

Gnetophyte assemblage from the Early Cretaceous of Transbaikalia

by

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With 10 plates and 2 text-figures

Abstract

The Baisa locality in the upper reaches of the Vitim River east of Lake Baikal (Transbaikalia) has previously yielded a few early angiosperm fossils as well as proangiospermous plants of gnetalean (*Eoantha*) and bennettitalean (*Baisia*) affinities (VAKHRAMEEV & KOTOVA 1977, KRASSILOV & BUGDAEVA 1982, KRASSILOV 1986). The Hauterivian to Barremian age of the locality is based on faunistic evidence and correlation. New finds in the same plant-bearing horizon provide additional information on the previously described genera and reveal new gnetalean reproductive structures. They include *Baisianthus ramosus* gen. et sp. nov., a branching axis bearing verticillate cupulate sporangiophores with synangia producing caveate anasulcate pollen grains, and *Vitimantha crypta* gen. et sp. nov., a flower-like pedicellate structure, with perianth bracts showing reticulate venation and follicle-like gynoecial structures. Polyplicate pollen grains are found stuck to the latter in the area of a papillate adaxial groove. A comparison of the vascular elements described for the newly found reproductive and foliar organs give evidence of the graminoid leaves *Praeherba spathulata* gen. et sp. nov. belonging to the *Eoantha* plant. The association of early angiosperms and diverse angiosperm-like plants suggests an innovative nature of this peculiar plant community. It is suggested that environmental changes, indicated by the evidence of mass mortalities of aquatic organisms in the same strata, might have affected terrestrial vegetation as well, promoting herbaceous habit and accelerate development in both the gnetophyte and angiosperm lineages.

Key words: angiosperm evolution, gnetophytes, graminoid leaves, pollen organs, Transbaikalia.

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1. Introduction

The Baisian locality in the upper reaches of the Vitim River east of the Lake Baikal in Transbaikalia has yielded several fascinating plant fossils, including “*Dicotylophyllum*” (VAKHRAMEEV & KOTOVA 1977), *Baisia* (KRASSILOV & BUGDAEVA 1982) and *Eoantha* (KRASSILOV 1986). The former genus was assigned to angiosperms, the latter two to proangiosperms of bennettitalean and gnetalean affinities, respectively. The

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locality also yielded trichotomosulcate and tricolpate pollen grains. Among the new findings are additional specimens of “*Dicotylophyllum*” as well as attached floral structures of both *Baisia* and *Eoantha* previously known as dispersed organs alone. Moreover, there are new reproductive structures of gnetalean affinities: the pollen-producing inflorescence *Baisianthus ramosus* gen. et sp. nov. and the flower-like *Vitimantha crypta* gen. et sp. nov. The material is partly preserved as compressions yielding cuticular fragments, pollen grains and tracheary elements. The latter proved suitable for comparing different organs coming from a single plant bed. In particular, such comparisons give evidence that the *Eoantha* floral axis was produced by the same plant as the associated graminoid leaves *Praeherba spathulata* gen. et sp. nov.

Jointly, these finds suggest a considerable diversity of endemic early angiosperms and angiosperm-like plants (*Baisianthus*, *Vitimantha*, *Eoantha*, *Baisia*) that played a significant role in the Baisian fossil plant assemblage giving it a peculiar innovative aspect. In contrast, the majority of contemporaneous plant assemblages consist only of conventional Mesozoic spore-plants and gymnosperms. However the earliest angiosperm macrofossil and pollen records are associated with gnetalean records in other localities as well, e. g., the Koonwarra Fossil Bed in Australia (DILCHER et al. 1996, KRASSILOV et al. 1996) and the Santana Formation in Brazil (OSBORN et al. 1993). Such assemblages are of interest as evidence of parallel evolution involving a number of plant species growing side by side in some special Early Cretaceous plant communities. Notably, in the case of the Baisian assemblage, these plants produced fairly small reproductive organs of a complex and elaborate structure. Such structures include the racemose inflorescences of cupulate sporangiophores in *Baisianthus*, the flower-like structures supposedly derived by shortening of a conventional gnetalean spike in *Eoantha* and perhaps also in *Vitimantha*. They indicate acceleration and condensation as the prevalent modes of their morphological evolution. These tendencies could have been directed by environmental changes.

