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# AN ANGIOSPERM CRADLE COMMUNITY AND NEW PROANGIOSPERM TAXA

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ABSTRACT. A few leaves and pollen grains from the Baisa locality in the upper reaches of the Vitim river, Transbaikalia, are recognized as angiospermous. This locality also yielded eight species that are considered proangiospermous, including the derived forms of gnetophytes, bennettites and cycadophytes. The Baisian assemblage is, thus, an example of an arogenic, or type-making, community that gave rise to several lineages trending towards angiosperm morphology. On the basis of ostracod zonation this assemblage is assigned to the Hauterivian or early Barremian. Most proangiosperm remains came from an open wetland vegetation that replaced the typical Mesozoic fern marshes. With the elimination of the latter a new type of wetland community was formed by the ecological expansion of preadapted gymnosperm groups developing new (partly herbaceous) growth forms in which proangiospermous characters appeared in the process. The vegetational change correlates with extensive rifting and basaltic volcanism. Mats of aquatic insects covering bedding planes indicate mass mortality perhaps related to sharp pH fluctuations that might also have affected the wetland plant community. Plant – insect interactions, as evidenced by pollen grains from the gut contents of fossil insects, may have played a significant role in proangiosperm evolution. A new species of *Eoantha* and four new genera are described, including a bisexual pre-flower *Preflosella nathania* gen. et sp. nov.

KEY WORDS: angiosperm origins, proangiosperms, morphological evolution, palaeoecology, Early Cretaceous

## INTRODUCTION

This paper reports on new finds of peculiar proangiospermous plants from the Baisa locality in the upper reaches of the Vitim river, Transbaikalia. The locality became famous due primarily to its extremely rich insect fauna, whereas the plant material seemed less promising. However Vachrameev and Kotova (1977) have reported, amid typical Mesozoic forms, a single angiosperm-like leaf, *Dicotylophyllum pusillum* Vachr., and a few *Clavatipollenites*-type pollen grains. These finds were repeated in our collecting trips to Baisa in 1979–1998. We also paid attention to some previously neglected, though numerous, fruit-like disseminules that were described as *Baisia*, our first proangiosperm find (Krassilov & Bugdaeva 1982). This was followed by *Eoantha*, a reproductive structure with transitional gnetophyte – angiosperm characters (Krassilov 1986). The 1996 entomological expedition brought additional specimens of *Eoantha* and associated vegetative parts, together with *Baisianthus* and *Vitimantha*, new genera of gnetophyte affinity based on reproductive structures (Krassilov 1997, Krassilov & Bugdaeva 1999). Three more genera are described below. The list of peculiar proangiospermous forms lengthened with each visit to the locality. At present they outnumber the conventional Early Cretaceous species, with a good prospect of further finds. With the accumulation of data it became clear that we are dealing with an evolutionary, innovative (arogenic) plant community. Putative environmental enhancers of morphological evolution are discussed later in the paper.

## PHYTOGEOGRAPHY AND ENVIRONMENTAL EVENTS

As the origin of angiosperms was a major event of the Early Cretaceous floristic evolution, the fossil floras of that age are looked upon as the possible cradle of this most successful group of vascular plants. A familiar *Ruffordia – Onychiopsis – Weichselia* (ROW) flora is known from the Wealden of Europe, as well as from North America and eastern Asia, including the roughly contemporaneous localities of Primirye (Russian Far East), Japan, eastern China and extending also to India. In terms of fossil plant abundance these localities represent fern assemblages with diverse bennettites and brachyphyllous conifers (or, more correctly, coniferoids, for some brachyphylls might belong to gnetalean plants, see Krassilov 1982a). The classic Wealden flora, mostly of Berriassian age (Watson & Kenneth 1996), lacks any angiosperm or angiosperm-like macrofossils (*Belhavstia,* described as a pre-angiosperm, is a thalloid form of dubious affinities, most probably a bryophyte). In Primorye the general aspect of the flora scarcely changed from the Berriassian to the Aptian when angiosperms first appeared as rare, though fully developed, forms lacking any indigenous precursors (Krassilov 1967). In eastern China they appeared somewhat earlier (Sun *et al.* 1993), but also as occasional invaders of persistent plant assemblages.

The Early Cretaceous floras of Siberia are also dominated by ferns, but with *Onychiopsis* replaced by *Dicksonia*. Most of the gymnosperms of these floras were deciduous, shedding their leafy spur-shoots, as well as their catkin-like strobili. Prominent among them were the Czekanowskiales (Leptostrobales) with bivalved many-seeded cupules and the Dirhopalostachyales with paired one-seeded cupules. These plants prompted the idea of Mesozoic proangiosperms (Krassilov 1975). However, reliable angiosperm records are lacking from Siberian floras until the Albian.

A quite different type of Early Cretaceous flora is represented by the fossil plant assemblages of Transbaikalia, Mongolia and northern China. This broad ecotonal area between the temperate *Phoenicopsis* and tropical to subtropical *Cycadoidea* zones (Krassilov 1972a) had a Siberian-type Jurassic flora with widespread fern assemblages. A major vegetational change occurred there at about the Jurassic/Cretaceous boundary. Along with the partial replacement of *Phoenicopsis* assemblages by *Cycadeoidea* assemblages, ferns became rare in comparison with the Jurassic floras of the same area (Krassilov 1982b). This apparently quantitative difference might signify a major restructuring of the wetland plant communities. The Mesozoic fern-beds were formed of fossil fern leaf mats representing a distinctive type of open wetland vegetation – the extensive coastal plain to riparian fern marshes (Krassilov 1972b: an alternative interpretation of the fern-beds as representing a "fern-savanna" is unlikely, for savanna is a xeric type of grassland with extremely xeromorphic arboreal components while the Mesozoic fern assemblages were helophytic, mostly recorded from coal measures). A sharp decrease of fern remains might then indicate a decline of the fern-marshes.

In the ecotonal area of central Asia the Jurassic/Cretaceous vegetational change was more abrupt than in both the *Phoenicopsis* and *Cycadeoidea* realms where floristic evolution across the boundary was rather gradual, with a few replacements at species level. It is only to be expected that climatic changes would have had a more profound impact on ecotonal communities than over the interior areas of vegetation zones. However, in Transbaikalia and Mongolia, the vegetational change correlates not only with a climatic change, but also with an extensive rifting and basaltic volcanism forming a major basaltic province comparable to the roughly contemporaneous basaltic provinces of the South Atlantic margins (a promising, yet insufficiently studied, area of floristic innovation). New landscapes appeared, with rift valleys and stratified lakes in which thick black shale sequences were deposited.

The bituminous black shale belt extended from Transbaikalia to the Yanji Basin in eastern China. The spatial and temporal correlation of black shale deposition with vegetational change suggests that both phenomena were related to intracontinental rifting and associated environmental events. The black shale facies required a high biotic productivity that was compensated by a rapid deposition of organic material rendering the surface waters oligotrophic. Such lacustrine ecosystems may have arisen through the acidification of water bodies by igneous bedrocks and volcanic surroundings and an insignificant influx of terrestrial material. Both factors seem causally related since a decrease of terrestrial influx might result from the demise of fern wetlands by acidification of the waterlogged soil. A new type of wetland, more tolerant of soil acidity, developed with morphological innovations arising in the process.

