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Megaspore assemblages in the Cretaceous of Minnesota

ABSTRACT

A mid-Cretaceous Minnesota lacustrine deposit, capped by a lignite and then channeled by a Cretaceous stream, has yielded a number of megaspores of both aquatic ferns and aquatic and terrestrial lycopods. Distribution of these megaspores shows differences in percentages in the several depositional environments. The lacustrine and fluvial deposits contain spores derived from the uplands, as well as those also occurring in the lignite. The lignite, representing deposition in a swamp, lacks *Costatheca* and *Spermatites*, and has a high incidence of *Tenellisporites*. Two new species are described: *Tenellisporites spinatus* Peake and *Ariadnaesporites varius* Hall and Peake.

INTRODUCTION

Geology

Isolated patches of mid-Cretaceous (Cenomanian) deposits occur in south central Minnesota, particularly along the Minnesota and Cottonwood Rivers. Sloan (1964) has described these beds as parts of the Ostrander Member of the Windrow Formation, mostly for lack of a better designation for them. Typical Ostrander deposits occur to the east and consist dominantly of fine-grained, loosely consolidated gravels. The name originally given to the local deposits, the Big Cottonwood Formation, is preoccupied by a Precambrian formation in Utah. Regardless of their nomenclature, they are mostly nonmarine of fluvial, lacustrine and deltaic origins. One of these deposits is a clay seam of the A. C. Ochs Brick and Tile Company near Springfield, Brown County, now mined to a depth of about 40 feet. Sloan (*loc. cit.*, p. 22) presented a generalized section of this pit which agrees with our observations of just a few years later. A ripple-marked veneer of marine shale lies below the glacial drift. Below this is a 1-foot lignite seam, and below the lignite a sequence of nonmarine varved clays containing scattered pyrite concretions and extending to the bottom of the pit. A Cretaceous stream has cut through the northwest corner of the nonmarine deposit. The stream channel has been filled with reworked lignite and varved clays, but at its base there is a small marine fauna of sharks, teleosts and a crocodile (Estes in Sloan, 1964, p. 25). The varved clays are lacustrine, and the lignite represents swampy conditions which developed when the lake was almost filled. The stream channel was one of a number produced by the rejuvenation of streams, flowing primarily from the east, as a result of a brief lowering of sea level. A later rise in sea level inundated the channel, filled it with reworked material, and deposited estuarine and marine clays above it and the swamp deposits.

Text-figure 1 gives a diagrammatic representation of the three sedimentary environments, lake, swamp and channel, together with the locations of the samples we have used for isolating megaspores.

Paleoecology

It was our original intention simply to compare the megaspore flora of the Springfield deposit with that described by Hall (1963) from Iowa, but, when we looked at the distribution of these spores in the three depositional environments, it appeared that they provided a means of distinguishing the purely paludal autochthonous deposits from the lacustrine and transported sediments, and that it was also possible to distinguish between those megaspores produced by aquatic plants and those produced by upland plants in cases where the habitat source had not been entirely clear.

