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A new heterosporous plant from the Cretaceous of West Siberia

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Abstract

A heterosporous free-sporing plant is described from the Upper Cretaceous of the Kem' River, West Siberia. The plant produced pinnate sporophylls with pinnules bearing a large solitary sporangium containing megaspores and microspores. The megaspores are numerous, in tetrahedral tetrads, with membranous laesural flanges forming an apical neck and the lateral pockets filled with monolete microspores. The plant represents a distinct line in the evolution of heterosporous pteridophytes with amphisporous sporangia retaining a great number of megaspores and developing an elaborate mechanism of joint dispersal of megaspores and microspores.

Keywords: plant morphology; evolution; heterospory; megaspores; Cretaceous

1. Introduction

We recently found in a collection of the Late Cretaceous plants from West Siberia what appears to be a new group of heterosporous plants, with megaspores and microspores mixed in a sporangiate structure. The material comes from an outcrop of sandstones and claystones of the Kemskaya Formation at the Kem' River 15 km downstream from the village Podgornaya in the Yenisey River Basin. Based on palaeofloristic evidence and correlation with marine deposits further north, the probable age of the Kemskaya Formation is Cenomanian (Lebedev, 1958). The collection is deposited in the Botanical Institute, St-Petersburg, No. 1198.

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2. Material

Five sporophyll fragments are preserved as impressions of thin axes bearing lateral pinnules with compressed spore masses. Most fragments are irregularly twisted at an angle to the bedding plane of a light brown claystone which also contains angiosperm leaf impressions. The sporophylls consist of an axis bearing lateral pinnules (Plate I, 1). The axis is more than 20 mm long (complete length unknown), 0.6–0.8 mm thick, slightly expanded at the pinnule nodes, straight, longitudinally grooved and with irregular striations. Only one pair of pinnules is preserved on each of the axes. The pinnules arise at about 45° to the axis, opposite or alternate, attached by a decurrent petiole 1.5–2 mm long (Plate II, 1). The blade is elliptical, 8–15 mm long, 6–9 mm broad, narrowly rounded at the apex, thick, flat, with raised marginal flanges. The venation is rather coarse, with the midrib extending to the apex and

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with six to seven pairs of lateral veins (Plate I, 2; Plate II, 3). The latter are opposite, rarely alternate, arising at about 45° to the midrib, slightly arcuate and reaching to the inner border of, but not extending to, the marginal flange. The ends of the lateral veins are slightly swollen. Occasional lateral veins fork near their point of departure. In a few impressions showing fine details, an irregular network of a higher order venation is discernible at greater magnification (Plate II, 2). A few pinnules are folded along the midrib, but this could be a preservational feature.

Each pinnule bears adaxially a thick solid spore mass of elliptical shape occupying all of the surface except the marginal flange (Plate I, 3, 4). No partitions, except irregular cracks, are discernible in the spore mass under magnifications of dissecting microscope. Parts of spore masses about 2–3 mm long from three sporophyll pinnules were removed from the rock with thin needles, washed in distilled water and mounted for SEM without any chemical treatment. As seen in SEM, the spores are compressed in a uniform mass showing neither interior sterile tissue nor any patterns preserved as distinct spore groups. It was, therefore, concluded that the spore mass represents a single sporangium.

When the sporangium is destroyed, which is often the case, the pinnules are strewn with spores and are pitted by their impressions on the incrusting film. The spores are of two distinct size categories which are also morphologically different obviously representing mega- and microspores. Each spore mass contains several hundred megaspores (Plate I, 5), some of them still in discernible tetrahedral tetrads (Plate III, 3; Plate IV, 3). The microspores are scattered between the megaspores or are contained in the laesural pockets of the latter (see below).

The megaspore tetrads easily fall apart and only few of them were extracted intact (Plate III, 2). The megaspores of a tetrad are equally developed. They are subspherical-prolate, rounded-triangular in equatorial view, triangular with projecting corners in side view, with the distal face broadly rounded, convex or occasionally concave, the contact facets slightly convex and the proximal face conical, extended into a 'neck' (Plate IV, 1, 2). The latter is dome-shaped, of a variable length, sometimes only slightly shorter than the polar axis of the body, three-lobed, apically thickened. The laesurae extend over about 3/4 distance to the equator. Their membranous flanges form two series of tubular extensions, or 'pockets' with an angular or elliptical mouth (Plate II, 4; Plate III, 1). The megaspore body between the laesurae is ornamented with a reticulum of irregular-polygonal lumina and with thick straight muri that are slightly raised at the corners. Close to the laesurae, the cells of the reticulum are stretched in the direction of and are connected to the membranous flange. The latter is irregularly folded and with minute perforations.