## THE BAISIAN ASSEMBLAGE

One such sequence outcrops on the left bank of the Vitim river near the mouth of Baisa brook giving name to a rich locality of lacustrine fauna mixed with terrestrial plant and insect remains. In the Baisa section, the granitic bedrock is overlain by conglomerates and coarse sandstones followed by thick black shales topped by several cyclothems of alternating sandstones, shales and marls. An ostracod species *Mongolianella kizhingensis* Scoblo, found in the lower part of the Baisa section, indicates Valanginian age, while the overlying ostracod assemblages of the main fossil beds are of the Hauterivian – early Barremian age (Skoblo & Lyamina 1986). Most plant remains came from two marl beds in the upper part of the section. The marls show a varve-like alternation of dark and light lamellae that indicate a seasonal climate, with a periodic massive influx of clastic material. They are covered with fossil mats formed of amassed larvae of mayflies, dragonflies, aquatic beetles and chironomids.

Since carbonate sedimentation requires neutral water chemistry and black shales would have been deposited in an acidic environment, their alternation must have been accompanied by the respective pH changes. The sequence of sedimentary events may conceivably have been related to pH fluctuations in the following way. During a black shale phase, organic deposition would have gradually increased pH to neutral. A carbonate phase would have then followed. The relatively frequent plant remains in the marl beds suggest an increased terrestrial influx from the expanding wetlands. Then a drop of pH at the next marl/shale transition may have caused a mass mortality of aquatic organisms sensitive to acidification as well as the simultaneous reduction of the wetland communities. Such cyclic environmental changes may well have enhanced morphological evolution.

The terrestrial insects found with proangiospermous plants often contain pollen masses in their gut, indicating widespread pollen-feeding that may have played a role in the morphological evolution of the source plants. Incidentally, the pollen grains of *Preflosella*, a bisexual flower-like structure, where found in the gut of two xyelid species (Krassilov & Rasnitsyn 1982) before the plant itself was discovered.

The marl bed fossil plant assemblages are dominated by the conifers *Podozamites* (shoots, leaves, *Swedenborgia*-type cone scales), *Elatides* (leafy shoots with seed-cones), and *Pseudolarix* (mostly cone scales, occasional spur-shoots), the last probably representing a slope vegetation. Less common are the coniferoids with *Brachyphyllum*-type shoots, the bennettitalean leaves of *Nilssoniopteris* and *Otozamites*, forked leaves of *Czekanowkia* and fragmentary fern pinnules. The rest of the assemblage contains eight species of peculiar plant provisionally assigned to the proangiosperms. With the single exception of *Loricanthus resinifer* gen. et sp. nov., a massive resiniferous pollen-cone of a larger, probably woody plant, they are small, inconspicuous, though sometimes fairly common, fossils, such as *Baisia hirsuta* Krassilov, (a comose one-seeded cupule), *Baisianthus ramosus* Krassilov et Bugdaeva (slender shoots bearing whorls of cupulate sporangiophores), *Eoantha zherikhinii* Krassilov (flower-like ovular structures and their associated graminoid leaves), *Praeherba spathulata* Krassilov et Bugdaeva and a second *Eoantha* species, *E. ornata* sp. nov. Their preservation suggests their proximity to the site of deposition. *Vitimantha crypta* Krassilov et Bugdaeva and *Preflosella nathania* gen. et sp. nov., though less common, are fragile flower-like structures that would not withstand long-distance transportation intact. Their source plants may have belonged to a single assemblage of supposedly herbaceous species forming a new type of wetland community which replaced the Jurassic fern wetlands.

## MATERIAL AND METHODS

The material is represented by light brown ferrugineous impressions with fragmentary compression remains preserved in light-grey marls. The impressions are actually incrustations or subcrustations (with the encrusting material deposited beneath the cuticle, hence reflecting the inner surface of the latter, see Krassilov & Makulbekov 1996). Small fragments of impressions were mounted for SEM to reveal microstructural features. The compressions were transferred to cellulose film by dissolving the matrix in nitric acid followed by fluoric acid and alkali or, if clear enough, without the last. The transfer preparations were then studied and photographed with the Amphioplan light microscope and Camscan SEM.

## SYSTEMATIC DESCRIPTION

The fossil plant material described in this paper came from the Baisa locality in the upper reaches of the Vitim river, Transbaikalia, fossil plant beds 11 and 31. The collection is deposited in the Palaeontological Museum, Moscow, No 4745.

### GENUS *EOANTHA* KRASSILOV 1986

#### ***Eoantha ornata*** Krassilov sp. nov.

Pl. 1, fig. 4

Name. Refers to the ornate appendages of the cupule.

Holotype. No 4745/31-1 (Pl. 1, fig. 4).

Diagnosis. Ovuliferous cupule lobed, shortly stalked, ellipsoidal, 5 mm long, 4 mm broad, with bracteal beaks spreading distally from each lobe. Ovules solitary per lobe, erect, elongate-elliptical, thickly cutinized.

Description. This species is based on a single impression of a longitudinally split cupule showing two lateral lobes in the bedding plane. Two large erect ovules, one per lobe, are prominent due to their thick shining cuticles. Two slightly asymmetrical horns or beaks, 6 mm and 4 mm long, spread distally from the backs of the lobes. The third beak along the midline belongs to a buried lobe of the median pair, the fourth one evidently split from the bedding plane. The beaks appear rigid, about 1 mm thick at the base, tapering to an acute apex, longitudinally grooved.

Remarks. Unlike the type species *Eoantha zherikhinii* (Krassilov 1986), which possesses a flower-like structure with a four-lobed ovuliferous cupule supported by a perianth of many free linear bracts, the new species lacks a free perianth. However, since the beaks of the new cupule are similar to the perianth bracts of *E. zherikhinii*, they are here considered as the free tips of perianth bracts basally fused to the cupule. Thus *E. ornata* is essentially of the same structure as the type species, but with the perianth bracts reduced to two decussate pairs adnate to the lobes.

Material. The holotype.

## GENUS *PROGNETELLA* KRASSILOV ET BUGDAEVA GEN. NOV.

Name. Referring to gnetophytes.

Type species. *Prognetella minuta* sp. nov.

Diagnosis. Inflorescence several times branched, with the penultimate branches spicate, bearing ovular spikelets in whorls on slender axes. Whorls proximally widely spaced, apically crowded, subtended by long pendent bracts. Spikelets of one to several bracteolate ovules. Bracts linear, with two veins. Axial and bracteal vascular bundles of spiral tracheids and reticulate vessels with scalariform-reticulate perforation plates. Ovules vascularized by spiral tracheids.

Remarks. Ovular spikes of the new genus are essentially like those of the extant *Ephedra*, but the inflorescence structure appears at least one order of branching more complex and the very long flexible bracts are unusual for the extant genus. This distinction also sets *Prognetella* apart from *Baisianthus*, a pollen organ from the same locality. *Drewria potomacensis* has a similar gnetophytic structure, but exhibits goniopteroid venation in the inflorescence bracts (Crane & Upchurch 1987). Moreover, as gnetophytes sometimes produced ovules and sporangiophores in similar cupules, the presence of pollen grains in *Drewria* indicates that it was actually a polliniferous inflorescence rather than an ovuliferous one.

### ***Prognetella minuta*** Krassilov et Bugdaeva sp. nov.

Pl. 1, ,figs 1–3, 5, 6

Name. Refers to the small size of the fossil.

Holotype. No 4745/31-2 (Pl. 1, figs 1–3, 5, 6).

Diagnosis. As for the genus.