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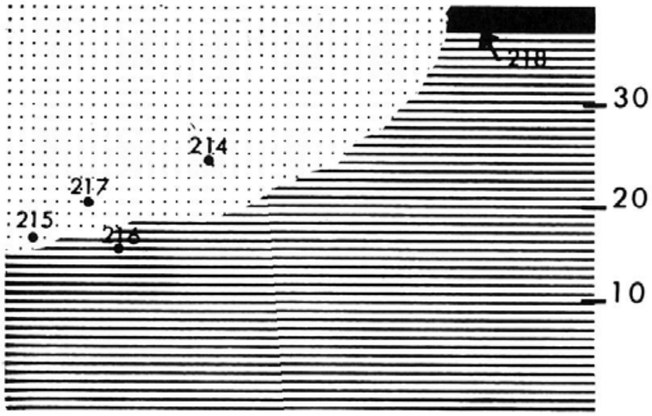
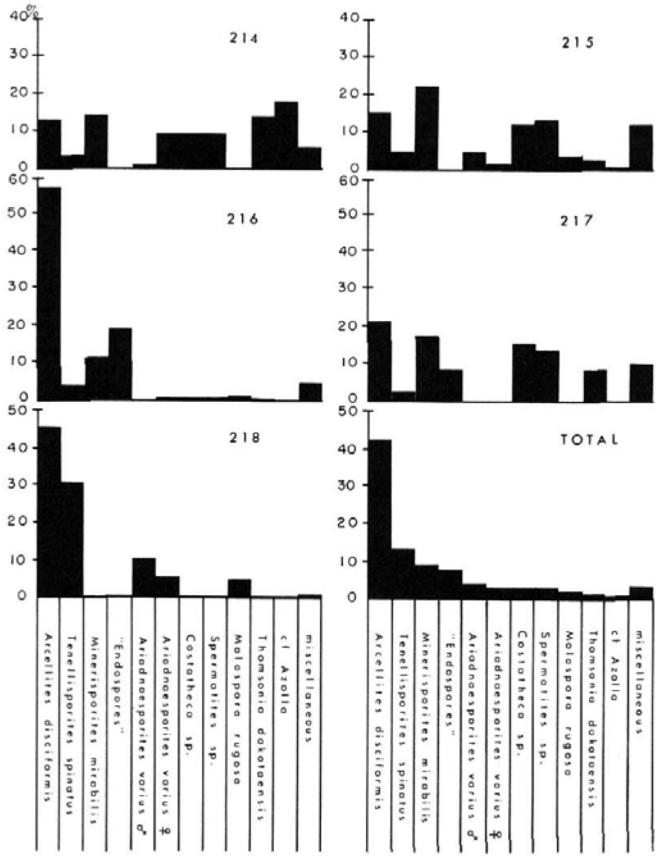


TEXT-FIGURE 1
Diagrammatic cross section of the Springfield pit. Stippled portion indicates stream channel deposits, lignite is shown in solid black, and the horizontally lined area represents varved lacustrine clays. Vertical scale in feet. Numbers 214 to 218 refer to sample locations.



TEXT-FIGURE 2
Bar graphs of percentages of each megaspore species in each of samples 214 to 218, and in all samples combined. Location of samples: 214, lower middle part of stream channel deposits; 215, bottom of stream channel deposits; 216, varved lacustrine clays below stream channel deposits; 217, just above bottom of stream channel deposits; 218, lignite overlying the varved clays.

Megaspores possess some inherent advantages over microspores for these purposes. Their large size (mostly greater than 250 microns) greatly reduces or even precludes the possibility of wind transport, hence those occurring in paludal deposits are very likely to be autochthonous, whereas those in lacustrine or fluvial deposits may be either autochthonous or water-borne. In the Cretaceous, plants of only two widely different habitats are represented by megaspores. The heterosporous ferns are all aquatic; *Arcellites, Ariadnaesporites, Molaspora* and *Azolla* are members of this group. The lycopods, with the exception of *Isoetes* today, are upland plants; among the fossils in this group are *Minerisporites, Thomsonia* and *Tenellisporites.* There are no other groups of free-sporing heterosporous plants today than these two, and there is no indication that there were more in the Cretaceous, either. Spore morphology in the two groups is diagnostically different. In the ferns, the megaspores have a perispore and are multiradially symmetrical, whereas megaspores of the lycopods lack a perispore and are usually triangular in outline or triradially symmetrical. Even fragments of megaspores can be placed in one of these two higher taxa, if not recognized at the generic level. Some objects of megaspore size still remain unassigned. *Costatheca* and *Spermatites* are two of these.

For the Springfield deposit there is the further advantage, mentioned above, that the megaspore flora of a contemporaneous deposit in nearby Iowa has been described by Hall (1963). Pierce (1961) has described the microspores from the Springfield pit, but his sample size was so small that no megaspores were found.

METHODS

We tried to obtain 250 or more spores from each sample. This was easy enough in the lignite (sample 218), but, after using an entire 5-pound portion of sample 216 to get this number, we processed only about a pound of each of the other three samples and picked all that could be obtained. These were samples from the channel, and their spore content was low.

Fragments, as well as whole spores, were picked. Each fragment was counted as a whole spore. Most of the fragments were larger than half a spore except in *Thomsonia.* Fragments of *Thomsonia* can be recognized by the "barbs" along the equator and the laesurae. Most of these fragments occurred in the channel deposits, and, even though this is not one of the more common forms, its numbers may be a little too high. The microspore masses of *Ariadnaesporites varius* and the individual megaspores of this species were tabulated separately.