The megaspore dimensions: equatorial diameter 75–80 μm, polar axis of the body without neck about 70 μm, neck 40–65 μm high, laesural pockets 25–30 μm high, their mouths 25–35 μm wide, lumina of the reticulum 5–6 μm wide in the middle of the contact facets, stretched to 10–15 μm at their contacts with the laesural flanges.

The microspores are commonly found in the tubular lobes of the neck and in the laesural pockets, typically a few per pocket, emerging from the mouth, occasionally in clumped masses transpiring through the closed membranes or seen through the mouth (Plate V, 1–3). Those stuck to megaspore reticulum were apparently shed from the laesural pockets.

PLATE I

New heterosporous plant from the Upper Cretaceous of the Kem' River, West Siberia.

1. Sporophyll axis with a pair of opposite pinnules. ×4.5.
2. Pinule slightly folded along the midrib. ×12.
3. Pinnule bearing intact sporangium. ×12.
4. Sporangium enlarged (arcuate lines are cracks). ×20.
5. Spore content of sporangium, SEM. ×60.

PLATE II (see page 78)

New heterosporous plant from the Upper Cretaceous of the Kem' River, West Siberia.

1, 2. Pinnules showing lateral veins. ×9.
3. Details of venation. ×15.
4. Megaspore, lateral view facing a laesura with membranous pockets, SEM. ×700.

PLATE III (see page 79)

New heterosporous plant from the Upper Cretaceous of the Kem' River, West Siberia, SEM.