Description. The holotype shows a dismembered inflorescence with slender penultimate axes about 20 mm long, 1 mm thick, radially spreading and some of them

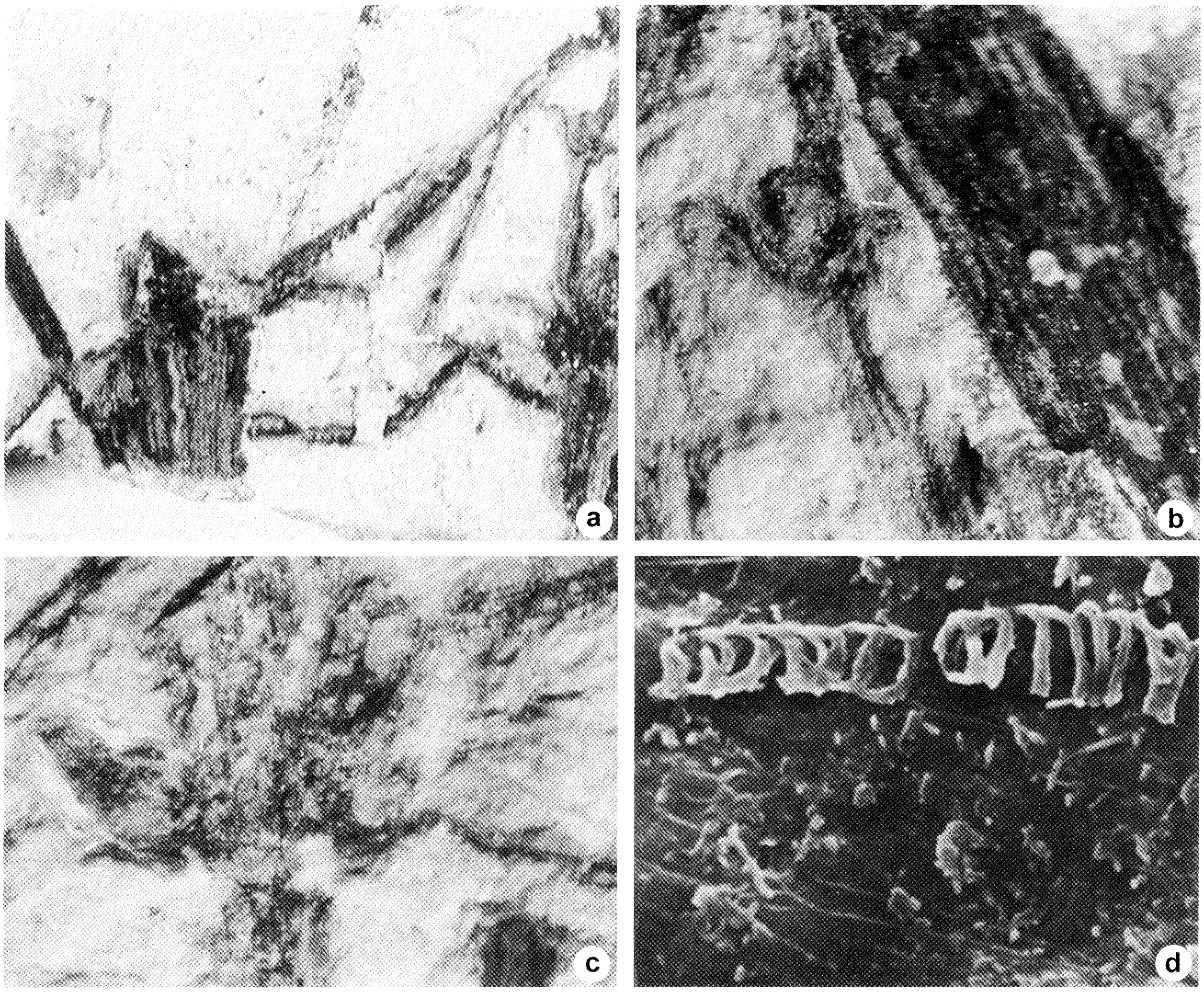

**Fig. 1.** *Prognetella minuta* gen. et sp. nov., holotype: (a) thick branching axis, × 4; (b, c) ovules with subtending bracts, × 8 and × 5; (d) spiral tracheid in the outer coat of an ovule, SEM, × 2700

still attached to the remnants of a higher order branch 5 mm thick (bottom right in Pl. 1, fig. 3). All the branches are longitudinally striate, with vascular tissue appearing as a dark central strand on the paler impressions. The penultimate axes are proximally terete, distally bearing a few whorls of spikelets at the decreasing intervals of 9, 3 and 1 mm (measured in a single better preserved branch 20 mm long), with the apical whorls crowded and overlapping. The spikelets are typically four per whorl, making an acute angle with the axis, 2–5 mm long, bearing from one to several ovules (just one in the apical spikelets). Each spikelet is subtended by a linear bract about 7 mm long, 1 mm broad, spreading almost horizontally from the node and then slightly pendent, often twisted as if flexible. The bracts are of the same width as the penultimate axes and of comparable length, but the axes are rigid, whereas the laminae of the bracts appear flat and thin, making a pale impression with two prominent dark ridges over the vascular bundles.

The ovules emerge as thickly cutinized shining bodies about 1.5 mm long, 0.8 mm broad, enveloped by delicate bracteoles (Fig. 1a, b) which occasionally persist at the nodes of empty spikelets that have shed their ovules (arrow in Pl. 1, fig. 1). The bracteoles appear decussate, basally connate, with three tips as minute teeth. The outer cuticle of the ovules shows elongate rectangular cells. Spiral tracheids are occasionally preserved adnate to the cuticle (Fig. 1d). The macerated vascular bundles of the thin axes and bracts consist of spiral tracheids about 18 mm wide and vessels more than twice as broad possessing short cylindrical members about 70 mm long. The perforation plates show scalariform bars connected by transverse elements to form a reticulate pattern (Pl. 1, figs 5, 6).

Material. The holotype and several scattered fragments of axes and spikelets in the same bedding plane.

## GENUS *LORICANTHUS* KRASSILOV ET BUGDAEVA GEN. NOV.

Name. From *lorica* (Gr.), armour, referring to the appearance of the peltate scales.

Type species. *Loricanthus resinifer* sp. nov.

Diagnosis. Large strobili of peltate scales, resiniferous with radially disposed resin bodies, bearing tufts of elongate sporangia producing spherical monolete prepollen with a sexinal gap over contact areas traversed by a laesural ridge.

Remarks. In general morphology this cone-genus is similar to *Aegianthus sibirica* (Krassilov & Bugdaeva 1988), a pollen cone from the Jurassic of eastern Siberia associated with ovular organs of gnetalean affinity. However, in *Aegianthus* the cone-scales are faceted and lack characteristic resin bodies, while the pollen grains are of a distally sulcate type. *Eucommitheca* from the Early Cretaceous of Portugal (Friis & Pedersen 1996) is similar in having peltate cone-scales with numerous elliptical bodies that were originally described as sporangia, though most of them did not contain pollen grains. At least some of them had the appearance of resin bodies of the type met with in *Loricanthus*, with *Eucommiidites* type pollen grains adherent rather than *in situ*. The pollen grains of *Loricanthus* occasionally resemble *Eucommiidites* with the depressed areas divided by a median ridge. Because of this feature they are also superficially similar to the dicolpate pollen grains of some extant angiosperms such as *Prosopanche americana* (Raflesiales). Because of the considerable morphological diversity of pollen organs allegedly producing *Eucommidites*-type pollen grains, and the controversial interpretations of the latter, one suspects that different pollen morphotypes have been lumped under the latter name.

### ***Loricanthus resinifer*** Krassilov et Bugdaeva sp. nov.

Pl. 2, figs 1–8, Plate 3, figs 1–5.