2. Age and environments

The Baisian locality occurs in a small depression that is part of an extensive rift system traversing the Vitim Highlands, Western Transbaikalia (KRASSILOV & BUGDAEVA 1982). Here the fossiliferous deposits onlap the granitic basement and are represented, from bottom up, by conglomerates with occasional shell beds, bituminous black shales and cyclically alternating fine-grained sandstones, siltstones and marls containing a rich fossil fauna of ostracodes, insects and fishes, as well as somewhat less abundant plant remains. The fish-beds are referred to as *Lycoptera* shales while the bivalve, ostracod and insect remains were included in, respectively, the *Limnocyrena*, *Lycopteroocypris* and *Ephemeropsis*–*Coptoclava* assemblages. The age assignments of these assemblages vary from Late Jurassic to early Neocomian (MARTINSON 1985, ZHERIKHIN 1979, KOLESNIKOV 1980, SKOBLO & LYAMINA 1986). In contrast, palaeobotanists have tended to give somewhat younger, late Neocomian to Aptian, ages basing their conclusions mainly on the angiosperm pollen records (VAKHRAMEEV & KOTOVA 1977) which are presently known from the older Neocomian deposits as well (HUGHES 1994).

Shortly before his untimely death in 1996, Dr. VLADIMIR SKOBLO drafted a comprehensive discussion of the Baisa Fossil Bed that he intended for a joint stratigraphic paper with the present authors. He argued that the ostracod species *Mongolianella kizhingensis* SKOBLO found in the lower part of the Baisa Section indicates a Valanginian age of the latter thus supporting the earlier conclusions based on bivalves, while the overlying ostracod assemblages of the main fossil bed are of Hauterivian–early Barremian age. His opinion is corroborated by correlation with the stratigraphically equivalent Jixi and Chengzihe formations of Heilongjian Province, China, the latter containing dinoflagellates and bivalves of Hauterivian to early Barremian age (SUN & DILCHER 1996).

An important characteristic of the Baisa Fossil Beds is the alternation of anoxic and oxygenic depositional environments represented by the black shale and oolitic marly facies, respectively. They also reflect pH fluctuations between approximately 5–6 for black shales and 7–8 for marls (KRASSILOV 1994). Several bedding planes within the marly beds are covered with large mayfly nymphs *Ephemeropsis* and the aquatic beetle larvae *Coptoclava*, intermingled with other insects, fish and fragmental plant material. Such fossil beds

are evidence of mass mortality of, in the first place, the pH-sensitive organisms. By analogy with extant lacustrine environments, mass mortalities could be caused by sharp pH fluctuations related to water pollution, in particular, by acid rains. In the case of these Cretaceous limnic faunas, acid rains could be related to intermittent volcanic activities in adjacent rift zones.

The same factor might have been of a critical importance for the terrestrial plant communities. Unlike other Neocomian localities, ferns are scarce in the Baisian plant-bed, while the common gymnosperms are represented only by fragmentary conifer remains perhaps coming from a distant upland community. The achene-like *Baisia* cupules that obviously came from a nearby source are the most abundant of all plant fossils. While *Baisianthus*, *Eoantha* and *Vitimantha*, although far less abundant, are extremely fragile and scarcely capable of withstanding much transportation, thus, also belonging to a proximal plant community. In addition, at the time of calcareous sedimentation, an influx of terrigenous material was minimal and perhaps originated from nearby sources alone. Probably, these reproductive structures were produced by waterside plants conceivably inhabiting coastal wetlands of the lake basin. It is well known that wetlands are particularly sensitive to acid rains that disturb their plant communities and thereby promote rapid expansion of their gap-filling and colonizer components. While such environments might have been unfavourable for fern growth, they provided opportunities for the newly emerging herbaceous gnetophytes and angiosperms perhaps inflicting in them a developmental acceleration tendency as indicated by their foliar and floral morphologies.

3. Systematics

Genus *Baisianthus* KRASSILOV et BUGDAEVA, gen. nov.

Type species: *Baisianthus ramosus* KRASSILOV et BUGDAEVA, sp. nov.

Derivation of name: From Baisa, the locality, and *anthus*-flower.

Diagnosis: As for the type-species.

Baisianthus ramosus KRASSILOV et BUGDAEVA, sp. nov.

Plates 1–5, Text-fig. 1

Holotype: N° 31-309, Institute of Biology and Pedology, Vladivostok, Pl. 1, Fig. 1, Text-fig. 1.

