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Isoetalean megasporophylls with megaspores from the Upper Cretaceous of Mongolia

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Abstract

Detached megasporophylls bearing relatively large sporangia with megaspores are described from the lower Maastrichtian dinosaur beds of the Nemegt Basin, eastern Gobi, Mongolia. The megasporophylls are fertile along their entire length except a short tip. The megaspore tetrads are aligned in a single file. On the base of these distinctions the Mongolian fossils are assigned to a new genus *Monilitheca* of the Isoetalean affinities. The megaspore casts show replicas of both the external and internal reticulate structures. The megaspores are comparable with dispersed spore genera *Horstisporites* and *Erlansonisporites* thus suggesting their isoetalean affinities.

1. Introduction

The Mongolian Cretaceous lacustrine deposits are rich in the remains of extinct lycopsids (Krassilov, 1982) presently added by the new findings in the Nemegt Basin, a depression south of the Altan Ula Highlands (Fig. 1) filled with Upper Cretaceous and Tertiary freshwater deposits. The Upper Cretaceous Upper Nemegt sequence is about 140 m thick, consisting of sands with gravel, silt and clayey interbeds in the lower 60 m, with alternating sand and silt above. On the evidence of its rich dinosaur fauna the Upper Nemegt beds are currently assigned to the lower Maastrichtian. Dinosaur and tortoise skeletons occur at several successive levels along the section (Gradzinski et al., 1968).

In the Ulan Bulak locality, an erosional remnant situated about 10 km northeast of the Naran Bulak Spring in the western part of the basin, the plant remains, mostly scattered stem and leaf impressions of cyperaceous monocotyledons, *Potomageton*-like shoots, lemnoid fruits and occasional *Isoetes*-like sporophylls, occur in a light grey siltstone 1 m thick beneath the lower dinosaur bed about 25 m above the base of the section. The spore-bearing megasporophylls, though detached, could hardly survive long-distance transport. In all probability they represent a small submerged plant constituting a minor element of the Ulan Bulak angiosperm-dominated assemblage of aquatic and semiaquatic herbs.

The preservational features are interesting in themselves for the megaspores, though preserved as casts, still show not only the outer but also the inner SEM discernible structural features. Though not as distinctive as in organically preserved megaspores the incasted structures allow taxonomic assignments thus extending the range of fossil

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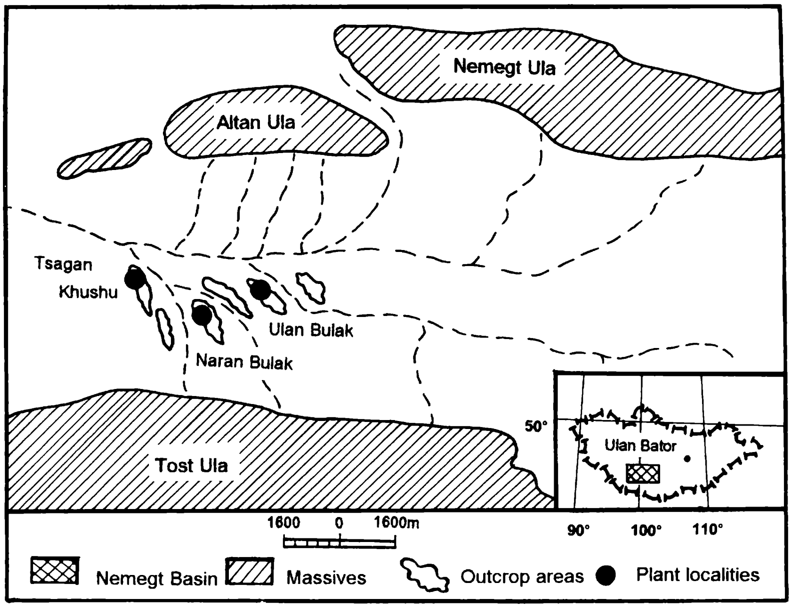


Fig. 1. Location of the study area and plant localities.

material suitable for structural studies. Incidentally, megaspores of the new genus are comparable with certain dispersed spore types of uncertain affinities.