Name. From the resin bodies.

Holotype No 4745/31-3 (Pl. 2, figs 1–5, 7, 8).

Diagnosis. As for the genus.

Description. The elongate strobili 50 mm long, 20 mm broad are preserved as compressions of spirally arranged scales, apparently attached to a central axis which, however, was not actually revealed. There were no fewer than 30 scales per strobilus. The scales are either tightly adpressed to one another forming a continuous armour, or separated by intervening wedges of rock matrix. This feature might depend on the developmental stage: the unripe strobili may have been compact, but expanded at maturity, with the scales gaping to expose the sporangia. The peltate apophyses of the scales are about 7 mm wide, apparently polygonal, 5–6-angular, concave between the vertices, but on closer inspection their outlines are irregularly angular or rounded with occasional angular curves that would arise from the compression of a hemispherical body which is preserved as a porous coal mass about 1 mm thick. The abaxial surface of the peltae is convex, smooth, covered with a thick shining cuticle, the adaxial one is concave, cup-like, with a rounded scar where the stalk was attached. Small bodies protruding from the adaxial surface of the peltae (Pl. 2, figs 1, 4) are infillings of resin cavities emerging from decaying tissue or still partly immersed in the coaly substance. Some scales are preserved as cuticular sacs with resin bodies inside. The resin bodies are radially disposed in one or two rings with centres at the stalk base. Their shapes vary from elongate to elliptical or ovate, 0.6–0.8 mm long (Pl. 2, figs 7, 8), their surface being irregularly pitted, sometimes preserving a sheath of thin tabular cells that could be epithelial.

The abaxial cuticle of the peltae is thick, externally papillate with hollow papillae (Fig. 2c) and with scattered stomatal pits bordered by small contiguous papillae. The inner surface of the cuticle shows irregularly polygonal cells with strongly ridged anticlinal walls. The cells are about 27–30 mm long, 15–17 mm wide, irregularly arranged, locally forming short rows or concentric rings. The stomata are widely spaced, with a slightly angular, occasionally incomplete ring of typically five subsidiary cells and with two or three (the third incomplete) rings of radially disposed encircling cells, the inner of which occasionally intrude between the subsidiary cells. The guard cells are reniform, about 40 mm long, with short, seldom preserved T-shaped polar extensions and with lateral crests 5.5 mm wide (Pl. 3, fig. 1). The aperture is either concealed or widely open.

The sporangia protrude from under the peltae in dense tufts of up to ten. Most scales show empty shrivelled sporangia that are irregularly ruptured and twisted (Pl. 2, figs 2, 5). The sporangia still filled with pollen grains are straight, fusiform, bluntly pointed, about 3 mm long, 0.3 mm broad (Pl. 2, fig. 6). The sporangial walls are one cell thick (which does not necessarily imply that they were not thicker earlier in their development), with narrow elongate cells in longitudinal rows (Fig. 2a, b).

The pollen masses filling the sporangia contain several hundred pollen grains, some of them still retaining a tetrad configuration (Pl. 3, fig. 4). The pollen grains are ellipsoidal or nearly spherical, diameters (larger diameter in ellipsoidal forms) 17–19.5 mm, slightly flattened on one side. The preserved tetrad configurations and paired grains left from desintegrated tetrads suggest that they are flattened on the proximal side. The contact area appears as a broad elliptical or irregular thickly bordered gap in the sexinal layer traversed by a median laesural ridge or occasionally by two diverging ridges of a vestigial trilete. The distal face is smoothly rounded or, in collapsed grains, irregularly depressed.

Material. The holotype and dispersed cone-scales from the same locality.

## GENUS *PREFLOSELLA* KRASSILOV GEN. NOV.

Name. From *flos* (Latin), flower.

Type species. *Preflosella nathania* sp. nov.

Diagnosis. Flower-like structure shortly pedicellate with single perianth-like whorl of broadly triangular parallel-veined bracts, with sporangial heads on thin axes axillary to the perianth bracts and with an ovuliferous cupule apical on the receptacle. Pollen grains bisaccate. Ovules apparently anatropous, two or more per cupule.

Remarks. The sporangial heads are arranged as in peltasperms, of which *Permotheca* is the most similar (Meyen 1984) and the pollen grains are of the same morphotype as those of *P. vesicasporoides*. However, in *Permotheca* the sporangia are free for most their length while in *Preflosella* they are free only at the tips. In *Caytonanthus*, another similar morphotype, the sporangia are fused along their entire length and the pollen grains show transitional monosaccate to bisaccate morphology (Harris 1951, Krassilov 1977). The cupule resembles *Caytonia*, superficially at least, but the ovules are relatively large and less numerous. Phylogenetic affinities are possible with both peltasperms and caytonialeans, for these two groups are interrelated. However, neither of the comparable organs ever formed bisexual structures. *Irania*, the only pre-angiospermous bisexual structure, had catkin-like pollen organs coaxial with the bilobed cupules of the apical raceme (Schweitzer 1977).

*Allisporites*-type pollen grains very similar to those of *Preflosella* had been previously found in the gut of xyelid insects from the same locality (Krassilov & Rasnitsyn 1982). Though visits by pollen-feeding insects may not necessarily have led to obligatory entomophily, in the case of *Preflosella* it may be surmised that a bisexual structure was developed as a consequence of this pollination mode.

### ***Preflosella nathania*** Krassilov sp. nov.

Pl. 4, figs 1–6

Name. From Nathan (Hebrew), gift.

Holotype. No 4745/31-1 (Pl. 4, figs 1–6).

Diagnosis. As for the genus.

Description. The species is based on the part and counterpart of a single specimen (Pl. 4, figs 1–3, with the counterpart transferred to cellulose film, Pl. 4, fig. 4) showing a compressed flower-like structure on a pedicel 2 mm long, 1 mm thick, apically expanded to 2.5 mm. Two perianth-like bracts are fully preserved on the left and the third bract is represented by a fragment on the right hand side of the pedicel. Since the bracts are radially spreading and the flower-like structure is split approximately in the median plane, there may originally have been four bracts.

The bracts are broadly triangular, flat or slightly adaxially concave, 11 mm long, about 4 mm broad in the lower third, gradually tapering to the apex, distally free, overlapping or perhaps shortly connate at the base. The venation of the bract consists of about ten coarse subparallel veins converging at the apex.

Two staminate spikes are seen on the right hand side. They are attached to the receptacle below the cupule. Each spike consists of a slender axis more than 8 mm long, 0.5 mm thick, spreading almost horizontally for a