1. Megaspore with three laesurae visible. ×700.
2. Megaspore tetrad. ×400.
3. Mass of megaspores. ×150.

PLATE I

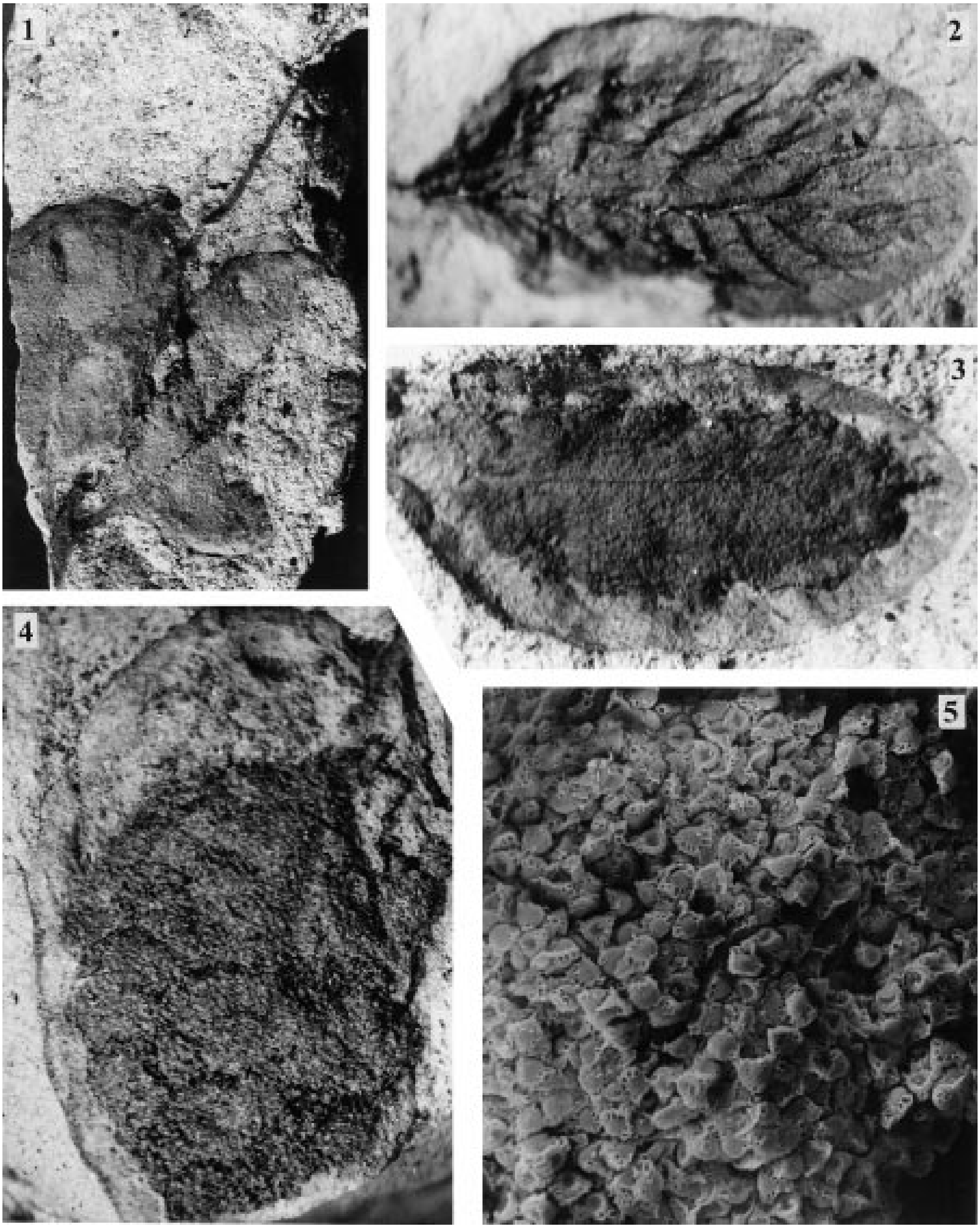
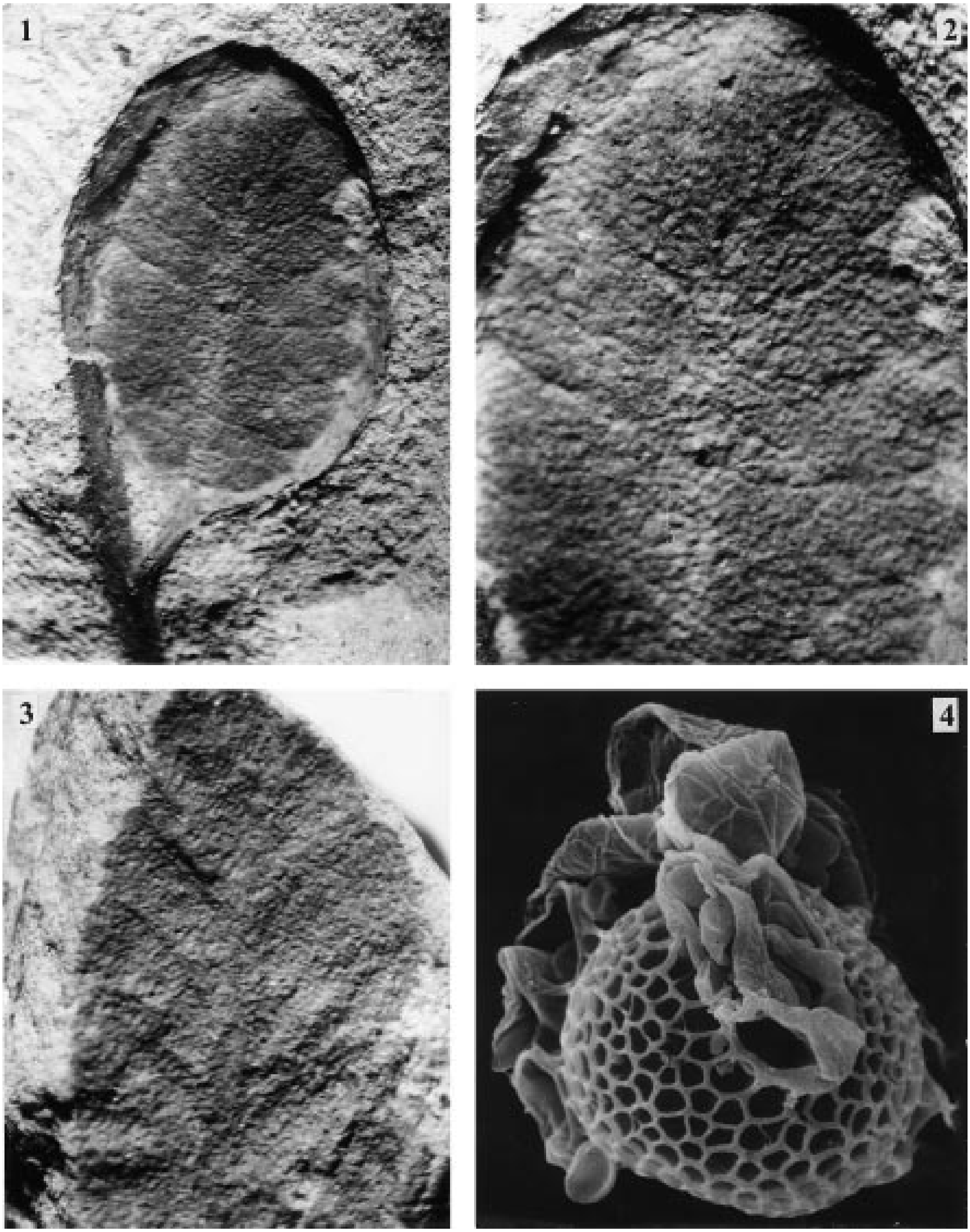
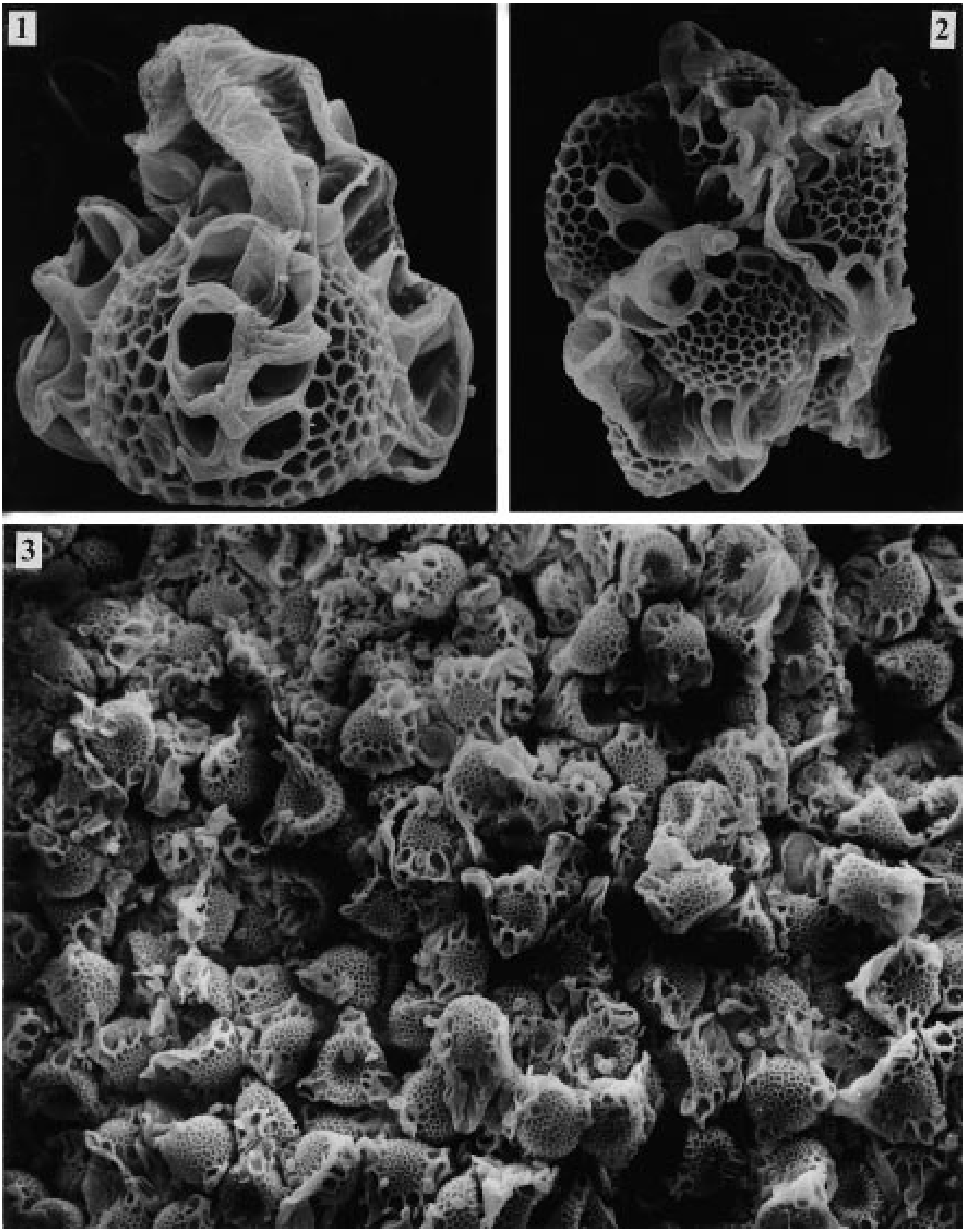