2. Systematic description

MONILITHECA Krassilov et Makulbekov, *gen. nov.*

Type: *Monilitheca minuta*, Krassilov et Makulbekov, *sp. nov.*
Diagnosis: Megasporophylls linear, about 1 mm wide, bearing a single sporangium along the whole length except a short sterile tip. Sporangium filled with tetrahedral megaspore tetrads linearly aligned in a single row. Megaspores trilete, with a membraneous external reticulum over the internal irregular reticulate layer.
Etymology: The generic name refers to the bead-like megaspore alignment.
Discussion: This genus is close to *Isoetes* but differs in the megasporophylls being fertile along their entire length except at the tip and the megaspores being linearly disposed in a single file.

Monilitheca minuta Krassilov et Makulbekov, *sp. nov.*
(Plate I, 1–6; Plate II, 1–4; Plate III, 1–5.

Holotype: No 4135/2-147a, an isolated megasporophyll (Plate I, 1–6; Plate II, 1, 3, 4; Plate III, 1–5).
Paratype: No 4135/2-148, an isolated megasporophyll.

PLATE I

Monilitheca minuta, Krassilov et Makulbekov, *gen. et sp. nov.*
1. Incomplete megaspore tetrad detached from the holotype (3). SEM, ×50.
2. Megaspore, proximal face. SEM, ×100.
3. Megasporophyll, holotype. ×10.
4. Part of the same, arrows on megaspore tetrads, ×12.
5. Megasporophyll, same as in 3 (arrow), on a siltstone slab among the monocot leaf debris. ×1.
6. In situ megaspores, holotype. ×30.