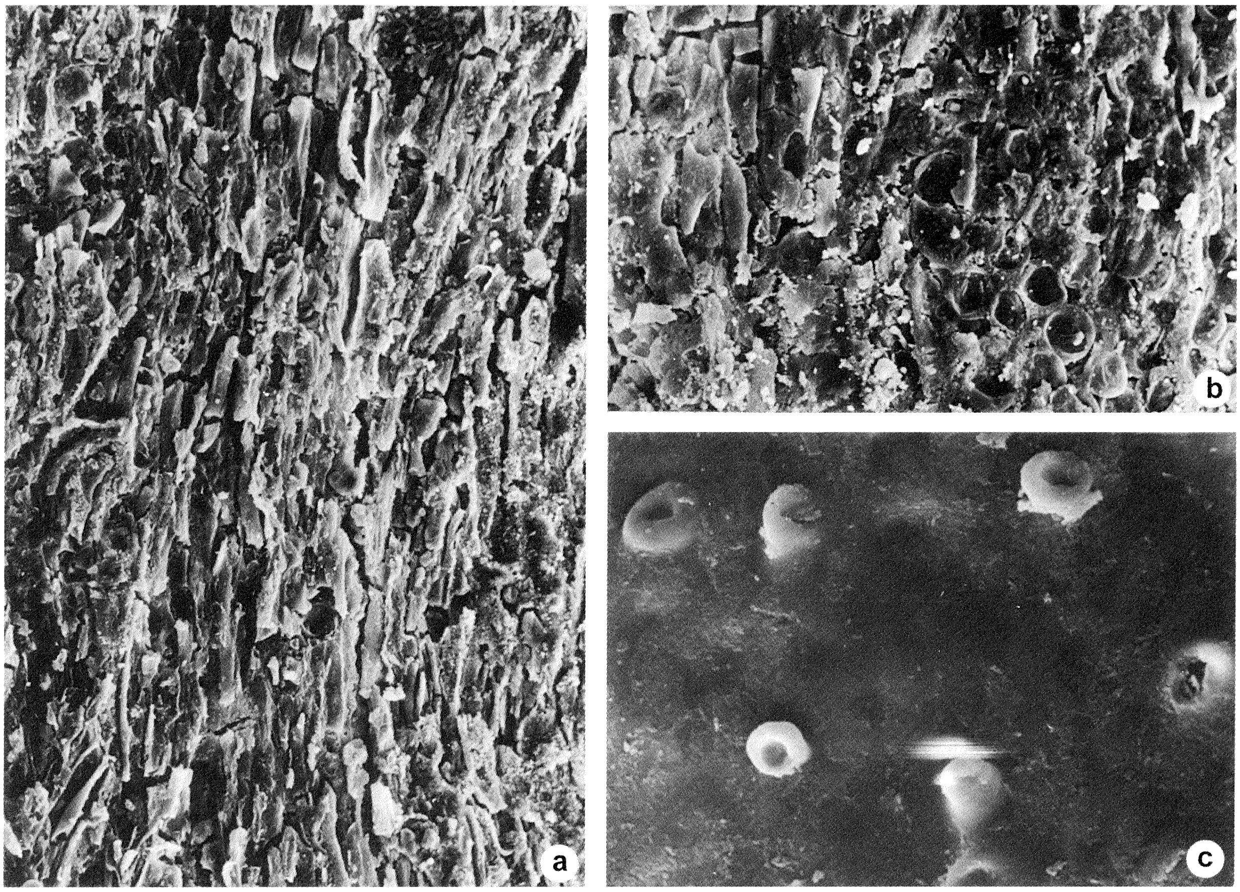

**Fig. 2**. *Loricanthus resinifer* gen. et sp. nov., holotype: (a) epidermal cells of sporangial wall, SEM, × 300; (b) same sporangium showing pollen grains immediately beneath a single layer of epidermal cells, SEM, × 300; (c) hollow papillae on the scale cuticle, outside view, SEM, × 500

short distance, then becoming upcurved, bearing a single row of sporangial heads turned outward and apparently extrorse. In the right hand spike, two basal heads are spread in the bedding plane appearing as radial, shortly lobed structures with a circular scar, making the stalk attachment, between them. Another spike shows two heads in side view, 1 mm apart, attached by a minute stalk, ovate, shortly incised at the apex. The better preserved head consists of five radially arranged sporangia connate along their whole length except at the apices which protrude as blunt teeth. The individual sporangia are crescent-shaped, 2 mm long, showing no evidence of dehiscence. The transfer preparation reveals another sporangiophore adpressed to the central bract, with sporangia preserved as pollen masses.

The pollen grains extracted from the sporangia are bisaccate, of variable dimensions (long equatorial axis 55–100 mm), with sacci of protosaccate infrastructure, laterally connected by a narrow stripe of sexine (Pl. 4, fig. 5). The sacci are crescent-shaoed to hemispherical, extended in the equatorial plane, in the smaller grains distally inclined, in the larger grains only slightly so. The corpus is keystone-shaped in side view. The cappa is broadly elliptical, transversely elongate, smoothly arched or with an irregular depression in the middle, minutely pitted. The cappula is narrow, traversed by a slit-like sulcus, often overlapped by the converging sacci.

The central part of the flower-like structure is occupied by a solitary cupule, apical on the receptacle. The cupule is spherical, 5 mm in diameter, showing two adpressed ovules (since the cupule is split in the median plane, the complete number of ovules may have been four) that are elliptic-obovate in outline, 4 mm long, with maximum width 2.5 mm slightly above the middle, attached at the base of the cupule, distally rounded, pointed at the base and apparently anatropous, yet lacking structural evidence of their polarity. The transferred ovules show a thick coat underlain by large stone cells.

Material. The holotype.

## CONCLUSIONS

With the accumulation of data the Baisan assemblage emerges as a peculiar association of plants showing transitional gymnospermous to angiospemous morphological characters. The high concentration of such forms suggests parallel evolution in which a morphological innovation was shared by the members of a biotic community bound by ecological and genetic limks (Krassilov 1998). Among the Baisian proangiosperms, *Baisia* is considered as a derived form of bennettitalean affinities (Krassilov & Bugdaeva 1982). *Preflosella nathania* gen. et sp. nov. is a bisexual flower-like structure, unique among the Mesozoic proangiosperms, with sporangial heads of peltasperm morphology and with ovuliferous cupules similar to those of *Caytonia*. The other genera show certain gnetalean features, but are not closely related to extant gnetophytes which are currently conceived as solitary survivors of different seed-plant orders. *Prognetella minuta* gen. et sp. nov. is a relatively primitive form morphologically related to *Ephedra*, but of a more elaborate inflorescence structure. *Loricanthus resinifer* gen. et sp. nov. belongs to a peculiar gnetophytic group with cupule-like cone-scales and angiospermoid palynological features. *Eoantha ornata* sp. nov. is a flower-like ovuliferous structure of gnetalean origin differing from the previously described *E. zherikhinii* (Krassilov 1986) in a supposedly derived state of the proximally connate perianth lobes and the lack of apical bracts.

Generally, gnetophytes and related forms may have played a more important role in the Mesozoic plant communities than had been previously anticipated (Krassilov 1982a and elsewhere). However, much more has to be learned of these recently discovered plants before their taxonomic position can be properly defined.

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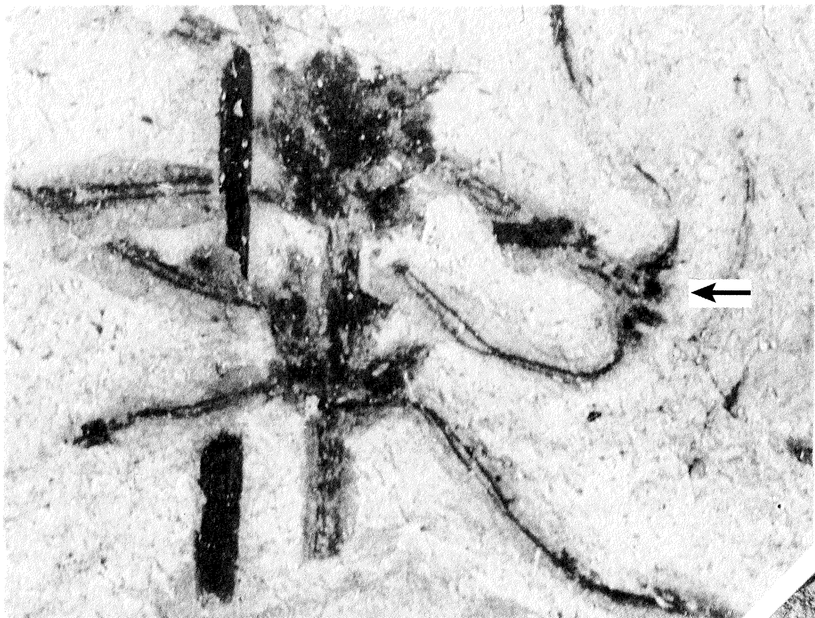
# PLATES