Percentages of each of the recognizable species and a category of miscellaneous spores, to include small numbers of as yet unnamed megaspores, are plotted in text-figure 2.

DISCUSSION

The suppositions of an autochthonous origin and a paludal environment for the plants which formed the lignite are substantiated by the occurrence in it of megaspores of known aquatic plants and by the absence of presumedly upland plants. *Molaspora, Ariadnaesporites* and *Arcellites*, the latter extremely common, are the aquatics; *Minerisporites* and *Thomsonia* the absent upland genera. Two unexpected distribution patterns turned up. *Costatheca* and *Spermatites* are both absent from the lignite, while the lycopod *Tenellisporites* is abundant. The latter must surely represent an aquatic or semiaquatic plant, perhaps related to the present-day *Isoetes*, a small aquatic, heterosporous lycopod, which has also been reported occasionally as a Cretaceous megafossil (Brown, 1939). Dispersed megaspores of *Isoetes* have not been reported. *Tenellisporites spinatus* is, however, quite similar to the megaspores of the present-day *Isoetes echinospora* Durand var. *braunii* (Durand) Engelmann.

Costatheca and, especially, *Spermatites* are very common in the Middle to Late Cretaceous. They occur in every shale from which we have isolated megaspores, but they are completely absent from the Springfield lignite. As yet we are not sure of their natural affinities, but they are rather seedlike (perhaps gymnospermous). Their occurrence in lake deposits suggests their transport thither. Those in the stream channel deposits were either reworked from the lake deposits or transported from a land surface.

The lake and stream channel deposits yielded all of the kinds of spores found in the swamp, as well as those from uplands carried in by streams flowing over the land surface. The latter include the lycopod spores *Thomsonia* and *Minerisporites*, as well as *Spermatites* and *Costatheca*. The high incidence of *Arcellites* and its relatively good preservation in the lake deposits suggest that it was common in both lake and swamp habitats. Most of the other spores show evidence of transport, although *Minerisporites* is usually well preserved. The aquatic ferns and *Tenellisporites* must have grown in shallow areas close to shore and been transported along with the land-derived spores to the deeper parts of the lake.

The spores referred to as cf. *Azolla* are also absent from the lignite. These spores resemble known *Azolla* megaspores from which the swimming apparatus and perisporal hairs have been lost. There is no other more authentic record of *Azolla* as early as the Cenomanian, however. Since *Azolla* is an aquatic heterosporous fern, it ought to occur in the lignite, if our identification of these spores is correct, but its occurrence only in the stream channel deposits presumes transport from the lake or an upland area.

Hall (1963) did not find either *Tenellisporites* or *Ariadnaesporites* in the Iowa "Dakota" deposit. Ours is the first record of *Tenellisporites* in this country, but *Ariadnaesporites* has been reported several times. Most of the megaspores, except *Tenellisporites*, have a relatively long Cretaceous range, though there are specific differences in time. Our comments about depositional environments and habitats need not be confined to deposits contemporary with this one.

Perhaps we have done no more than reinforce our ideas as to the habitat preferences of the plants which produced these Cretaceous megaspores. As expected, the aquatic ferns occurred in swamps, and the upland lycopods did not. There are a few unexpected results, though. One is the absence of *Spermatites* and *Costatheca* from the lignite; and a second is the occurrence of the lycopod *Tenellisporites* in this lignite. Deposits which contain all of these megaspores, or even certain combinations which include terrestrial lycopods, must be allochthonous to a certain extent. Deposits of autochthonous plants are the more difficult to identify, since it is the absence of terrestrial spores which distinguishes them.

SYSTEMATIC DESCRIPTIONS

Division PTERIDOPHYTA
Class LYCOPSIDA
Order SELAGINELLALES (provisional assignment)
Family SELAGINELLACEAE (provisional assignment)
Genus THOMSONIA Mädler, 1954

Thomsonia dakotaensis Hall
Plate 1, figure 1

Thomsonia dakotaensis HALL, 1963, p. 438, text-figs. 37–39.

Comments: Most specimens are fragments, but they all resemble *T. dakotaensis* Hall. In the few intact spores, barbs seem to be lacking on the distal surface. The sculpture of the barbs is braided or ropelike, and long, tortuous fibrils, with few irregular intervening spaces, contribute to the composition of each barb. The spines of *Tenellisporites spinatus* have a similar pattern.