PLATE I

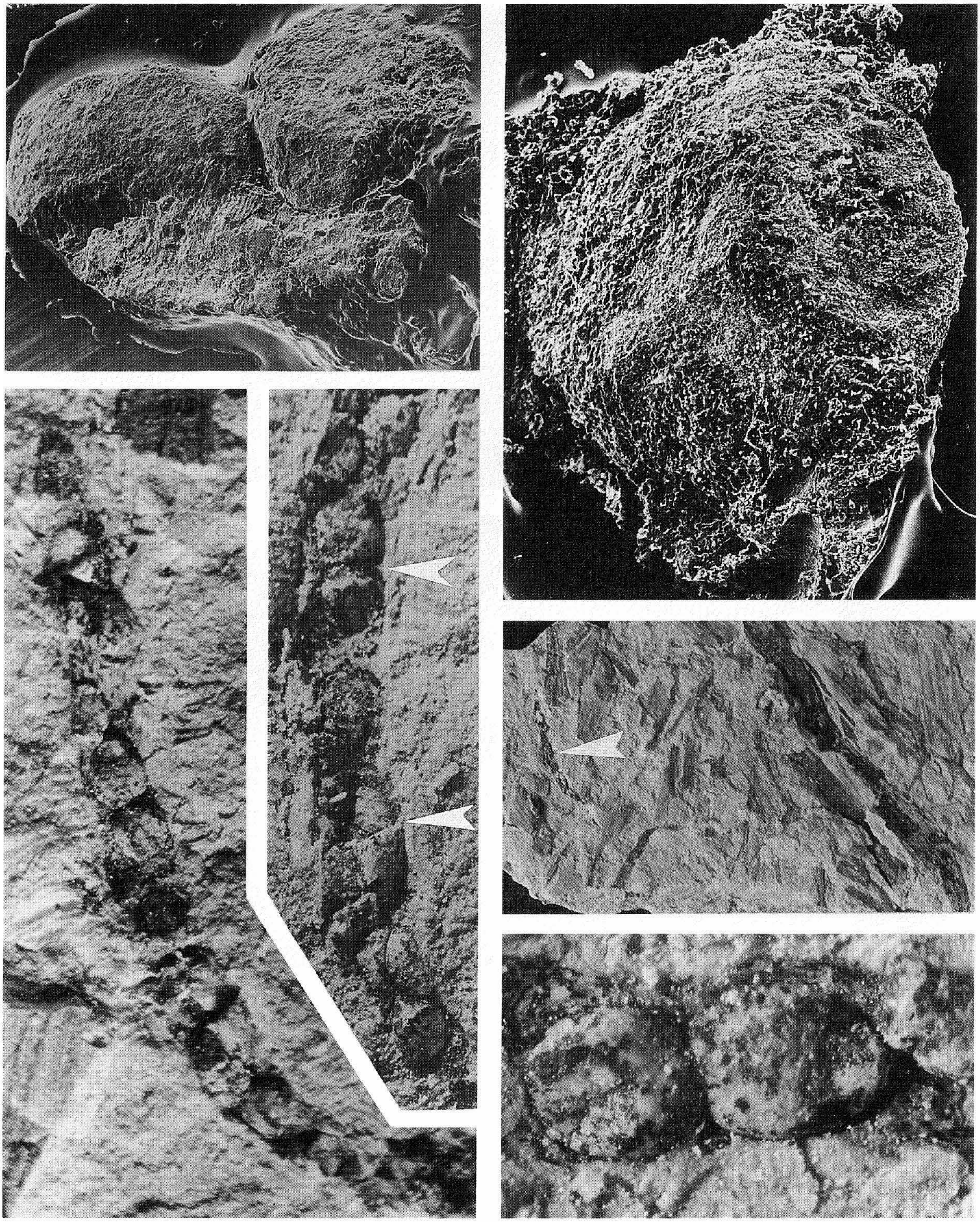