Plate 1

figs 1–3, 5, 6. *Prognetella minuta* gen. et sp. nov., holotype, spicate branches arising form the remnants of a thicker axis (bottom right in fig. 3, × 1) and detached, bearing long bracteate whorls of ovuliferous spikelets (figs 1, 2, × 4); vascular bundles of bracts showing spiral tracheids and broader reticulate vessels (fig. 6, SEM, × 1500) with scalariform-reticulate perforation plates (fig. 5, SEM, × 3000)

fig. 4. *Eoantha ornata* sp. nov., holotype, cupule showing two seeds, × 10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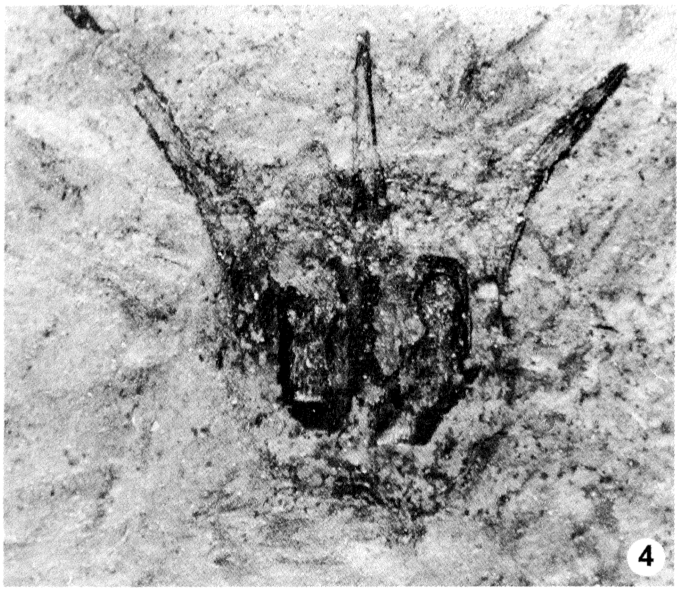
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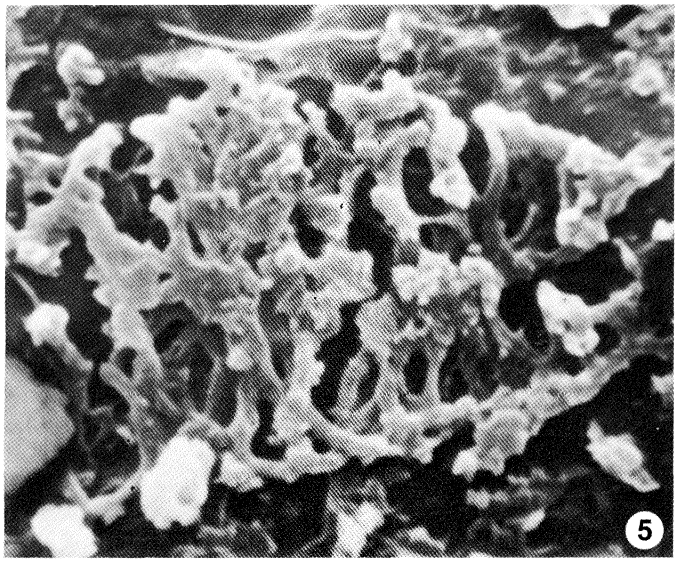
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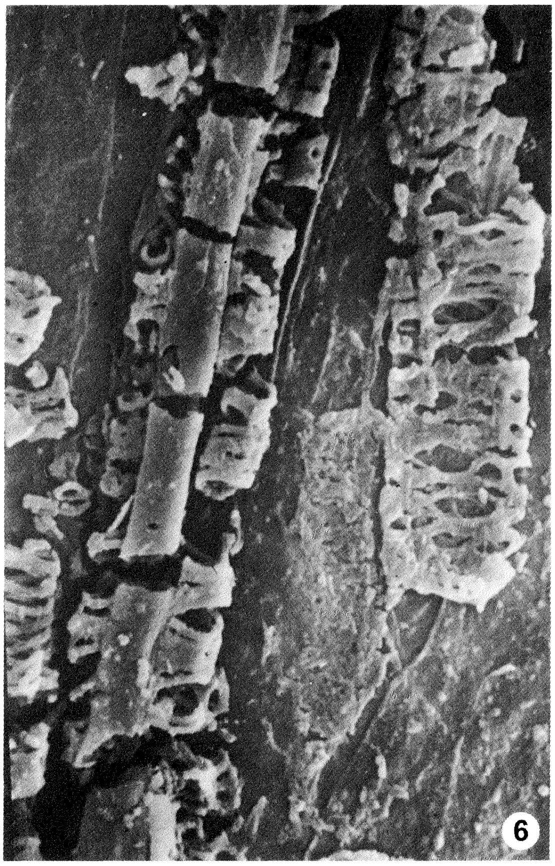
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Plate 2

figs 1–8. *Loricanthus resinifer* gen. et sp. nov., holotype. pollen cone (fig. 3, × 2) with peltate scales showing resin bodies (figs. 1, 4, × 10) and shrivelled sporangia (figs 2, 5, × 10), as well as straight fusiform sporangia filled with pollen grains (fig. 6, SEM, × 50). Resin bodies showing remains of an epithelial sheath (figs 7, 8, SEM, × 100)