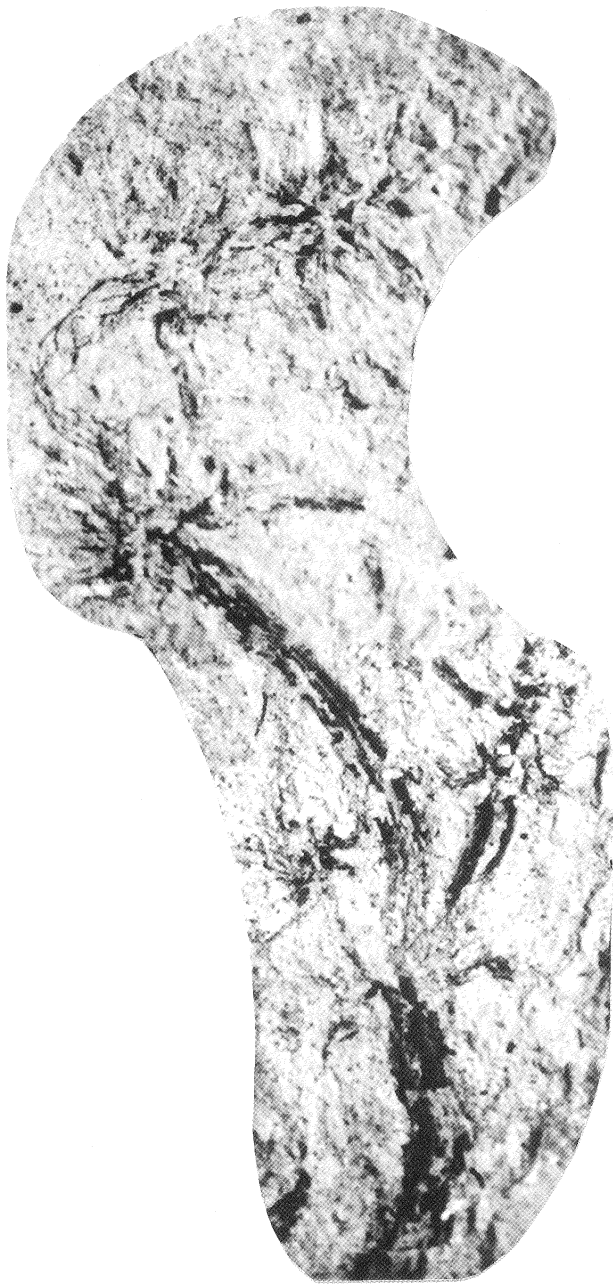
Locality: Left bank of the Vitim River downstream of the mouth of its tributary Sololy Creek, Transbaikalia.

Age: Early Cretaceous, Hauterivian–Barremian.

Derivation of name: *ramosus*, branching, refers to the morphology of the pollen-producing organs.

Diagnosis: Slender articulate shoots bearing verticillate sporangiophores on lateral branches and on the main axis distally. Lateral branches in a candelabrum-like bracteate whorl at the basal node separated by a long internode from the crowded distal whorls of cupulate sporangiophores. Nodal bracts linear, with a single vein. Sporangiophores enclosed in cupules, protruding at maturity, bearing 2–4-sporangiate synangia or rarely distinct sporangia on the lateral and terminal branches. Pollen grains produced in tetrahedral tetrads, anasulcate, caveate, with a separable nexinal body. Tracheary elements of the shoot axis divided into short segments, with uniseriate large pits and with helical secondary thickenings, those of the sporangiophore axis with helical thickenings, both forming scalariform junctions of many bars.

Description: The material consists of seven branching shoots and numerous fragments of unbranched axes or detached pollen organs. The shoots might have been borne in clusters as suggested by their arrangement in Pl. 1, Fig. 2. They are articulate, bearing whorls of bracteate pollen organs at the nodes. The shoot axes are slender, about 0.6 mm and up to 1 mm thick, straight or gently curved, some bent at the lower node, scarcely rigid, with a few distinct longitudinal ribs with a fine striation between them. All the shoot specimens seem torn off rather than abscised, so that their complete length is unknown. However, the specimens about 15 mm long seem almost complete, showing up to five nodes, with the proximal internodes much longer than the distal. In the holotype (Pl. 1, Fig. 1, Text-fig. 1) the basal internode is 4.5 mm long, the lower node producing a whorl of short branches axial to pending bracts. The latter are linear, about 3 mm



Text-fig. 1. *Baisianthus ramosus* gen. et sp. nov., reproductive shoot bearing sporangiophore whorls terminal on the lateral branches and sessile on the main axis distally, Holotype, 12 \times .

long, 0.5 mm broad. Two branches compressed in the bedding plane are 4 mm and 5 mm long, diverging at acute angle and each bearing a terminal cluster of pollen organs. The subsequent nodes bear bracteate whorls of pollen organs directly on the main axis. The second node is 6 mm above the first one, while the distal nodes are more crowded, the internodes progressively decreasing to 2.5 mm and 1 mm. Two terminal nodes seem almost contiguous, with the pollen organs helical rather than verticillate. The whorls and their subtending bracts decrease in the same direction.