PLATE II



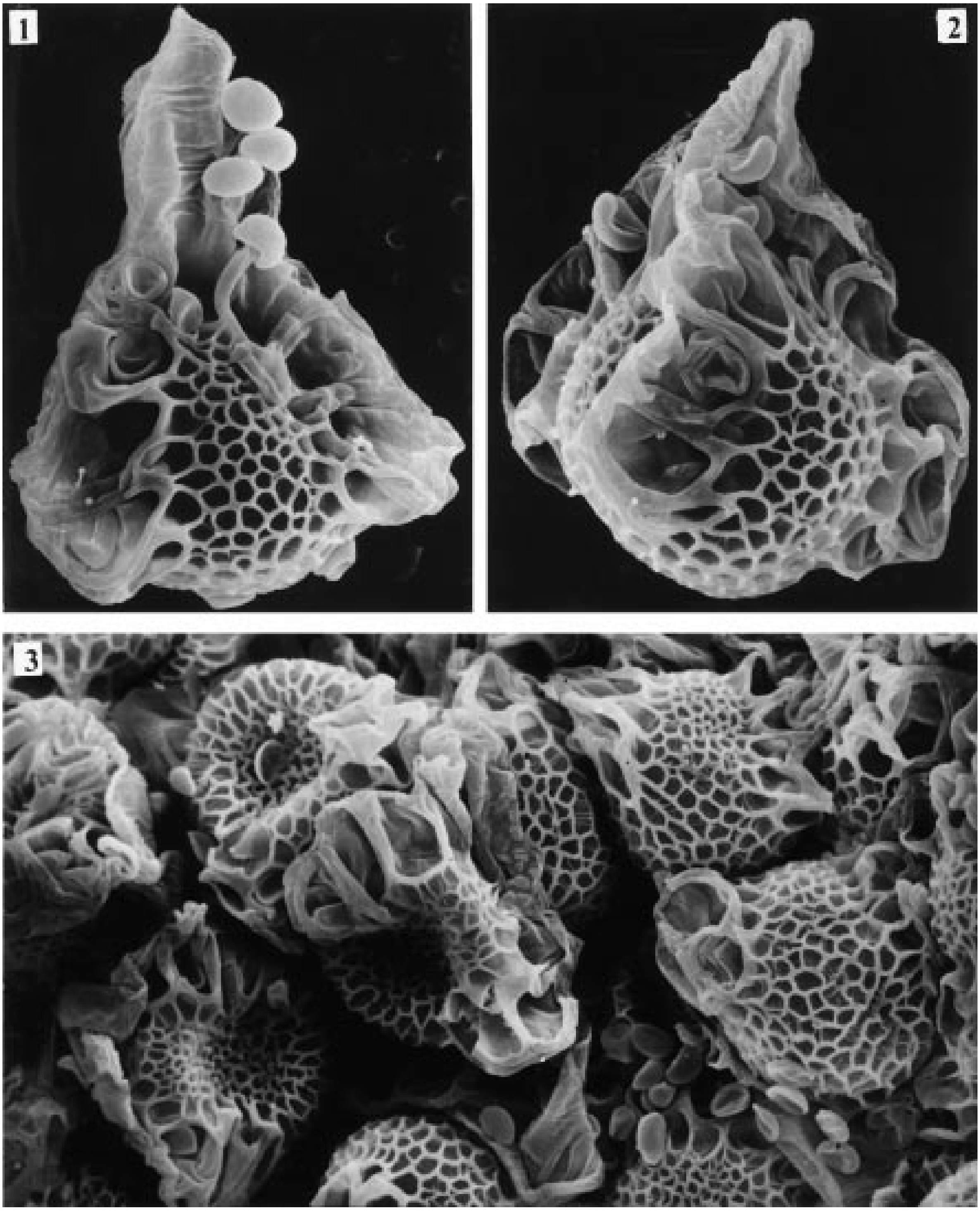
For description see p. 76.