Genus MINERISPORITES Potonié, 1956

Minerisporites mirabilis (Miner) Potonié
Plate 1, figure 2

Selaginellites mirabilis MINER, 1935, p. 618, pl. 23, figs. 1–6.
Minerisporites mirabilis (Miner). – POTONIÉ, 1956, p. 67, pl. 9, figs. 87–88.

Dimensions: Diameter 320 (480) 625 μ.

Comments: This is a highly variable assemblage of specimens, especially in size and sculpture of the wall. In all specimens the wall is relatively thin (*ca.* 2–5 μ), the laesurae extend to the equator, or somewhat beyond the body onto an equatorial flange. The sculpture ranges from the characteristic reticulate pattern with lumina of uniform size to the faintly rugulate pattern in the illustrated specimen.

Order ISOETALES (provisional assignment)
Family ISOETACEAE (provisional assignment)
Genus TENELLISPORITES Potonié, 1956

Tenellisporites spinatus Peake, **n. sp.**
Plate 1, figure 3

Holotype: Slide 218–19, coordinates 114.5×32.5, reference 11.8×119.8, paleobotanical collection MIN. Plate 1, figure 3.

Type locality: Springfield, Minnesota.

Stratigraphic horizon: Ostrander Member of Windrow Formation.

Description: Trilete megaspore; laesurae extending to equator; outline subcircular to triangular. Both proximal and distal surfaces covered with evenly but widely spaced simple or once-forked spines; spines 4 (5.8) 7 μ wide, 25 (39), 50 μ long; wall of spines foveo-reticulate. Megaspore wall 3–4 μ thick, foveolate to granular in areas between the spines.

Dimensions: Diameter 240 (327) 400 μ.

Comments: This species is distinguished by its relatively long and occasionally bifurcate spines.

Class FILICOPSIDA
Order MARSILEALES
Family MARSILEACEAE
Genus MOLASPORA Schemel, 1950

Molaspora lobata (Dijkstra) Hall
Plate 1, figure 4

Triletes lobatus DIJKSTRA, 1949, p. 25, pl. 2, fig. 9.
Molaspora rugosa SCHEMEL, 1950, p. 753, text-fig. 12.
Pyrobolospora lobata (Dijkstra). – HUGHES, 1955, p. 211.
Arcellites lobatus (Dijkstra). – POTTER, 1963, p. 228.
Molaspora lobata (Schemel). – HALL, 1963, p. 432.

Comments: Most of the specimens of this species are broken or corroded, but they are unmistakable and compare closely with specimens from the Dakota Formation of Iowa (Schemel, 1950; Hall, 1963).

There are no valid reasons for not including these megaspores in the extant family Marsileaceae. Their resemblance to the megaspores of the living *Regnellidium diphyllum* is unmistakable, and no purpose is served by placing them in artificial higher taxa. Only because their vegetative remains are unknown do we continue to assign them to the genus *Molaspora* rather than to *Regnellidium.*

Dimensions: Diameter 370 (483) 528 μ.

Family MARSILEACEAE (provisional assignment)
Genus ARCELLITES Miner, 1935

Arcellites disciformis Miner
Plate 1, figure 5

Arcellites disciformis MINER, 1935, p. 600, pl. 20, figs. 61, 64–66.
Arcellites crillensis SCHEMEL, 1950, pp. 751–752, text-figs. 16–19.
Arcellites cf. *A. hexapartitus* (Dijkstra). – POTTER, 1963, p. 227, pl. 1, figs. 1–7.

Comments: This is a common, distinctive megaspore, and, even when the trifolium and body floats have been broken, it is easily recognized. A number of specimens in both the lignite and the clays has the *Crybelosporites* type of microspore among the trifolium segments.

There is less assurance than for *Molaspora lobata* that *Arcellites disciformis* can be correctly assigned to the family Marsileaceae. The most striking differences from megaspores of living members of that family are the pronounced coiled trifolium, the floatlike appendages, and the development of the male gametophyte within the confines of the trifolium. This last feature is in contrast to the analogous situation in *Marsilea vestita,* described by Machlis and Rawitscher-Kunkel (1967), where the freely shed sperm accumulate at the proximal end of the megaspore in a "sperm lake". The microspores of *Arcellites* (*Crybelosporites*) are similar to those of *Marsilea,* however.