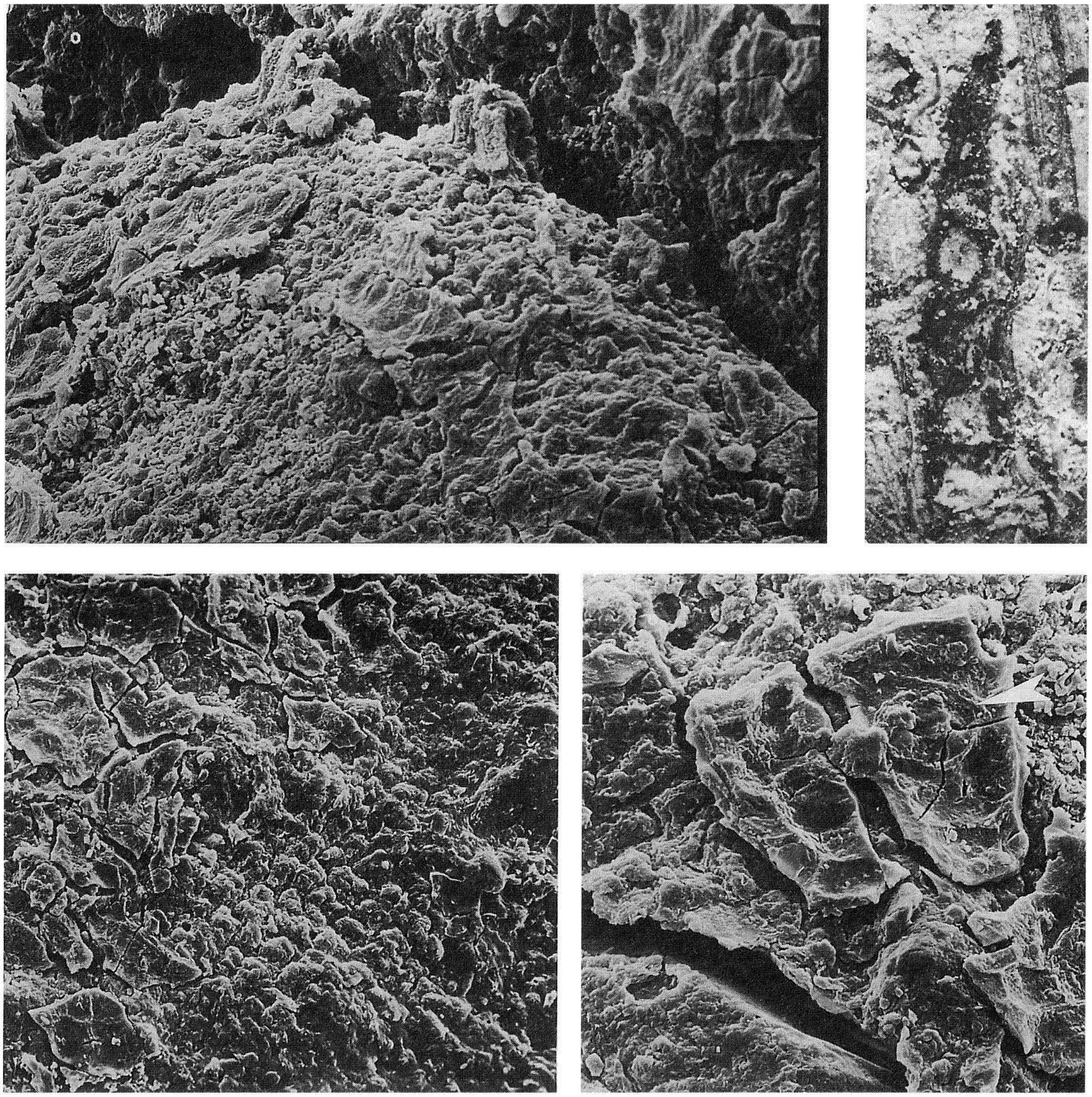