PLATE III



For description see p. 76.

PLATE IV



The microspores are elliptical to rounded-elliptical in equatorial view, bean-shaped with rounded ends in side view, 12–17 μm long, 10–13 μm wide, proximally slightly concave, with a single laesura slightly shorter than the long axis, slit-like or occasionally open, with the ends, or one end only, bifid, but usually onlapped by exinal folds (Plate V, 4). Occasional microspores are split into halves along the equator. The exine is irregularly folded with the folds occasionally appearing as an Y-mark, but none of the observed microspores is convincingly trilete. The exinal sculpture is rugulate-microreticulate with irregular lumina (Plate V, 4).

3. Discussion

Our material is unusual in showing amphisporous sporangia with spores of two widely different dimensional and morphological categories. The megaspores are numerous and they have special laesural outgrowths that contain microspores. Such associations are regular and they can hardly be explained as a preservational feature. It seems beyond reasonable doubt that megaspores and microspores were produced in the same sporangial structure. A possibility of a heterosporangial synangium containing both mega- and microsporangia that were resorbed at an early developmental stage, their spore contents being mixed in a uniform mass, cannot be ruled out. This is unlikely, however, for in the known cases of dissolved sporangial walls, their spore contents retain the sporangial shape and the intimate association of spores from different sporangia does not take place (e.g., Chitaley and Paradkar, 1972). Rather this kind of association can be explained by a diachronous development of megaspores and microspores. This suggestion agrees with their dissimilar tetrad configuration–multiplanar (tetrahedral) in the megaspores vs. presumably uniplanar (producing monolete grains) in the microspores. The flanges of developing megaspores might penetrate the mass of microsporocytes that were caught inside the tubular laesural outgrowths where they then underwent meiotic divisions. This mechanism might provide for attachment of the mega- and microgametophytes after dispersal of the megaspore–microspore complexes.

Among water ferns, the salviniacean genera produce superficial sori, typically homosporangial, with a few exceptions, while in the Marsiliaceae the sori are born in the spherical sporocarps. However, *Rhodeites*, a fossil genus from the Lower Palaeocene Intertrappean beds of Mohgaon–Kalan, India, has pinnule-like sporocarps with sori containing both megasporangia and microsporangia. The megasporangia are preserved as a thin film surrounding a single megaspore. The microsporangia are much more numerous, discernible as distinct spore masses even when the sporangial wall is destroyed (Chitaley and Paradkar, 1972, 1973). This situation is quite different from what we observed in our Cretaceous form with numerous megaspore tetrads, the microspores typically born in the laesural pockets of megaspores. Both mega- and microspores are trilete in *Rhodeites*, the former showing an ‘aspidote aperture’ and compared with a dispersed spore genus *Arcellites*.

Widespread in the Cretaceous are megaspores with long necks, such as *Arcellites* Miner emend. Ellis et Tschudy, a genus of formal classification for dispersed spores (Miner, 1935; Ellis and Tschudy, 1964). In *Arcellites*, a well developed proximal neck typically consists of three to six lobes or ‘leaflets’ developed over a short triradiate mark. In *A. incipiens* Singh from the Lower Cretaceous of Alberta (Singh, 1964), the megaspore body bears pocket-like tubular structures, but these are not related to laesurae. Microspores attached to the neck were described by Ellis and Tschudy (1964) from the Lower Cretaceous of North America and then by Li and Batten (1986) from the Upper Cretaceous of Inner Mongolia. These microspores were assigned to *Perotrilites* and *Crybelosporites* respectively. Ellis and Tschudy suggested that the megaspores floated necks downwards entrapping dispersed microspores between gelatinous ‘leaflets’. Hughes (1955), who described this type of megaspore under the name *Pyrobolospora* Hughes, later synonymized to *Arcellites*, compared them with