Dimensions: Trifolium length 210 (303) 380 μ, total length 429 (548) 660 μ, body diameter 200 (280) 350 μ.

Genus ARIADNAESPORITES Potonié, 1956

Ariadnaesporites varius Hall and Peake, **n. sp.**
Plate 1, figures 6–7; plate 2, figure 1

Holotype: Slide 218–1, coordinates 122.5×24.3, reference 14.8×116, paleobotanical collection MIN. Plate 1, figure 6.

Type locality: Springfield, Minnesota.

Stratigraphic horizon: Ostrander Member of Windrow Formation.

Description of megaspores: Wall composed of an outer perispore and an inner endospore, each about 6 μ thick. The endospore has a psilate to foveolate wall, more like that in *A. intermedius* Hall than that in *A. cristatus* Tschudy. The hairs which form part of the perispore are both numerous and very long, though, as is usual in this genus, the total length is virtually impossible to obtain, because they intertwine. A distinctive feature is the occurrence of hairs of two widths. The wider hairs, about 2–3 μ wide, are most numerous, but in addition there are some narrow hairs 1 μ wide. All are apparently attached to the distal hemisphere of the perispore, but they tend to overflow the trifolium, which is always difficult to see.

Dimensions: Body diameter 200 (328) 440 μ.

Description of microspores: Wall 2–3 μ thick, psilate to granular; 4–6 hairlike processes on distal hemisphere. The processes resemble those on the megaspore in being long and tortuous. The width of the processes varies among microspores from 2 μ to 4 μ. The number of microspores in each aggregation is usually only from 2–4, but an occasional aggregation has as many as a dozen. The hairs in the microspore aggregations are of two widths, the narrower being only 1–2 μ wide, the wider as much as 6 μ wide. The narrow hairs seem not to be attached to the spores, and their source remains obscure.

Dimensions: Width of spore body 36 (49) 61 μ, total length 88 (96) 110 μ.

Comments: This is a doubtful member of the Marsileaceae, because the microspores are more nearly like the megaspores than they are like the microspores of the living species of this family, and because, as in *Arcellites*, there are distinctive appendages on the spore body and a pronounced trifolium. Although *Ariadnaesporites* does not occur in the Iowa deposit, it is a common Cretaceous genus (Hills, MS.; Hall, MS.).

The difference in diameter between megaspores and microspores is much greater than that recorded for those other species of the genus where both kinds of spores are known (Hall, MS.). Elsik (personal communication) has commented that several of his specimens of *Caudaspora spinosa* (=*Ariadnaesporites spinosa*) (Elsik) Hills (Hills, MS.) consist only of apparently sterile masses of the hairlike processes, as is the case with *A. varius* as well.

SPORAE INCERTAE SEDIS
Genus COSTATHECA Hall, 1967

Costatheca spp.
Plate 2, figure 2

Comments: The name *Costatheca* was introduced by Hall (1967) to replace the preoccupied name *Chrysotheca* Miner, 1935. Members of the genus are elongate, saclike, and ribbed or ridged structures, somewhat

PLATE 1
All figures ×100

1 *Thomsonia dakotaensis* Hall
Oblique proximal view. Slide 214–3. Coordinates 120.5×26.5. Reference 13.1×117.2.