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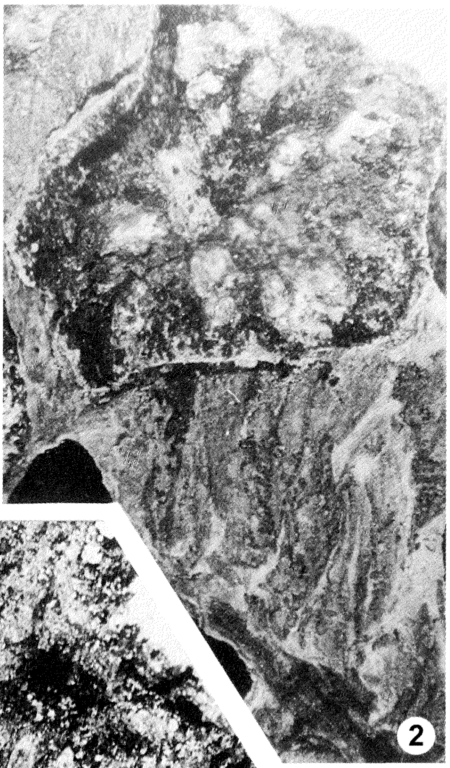
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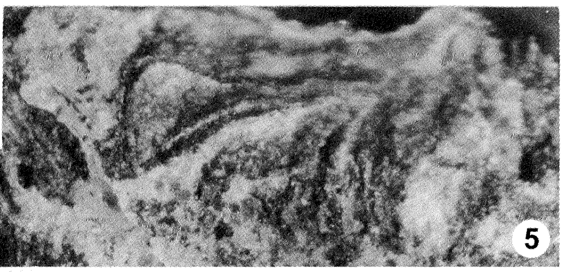
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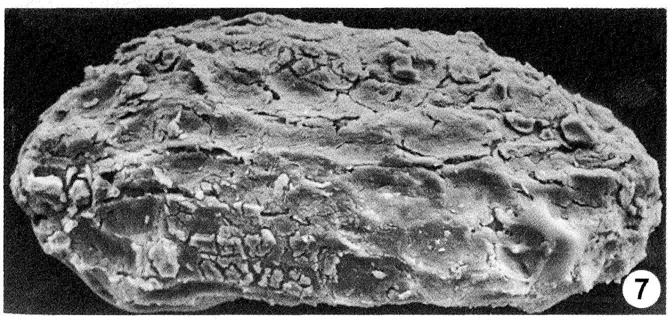
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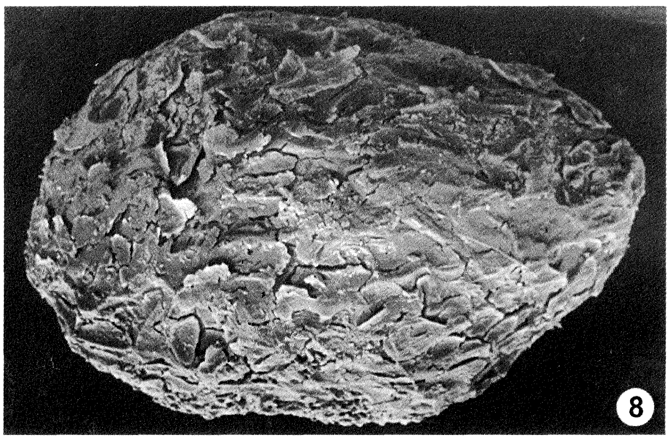
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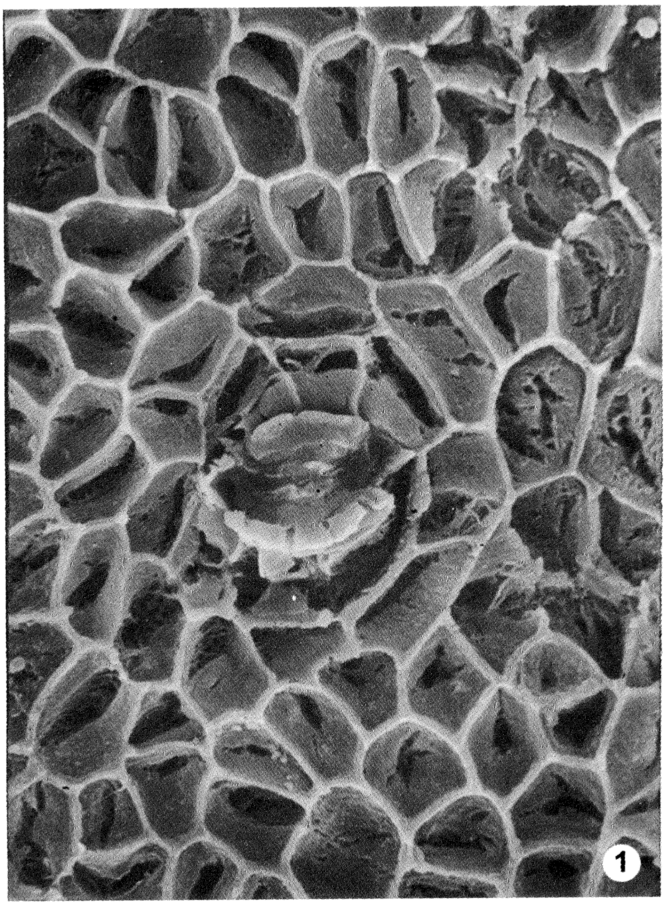
Plate 3

figs 1–5. *Loricanthus resinifer* gen. et sp. nov., holotype, scale cuticle showing amphicyclic stoma (fig. 1, SEM, × 700) and pollen grains from sporangia shown in Plate 2, fig. 6, with partly preserved tetrad configurations, SEM (fig. 2, × 1500; fig. 4, × 1000; fig. 5, × 2500) and proximal face with a depressed contact area traversed by a laesural ridge (fig. 3, × 4000)



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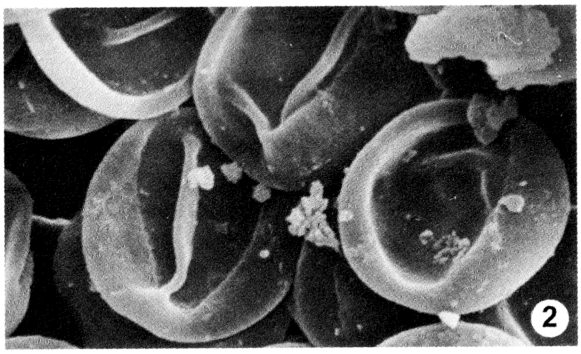

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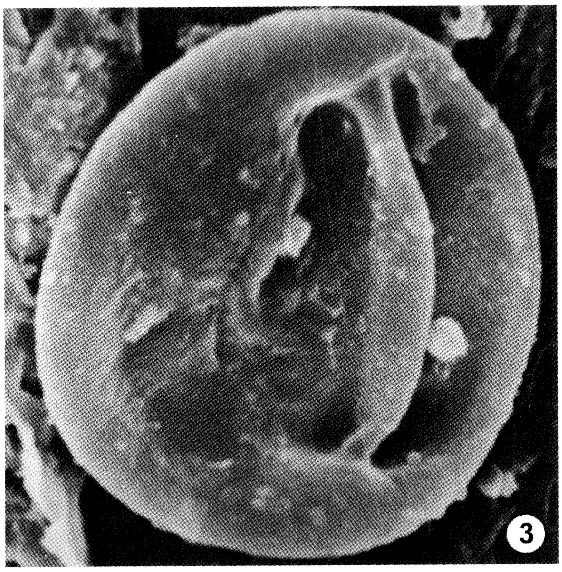

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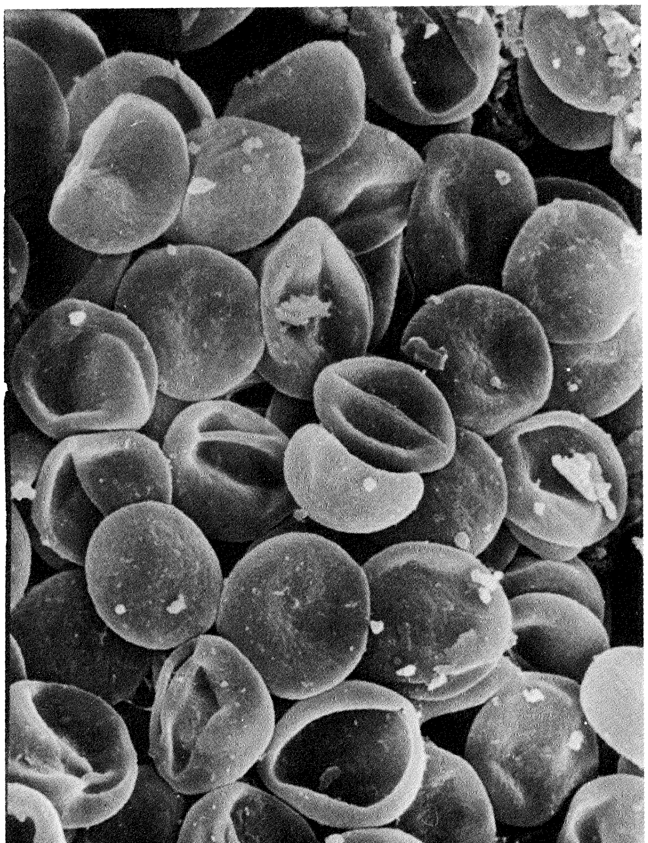