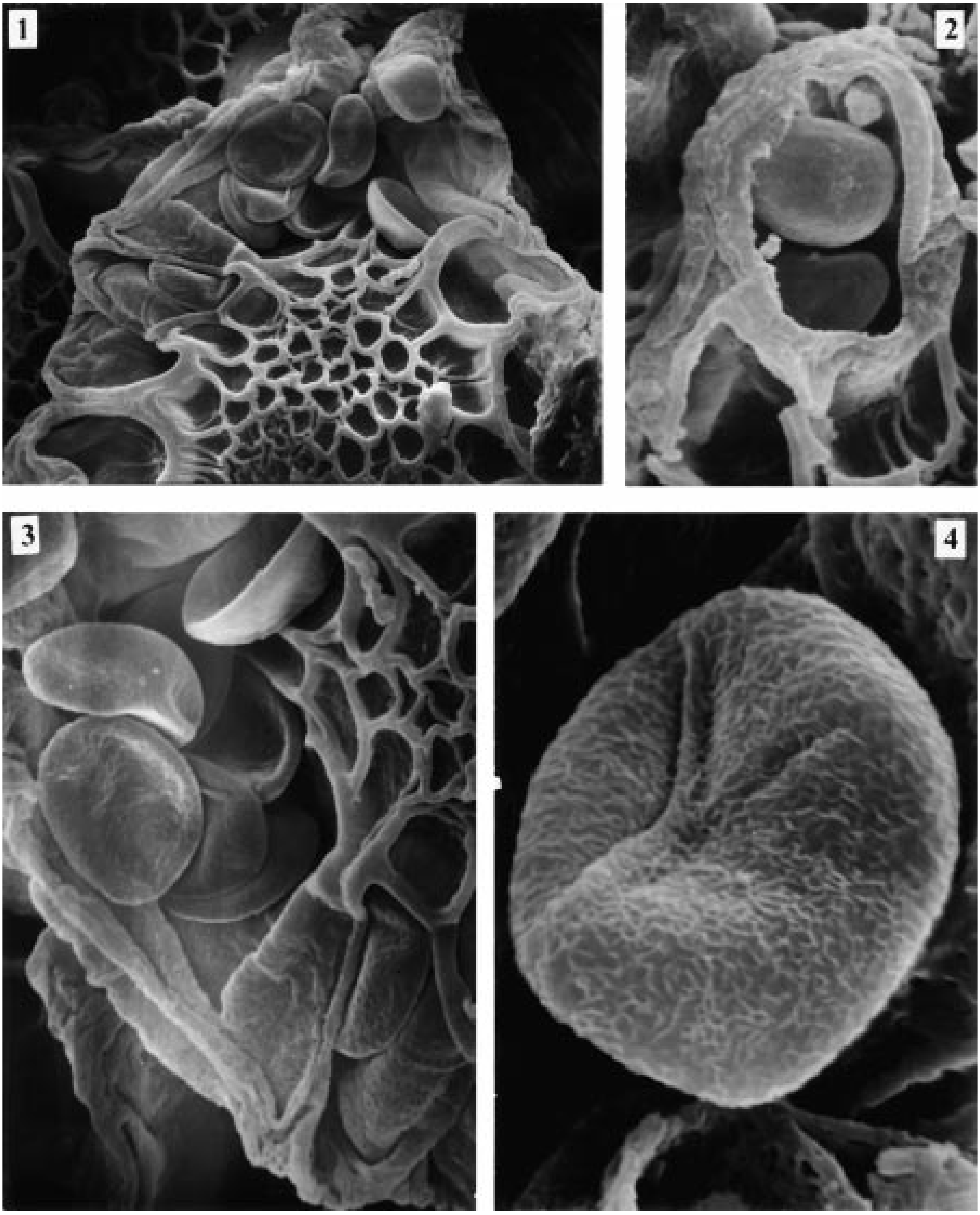
PLATE IV

New heterosporous plant from the Upper Cretaceous of the Kem’ River, West Siberia, SEM.

1, 2. Variations of neck and lateral laesural outgrowths. ×700.

3. Megaspores and microspores inside sporangium, a tetrad is visible in central part. ×500.

PLATE V



Kryshtofovichia which, in his opinion, could be a *Lagenicula*.

