 1956, or *Ghoshispora* Srivastava, 1967 emend. Srivastava, 1978 rather than *Arcellites*. Exine channeling possibly homologous with that in *Arcellites* has been observed in some species of *Salvinia* [e.g., *Salvinia cerebrata* Nikitin, 1948 ex Dorofeev, 1955a illustrated in Kempf, 1971 and in Collinson et al., 2001; *S. intermedia* complex sensu Collinson et al., 2001; *S. natans* (Linnaeus, 1753) Allioni, 1785 as illustrated in Kempf, 1971; and *S. rhenana* Kempf, 1971]. In *Azolla*, exine ultrastructure appears spongy rather than narrowly channeled but may be homologous (e.g., *Azolla nikitinii* Dorofeev, 1955a and *A. ventricosa* Nikitin in Dorofeev, 1955b ex Dorofeev, 1959, illustrated in Friis, 1977). The perine of modern salviniaaceous megaspores is either diffuse and vacuolate (e.g., *Salvinia* and some species of *Azolla*) or densely fibrous (e.g., some species of *Azolla*) (Kempf, 1969, 1971; Perkins et al., 1985; Collinson et al., 2001) and is not obviously similar to the perine of any species of *Arcellites*, or to the perine of taxa in its sister clade, Marsileaceae (Pryer et al., 2001; Schneider and Pryer, 2002). Phylogenetic analyses of all characters and all taxa are necessary to establish homologies and are part of ongoing studies of SEM and TEM sections of extant and fossil salvinialean megaspores.

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FIGURE 2—1–5, TEM and SEM micrographs of *Arcellites* Miner, 1935 emend. Ellis and Tschudy, 1964. 1–3, *Arcellites stellatus* n. sp. 1, TEM micrograph of median longitudinal section through megaspore wall near equator, FMNH PP46725; 2, SEM micrograph of section through fractured megaspore spore wall, FMNH PP46722; 3, enlarged TEM micrograph of median longitudinal section through megaspore wall near equator, FMNH PP46725. 4, 5, *Arcellites hexapartitus* (Dijkstra, 1951) Potter, 1963. 4, TEM of median longitudinal section through megaspore wall near equator, FMNH PP46714; 5, SEM micrograph of section through fractured megaspore wall, FMNH PP46711. 6–8, Light micrographs of *Arcellites stellatus* n. sp. 6. Reflected light micrograph, FMNH PP46723; 7, transmitted light micrograph, FMNH PP46724; 8, close-up of specimen in 7 showing trilete laesura beneath acrolamella, FMNH PP46724. e = exine, p1 = inner perine, p2 = outer perine, dse = dimpled sculptural element, L = trilete laesura. Scale bar 5  $\mu\text{m}$  in 1–5; 100  $\mu\text{m}$  in 6–8.

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