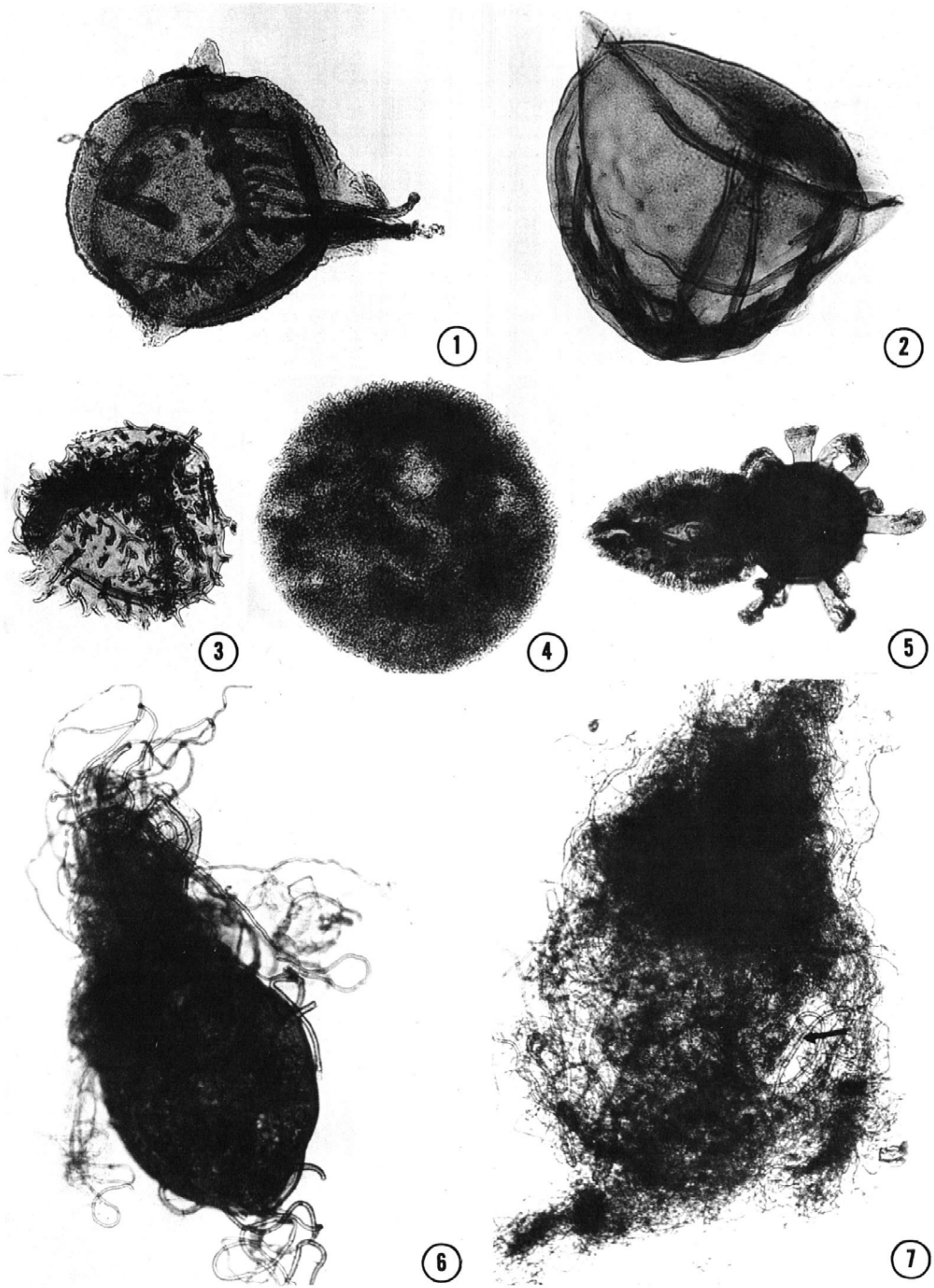
2 *Minerisporites mirabilis* (Miner) Potonié
Wall sculpture appears as undulating ridges when seen in transmitted light. Mounted in euparal, index of refraction 1.483. Slide 215–1. Coordinates 115×25. Reference 12.7×119.1.

3 *Tenellisporites spinatus* Peake, n. sp.
Holotype. Slide 218–19. Coordinates 114.5×32.5. Reference 11.8×119.8.

4 *Molaspora lobata* (Dijkstra) Hall
Distal surface, with clavate projections of perispore; slightly corroded specimen. Slide 218–11. Coordinates 116.5×38.5. Reference 11.5×115.3.

5 *Arcellites disciformis* Miner
Slide 218–9. Coordinates 123×23. Reference 12.1×121.4.

6–7 *Ariadnaesporites varius* Hall and Peake, n. sp.
6, holotype. Slide 218–1. Coordinates 122.5×24.3. Reference 14.8×116. Megaspore, partly crushed. Long twisted hairs obscure the trifolium at the proximal (upper) end of the spore. 7, mass of hairs in which microspores are imbedded but are not evident at this magnification. The two types of hair, narrow and broad, can be seen on the right. The microspore figured in plate 2, figure 1, is at the lower right. Arrow points to another microspore. Slide 218–10. Coordinates 115.5×32. Reference 14.2×117.4.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resembling small seeds. Commonly, one end is darkened and possesses a chalaza-like orifice. Cell-like outlines are sometimes seen on the surface. The wall may be double in some specimens. Neither the natural affinities nor the taxonomy of this genus is clear. There is a large number of species, some of which are rather like specimens of *Spermatites.*

Many of the specimens of *Costatheca* in the Springfield deposit are broken. They occur only in the lake and stream deposits, as noted above. The figured specimen is *C. diskoensis* (Miner) Hall. There are other species in this assemblage, but no attempt was made to distinguish among them, and all were counted as members of the genus.