Actually, despite an enormous time gap between them, *Kryshtofovichia* and *Arcellites* are quite similar. A related spore genus *Balmeisporites*, a Cretaceous Southern Hemisphere form (Baldoni and Batten, 1991) shows deeply invaginated lumina of triradiate acrolamellae resembling the laesural pockets of our Siberian form. Microspores were not reported in association with this genus.

Megaspores found in sporangia of the heterosporous plant from West Siberia belong to the same morphological group being most similar to *Balmeisporites* while differing from both *Kryshtofovichia* and *Arcellites* in having much longer triradiate acrolamellae extending beyond the neck and bearing the membranous 'pockets'. Here microspores were caught in the neck and pockets before dispersal which might also be the case in *Arcellites*.

Batten et al. (1996) suggested a marsilialean affinity for *Arcellites* perhaps representing an extinct family. Earlier a similar conclusion has been reached by Chitaley and Paradkar (1973) for *Rhodeites*, once compared with *Regnellidium*, an extant Brasilian genus of water ferns. *Kryshtofovichia*, predating the appearance of water ferns by at least 200 m.y., might have been produced by a heterosporous early vascular plant. It was compared to *Lagenicula*, a widespread morphotype of gulate Carboniferous megaspores produced by lepidodendralean lycopsids. In the typical Carboniferous *Lagenicula*, the proximal neck is thought to be a float or an anchoring structure (Zerndt, 1934) unrelated to microspores.

Bisexual (amphisporous) sporangia are totally lacking in the Mesozoic to extant plants, but they occur in the Devonian Barinophytales and occasionally in the roughly contemporaneous Archaeopteridales. Both groups are leafless with sporangia in two rows on ultimate fertile branchlets. In the better studied *Barinophyton citrulliforme* (Brauer, 1980), the sporangia contain about 30 large megaspores that are immersed in the mass of several thousands of microspores. Both megaspores and microspores are trilete. The heterosporous archaeopterids are mostly heterosporangial, but amphisporous sporangia are described in *Chaleueria* and in a single species of *Archaeopteris* (Medyanik, 1982). No special megaspore–microspore complexes were ever found. However, such complexes might occur in the Devonian plants represented by *Kryshtofovichia*, the dispersed megaspores bearing microspores in the extensively developed apical three-lobed gula that was originally described as 'androcamera' (Nikitin, 1934). Here also the megaspores are trilete whereas the microspores are monolete.

As for the systematic position of the Siberian plant, the morphology of sporangiferous pinnules with pinnate venation suggest a water fern affinity. However, in water ferns, sporangia arise in sori that could be heterosporangial but never contain amphisporous sporangia. Moreover, the morphology of a single adaxial sporangium is more like that of lycopsids than water ferns. The megaspore morphology finds analogies both in water ferns and lycopsids. In particular, *Lagenicula* represents a similar, although geologically much older, morphotype. However, *Lagenicula* is typically produced in megasporangia as a solitary functional megaspore, with the remaining members of a tetrad aborted. The situation in barynophytes is more similar to that of the Cretaceous group, although here also the ratio of microspores to megaspores per sporangium suggests a numerical reduction of the latter.

The barynophytes belong to an early evolutionary stage of heterospory involving forms with amphisporous sporangia as well as those with morphologically similar but functionally differentiated microsporangia and megasporangia, as in the heterosporous archaeopterids. Later, the amphisporous line seemed to disappear while in several heterosporangial lines the two kinds of sporangia underwent a morphological divergence, with megaspores reduced to few or one per megasporangium.

Our material suggests a resurrection of the amphisporous line, although direct phylogenetic links with barynophytes or other progymnosperms seem

PLATE V

New heterosporous plant from the Upper Cretaceous of the Kem' River, West Siberia, SEM.

1, 2. A series of megaspore laesural pockets filled with microspores. ×1100 and 1800.

3. Two microspores at the mouth of a laesural pocket. ×1800.

4. Microspore showing reticulate surface sculpture. ×6000.

unlikely in view of an enormous time gap. Moreover, in the Cretaceous plant, the megaspores are produced in unprecedented quantities and are bearing microspores in the elaborate flange structures of their Y-mark laesurae. Abundant relatively small megaspores, as well as a close association of the latter with microspores would be advantageous for a colonizing species. We consider this plant as representing a special line in the evolution of heterospory, appearing at the time of an adaptive radiation burst in the vascular aquatic plants.

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