PLATE II



Monilitheca minuta, Krassilov et Makulbekov, *gen. et sp. nov.*

1. Megaspore, distal face showing partly preserved surface reticulum overlaying the interior reticulum. SEM, × 700.
2. Megasporophyll, paratype No 4135/2-148 showing sterile tip. × 8.
3. Megaspore, contact facets showing baculae of the inner sculpture beneath the fragmented outer layer. SEM, × 500.
4. Megaspore, surface reticulum fragments with spine bases (arrow). SEM, × 500.

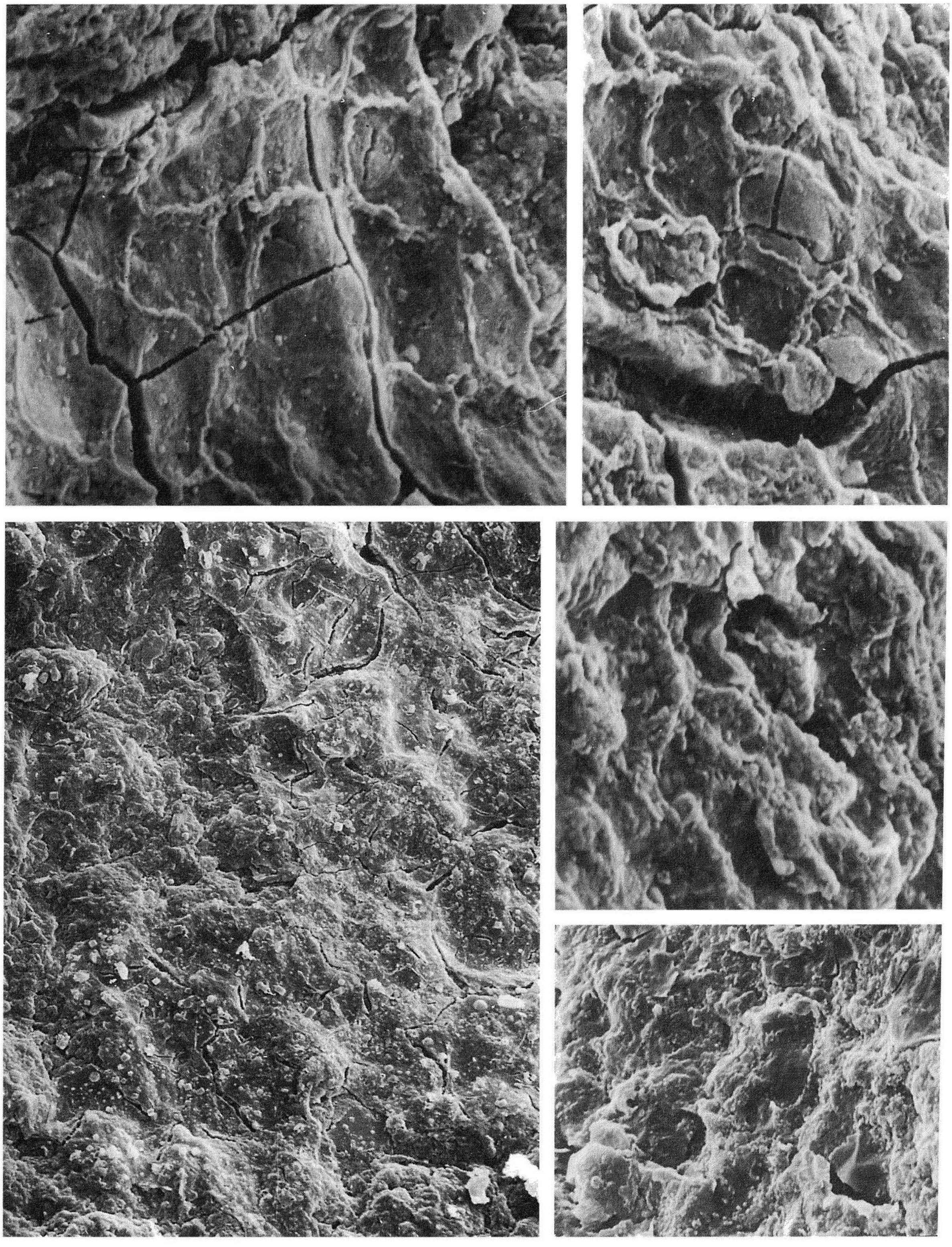
PLATE III

Monilitheca minuta, Krassilov et Makulbekov, *gen. et sp. nov.*

1, 2. Details of surface reticulum. SEM, × 2600.

3–5. Details of internal reticulum. SEM, × 850 (3) and × 1500 (4, 5).

PLATE III



Material: Two isolated megasporophylls with megaspore casts.
Repository: Palaeontological Institute, Moscow.
Type locality: Ulan Bulak, the Nemegt Basin, eastern Gobi, Mongolia.
Stratigraphic horizon: The Upper Nemegt Beds.
Age: Lower Maastrichtian.
Diagnosis: As for the genus.
Etymology: Latin *minutus*, made smaller, referring to small megasporophylls.

Description: Two megasporophyll fragments are preserved on two different slabs of finely laminated siltstone with abundant plant debris. One of them, the holotype, is 18 mm long, 1 mm broad, proximally curved, the base torn off, the sterile apex pointed, 1.5 mm long, the rest of the blade entirely covered with megaspore casts constituting approximately ten tetrads which are aligned in a single row along the sporophyll axis. Another fragment (Plate II, 2) also represents a distal part of sporophyll 9 mm long, 1.1 mm broad, the sterile apex slightly constricted, acuminate, 1.5 mm long. The fertile portion shows eight megaspore casts. Details of sporangial morphology are not discernible in either of the specimens.

An incomplete tetrad and several megaspore casts have been detached from the holotype and mounted for SEM (Plate I, 1, 2). The megaspores are biconvex, their equatorial outline circular or rounded-ovate, diameter ranging from 850 mm to 940 mm, with conspicuous size differences within a tetrad. The laesurae are raised, gently sloping to the contact facets, about 150 mm wide, reaching to the equator. The curvatures are distinctly marked. Two sporoderm layers are preserved: the surface reticulum and the underlying sculptured layer. This kind of preservation might be due to the encasting mineral solution penetrating between the two loosely coupled sporoderm layers, thus forming not only the external, but also the internal replica, the latter showing the inner reticulum.

The outer reticulum is fragmented and lost over much of the spore surface, but the fragments occur on the both proximal and distal faces. The muri are ridged, raised at the corners, forming a perfect network with polygonal or irregular lumina and with spine bases about 20 mm thick (Plate II, 4, Plate III, 1,2). The underlying layer is ornamented with a low reticulum showing more regular rhombic lumina on the distal face (Plate II, 1, and Plate III, 3) while proximally the muri are indented as if consisting of fused bacula, the lumina appearing as irregular cavate depressions (Plate III, 4, 5). Distinct conical or clavate bacula are seen on the contact facets between the rays (Plate II, 3).