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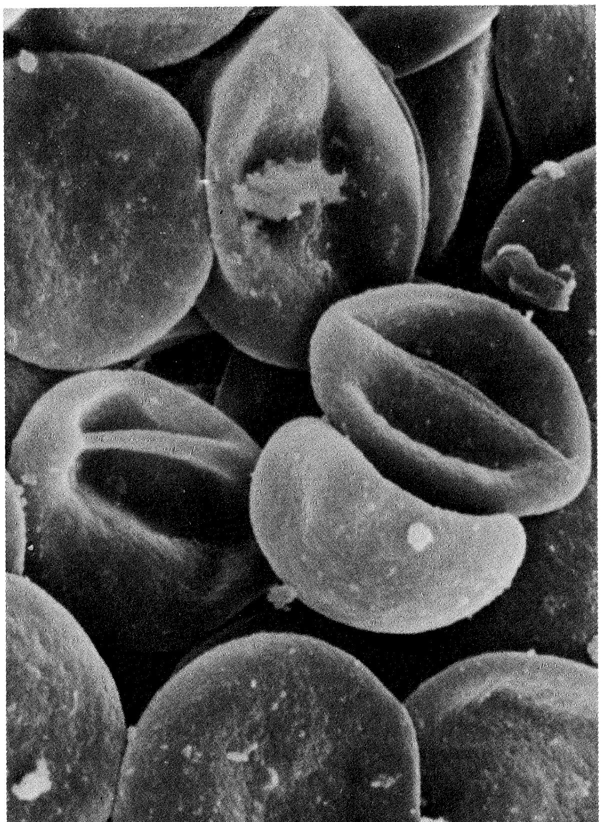

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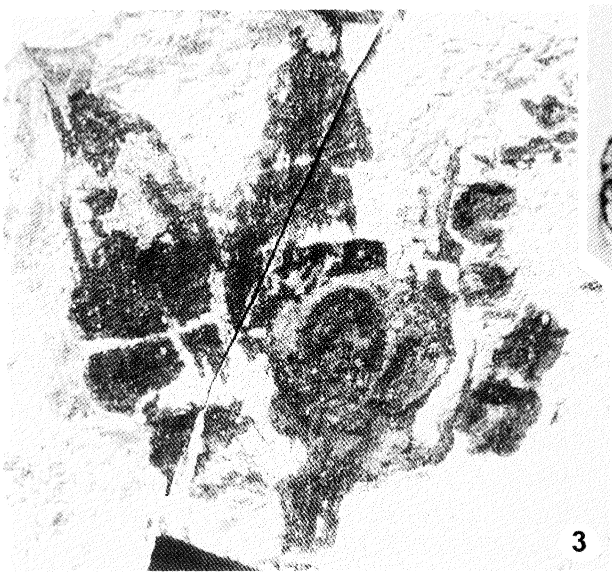
Plate 4

figs 1–6. *Preflosella nathania* gen. et sp. nov., holotype, a flower-like structure with perianth bracts, spikes of sporangial heads a central cupule (fig. 3, × 5); close-up of sporangial heads and cupule (fig. 1, × 7; 2, × 8) and transfer of the counte (fig. 4, × 10, arrow on sporangium). Pollen grains from sporangium showing protosaccate infrastructure and narrow la connection of the sacci (fig. 5, LM, × 1000; fig. 6, SEM, × 300)


1


2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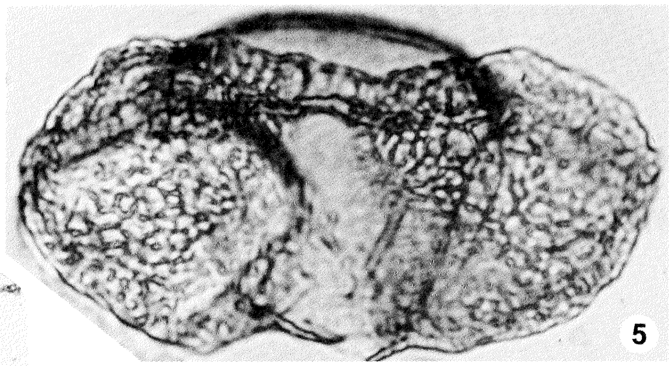
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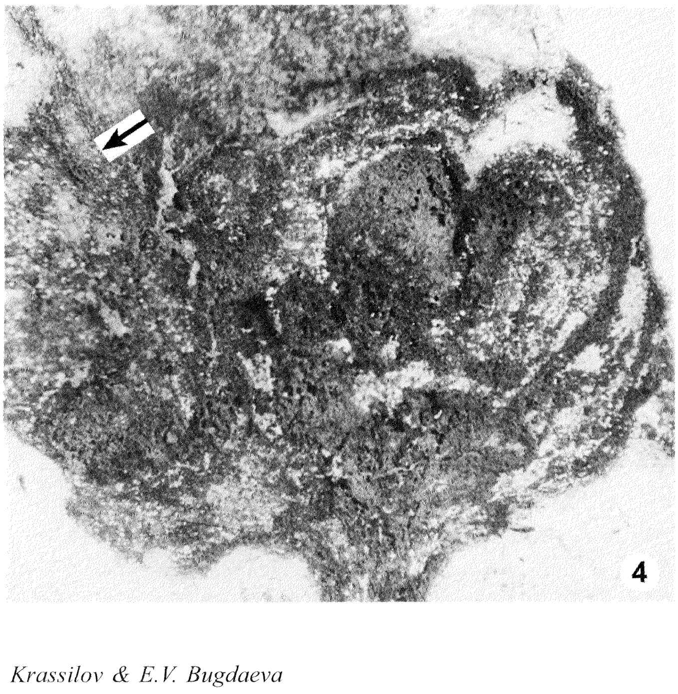
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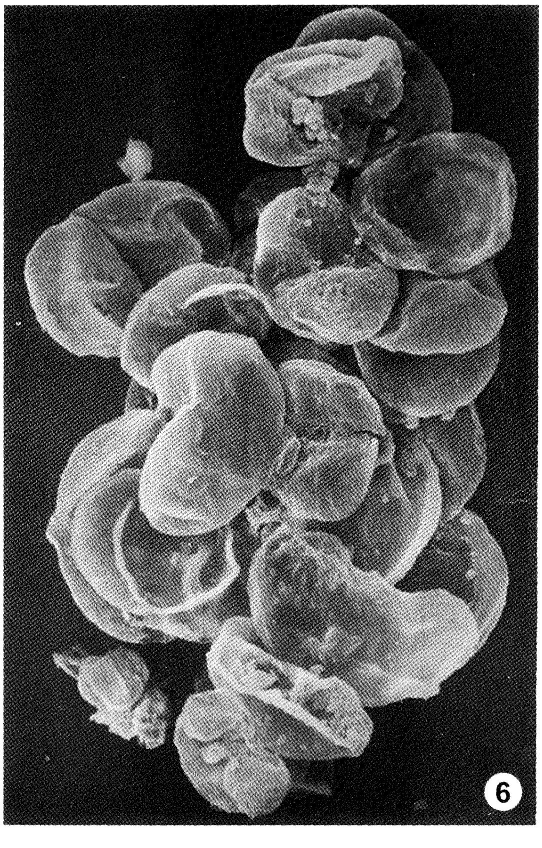
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