Dimensions: 595 (822) 1300 μ long by 250 (360) 462 μ wide.

Genus SPERMATITES Miner, 1935

Spermatites sp.
Plate 2, figure 3

Comments: Like *Costatheca,* the specimens assigned to *Spermatites* Miner, 1935, are hollow sacs, but there are generally no longitudinal ridges, and the outlines of cell walls are generally quite clear. An orifice is present at one end. The opposite end of the sac is sometimes micropyle-like (as in the figured specimen), but the so-called micropyle is not open at the tip. The cells just below this beak often have sinuous outlines and are somewhat like the cap of cells at the apex of the sporocarp of present-day *Azolla*. No spores have been found in any of the specimens of *Spermatites* that we have seen. Some seed cuticles are like *Spermatites* (see Harris, 1954). The figured specimen is most nearly like *Spermatites elongatus* Miner, but this is such a heterogeneous genus that we are reluctant to assign specific names until more is known about its taxonomy.

Dimensions: Average length of specimens 850 μ, width 350 μ.

Sporae incertae sedis, forma 1
Plate 2, figures 4–5

Comments: A number of spherical objects, designated as "endospores" in text-figure 2, occur in the lake and channel sediments. They have a thin wall, 1–2 μ thick, which is psilate to foveolate, except where corrosion has occurred. The spores are inaperturate. Diameter of the spores is 230 (287) 410 μ. One or two folds may usually be seen in the wall.

These objects are of about the same diameter as the spore body of *Arcellites disciformis.* There are 3 laesurae in *Arcellites,* but these are rarely seen. Perhaps some specimens of *Arcellites* are actually inaperturate and are represented by these corroded endospores. The endospores occur in certain of the transported sediments in which *Arcellites* also occurs, but are absent from others and from the lignite. In the lake sample (no. 216), the endospores and *Arcellites* are the two most abundant spore types, attaining 20% and 57% of the assemblage respectively; but, of the samples from the stream channel deposits, only one has both types. If abrasion caused by transport was responsible for removing the perispore,