3. Discussion

Single large sporangia proximal on linear sporophylls occur in Isoetales and the fossil sporangia rank among the largest, though in the extant *Isoetes* the upper limit is up to 30 mm long. However, our sporophylls differ from *Isoetes*, both fossil and extant, as well as *Stylites*, in being almost entirely fertile, sparing a very short sterile apex alone. Moreover, the spore tetrads are longitudinally aligned in a single row and they seem to have been dispersed with detached sporophylls rather than being liberated from decaying sporophylls as in other genera. Whether the sporophyll shedding in *Monilitheca* was regular (and, perhaps, functional) or occasional is still to be learnt.

The megaspores belong to the *Erlansonisporites–Horstisporites* group of dispersed spores (Infraturma Murornati), having a perfect surface reticulum over the spore body including, or sometimes excluding, the contact facets. In *Erlansonisporites* the external reticulum is diaphanous and readily separable from the spore body revealing the inner surface which shows a trilete mark and is, at least in some species, ornamented with a differently structured internal reticulum. Incidentally, a fairly distinct internal reticulum is illustrated by Taylor and Taylor (1988) in *E. sprassis* from the Lower Cretaceous of Argentina. A less regular inner reticulum of anastomosing rugae was observed through the diaphanous external layer in *E. singhii* from the Maastrichtian of Alberta (Binda and Nambudiri, 1988). Specimens of *Erlansonisporites* striped of their external reticulum might appear not unlike some species of *Horstisporites* and, in fact, an additional form-genus *Kerhartisporites* has been erected by Knobloch (1984) as intermediate between the two.

The external and internal sculptured layers of megaspore sporoderm have been variously termed exo- and mesosporium (Fitting, 1900; Hoeg et al., 1955), perine (Kempf, 1973; Begard, 1978), outer and inner exoexine (Hughes, 1955; Li and Batten, 1986) or layers B and C–D (Taylor and Taylor, 1988), respectively. Kempf has consistently assigned to perine (notably in *Horstisporites semireticulatus*, but also in angiosperm pollen grains) the layers forming sexine or ectexine of the more conventional classifications. Other authors either did not mention perine at all or reserved this term for the tapetal surface deposits, e.g., siliceous incrustation in lycopods or pollenkitt in angiosperms. Morbelli (1995) has reviewed the controversial issue of mesosporium, or mesospore, an inner stratum of the spore wall separable (at least in immature and aborted megaspores) from the exospore proper. She found that in *Selaginella* both layers have a similar ultrastructure supposedly indicating a common origin.

In our material and in a number of figured specimens (e.g., in the *Minerisporites*-like megaspores of the aquatic lycopsid *Limnoniobe*, see Krassilov, 1982, fig. 27) the external membraneous reticulum seems to have been developed irrespectively of the proximal trilete mark haphazardly overlapping the laesurae. This makes it developmentally different from exinal structures traversed and, to various degrees, modified by the trilete, perhaps suggesting a membrane of tapetal origin scarcely homologous to the nonseparable reticulate ornamentation of other megaspore genera.

The megaspores fall in the size range of *Erlansonisporites erlansonii* (Miner, 1932; Kovach and Dilcher, 1988), being much larger than *E. singhii*, *E. alatus*, *E. dubius* and other Cretaceous species typically having a coarser reticulum, with muri extended into thin lamellae, and shorter laesurae relative to spore radius (Potonié, 1956; Binda and Nambudiri, 1988; Knobloch, 1984; Kovach and Dilcher, 1988). *Erlansonisporites spinosus* is similar in having spines in the external reticulum which is, however, lacking on the proximal face (Begard, 1978). *Horstisporites iridodea* is of comparable dimensions but has a much coarser reticulum. This species might have a residual perinal membrane described as an anastomosing network over the proximal reticulum (Taylor and Taylor, 1988). In the much smaller *H. reticuliferus* and *H. cenomanicensis* the surface ornamentation resembles the interior reticulum of the *Monilitheca* megaspores. However, these European species lack any evidence of a membraneous external layer (Knobloch, 1984).

The dispersed *Erlansonisporites*-type megaspores have been thought of as representing plants of sellaginelloid affinities (previously assigned to *Selaginellites*) though Binda and Nambudiri (1988) have extended the comparison to *Isoetes*. Our in situ material, though not assignable to any of the species for dispersed megaspores, nonetheless gives a definite evidence in favour of the Isoetalean affinities of the group.

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