PLATE 2

Figure 1 × 520, figures 2–6 × 100

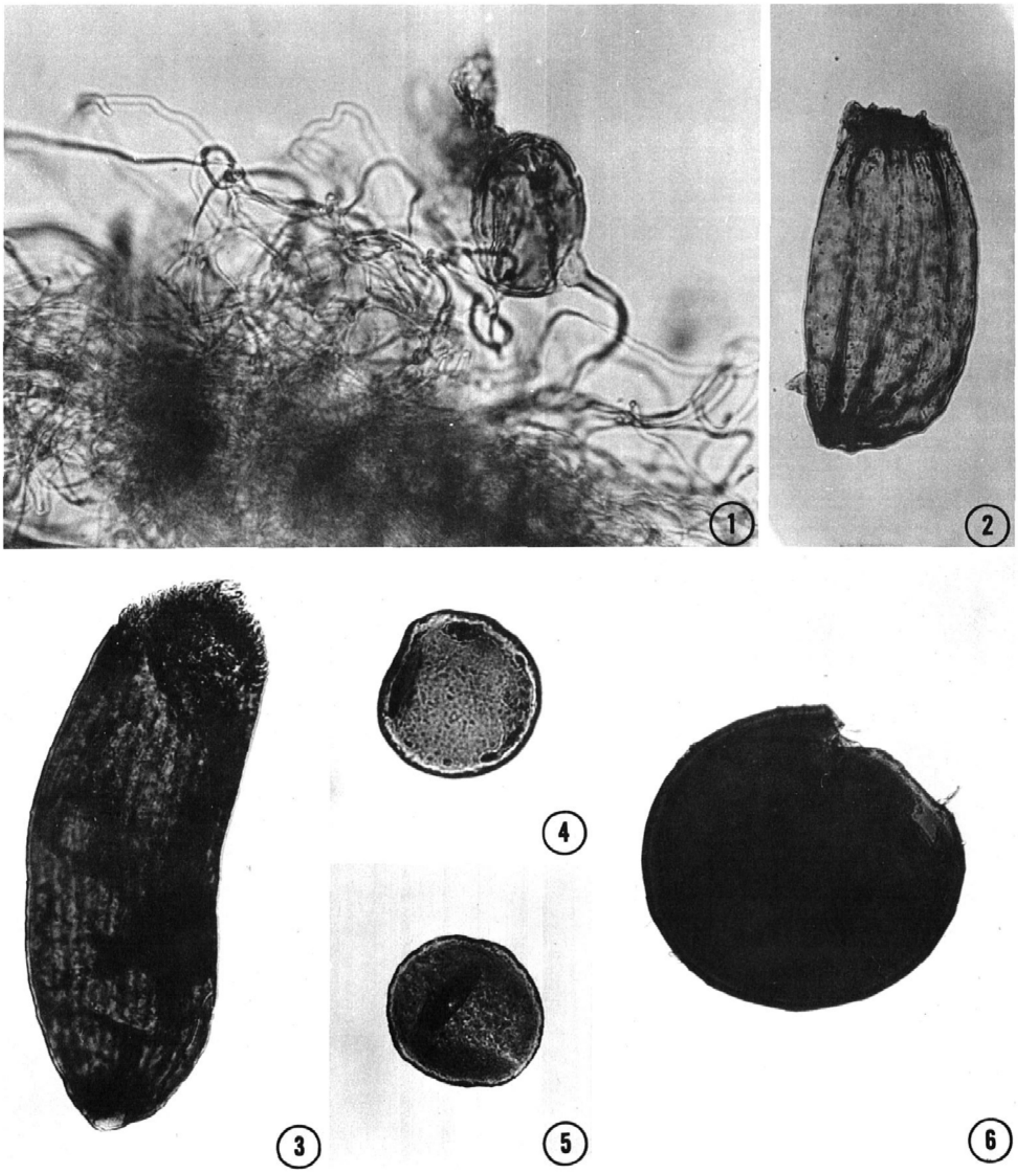
1 *Ariadnaesporites varius* Hall and Peake, n. sp.
Microspore and mass of hairs, enlargement of lower right portion of plate 1, figure 7. Slide 218–10. Coordinates 115.5 × 32. Reference 14.2 × 117.4.

2 *Costatheca diskoensis* (Miner) Hall
This specimen is almost identical with the lectotype of the species. Slide 217–1. Coordinates 116 × 24. Reference 67.7 × 119.

3 *Spermatites* sp.
Slide 215–4. Coordinates 112 × 33.5. Reference 11.6 × 111.1.

4–5 "Endospores"
Cf. spore body of *Arcellites disciformis* for size, plate 1, figure 5. 4, slide 216–3. Coordinates 126 × 27.5. Reference 38.5 × 121.8. 5, slide 216–1. Coordinates 124.5 × 31. Reference 17.5 × 119.

6 Cf. *Azolla*
Slide 214–3. Coordinates 121.5 × 25. Reference 13.1 × 117.2.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one would expect endospores in all of the channel deposits, as well as in deposits from other localities in which *Arcellites* is abundant.

These nondescript objects may not be spores at all, for inaperturate free-sporing megaspores are not known to exist.

Sporae incertae sedis, forma 2
Plate 2, figure 6

Comments: A few specimens of a large spherical spore occur in the stream channel deposits and are designated as cf. *Azolla* in text-figure 2. A large, gaping, irregular opening occurs on one side of the spore, presumably the proximal end. This opening is reminiscent of the one which results when the swimming apparatus is removed or lost from the megaspores of some species of *Azolla*, and the contact area of the megaspore is removed as well. Although these spores may resemble such specimens of *Azolla*, it is doubtful that they are, in fact, *Azolla*. These spores average over 500 μ, which is larger than any as yet described *Azolla* megaspore. There is no evidence of the kind of perispore that is so characteristic of *Azolla*, nor is there a swimming apparatus. The fact that there is no other valid *Azolla* known from this early in the Cretaceous also has a bearing. The wall of these spores is 4–5 μ thick, and the spore diameter is 440 (514) 660 μ. Outline of spores circular. Their surface is psilate, except for a few branched hairs at the apertural end.

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