This shoot structure seems typical, for in other specimens the proximal node is similarly branched and is distant from the more condensed distal part, the latter variable, sometimes consisting of two fertile nodes alone (Pl. 1, Figs. 3, 5). A single fragment of a somewhat larger shoot (Pl. 1, Fig. 4) shows a candilabrum of four branches of which the better preserved one (left) is about 6 mm long, is subtended by a bract 4 mm long. It is apically forked with each terminal ramification bearing crowded pollen organs. A smaller shoot on the same slab (right in Pl. 1, Fig. 4) is not actually connected to the larger shoot. It is peculiar in the

Table 1. Correlation of lower Cretaceous deposits of the Baisian Basin and NE China (the latter after SUN & DILCHER 1996 and SUN 1997, personal communication).

Stages	Baisian Basin, Transbaikalia	Jixi Basin, NE China
Aptian	Coal-bearing strata (better developed in adjacent basins) with fern - gymnosperm flora	Muling Formation, coal-bearing strata with fern - gymnosperm flora
Barremian	Unconformity	Chengzihe Formation, coal-bearing sandstone/shale cycles with early angiosperms
Hauterivian	Zazinskaya Formation, lacustrine black shales, marls, sandstone/shale cycles, with the Baisian flora	Chengzihe Formation, marine shales with <i>Buchia</i> , conglomerates
Valanginian	Yendondinskaya Formation, conglomerates, sandstones, coaly shales	Didao Formation
Berriasian		

branching of not only the basal, but also the next node, with both miniature candilabra either sterile or having pollen organs shed before fossilization.

Vascular tissue macerated from compressions of the axes consist of long tracheids, elliptical in cross-sections and about 20 μm in the largest diameter. The radial walls show a “vertebrate” structure of short segments separated by scalariform slits with uniseriate large pits. The secondary wall thickenings are helical of irregularly spaced coils (Pl. 2, Fig. 6). In the “vertebrate” structure, the segments are about 10 μm long, their surface is scabrate with minute warts, the pits are rounded-rhomboid, with a lenticular aperture (Pl. 2, Fig. 9). In the helical thickenings, an average coil spacing is 1.5 μm , but some coils are closer together, almost contiguous or else the coils are reticulate (Pl. 2, Fig. 7). Occasional tracheids show what appears to be a tertiary structure of thin irregularly reticulate striations with large distant pits about 3.5 μm wide (Pl. 2, Fig. 8). Small tangential pits are sometimes discernible. A junction of tracheary elements in Pl. 2, Fig. 10 appears as a stretched helical structure transformed into a series of irregular scalariform pits or pores, similar to oblique perforation plates. However, it is not clear whether it is actually perforated.

The nodal whorls of pollen organs typically consist of four to eight cupules enclosing sporangiophores that protrude at maturity. The cupules are paired, shortly stalked, subtended by linear bracts and small lanceolate bracteoles that are scarcely discernible in the compressions but separate during maceration (Pl. 3, Fig. 18). The bracteoles are of variable dimensions, from 0.3 mm long, 0.1 mm broad to about 1 mm long, 0.3 mm broad, bluntly pointed, sometimes with apical pits, perhaps glandular. They are thinly cutinized, with indistinctly marked longitudinal files of cells.

The supposedly unripe cupules are ovate, pointed, about 1 mm long, longitudinally striate, thinly cutinized, with the cuticular features as in the bracteoles. Pl. 3, Fig. 14 shows a pair of immature cupules, the outlines of a sporangiophore are visible through the cupule wall in the right one. In a split cupule shown in Pl. 3, Fig. 13 the unripe sporangiophore completely fills the locule, with synangia adpressed to the wall. A macerated cupule reveals a sporangiophore axis with a single vascular bundle consisting of long, narrow (about 7 μm in diameter) tracheary elements that are bent around an elliptical object that could be a resin body. The tracheary elements show steep helical thickenings, their junction seen in Pl. 3, Fig. 17 appearing as a long perforation plate with about 20 scalariform bars and irregular pits or pores between the bars.

At a more advanced developmental stage, the sporangiophores protrude from their ruptured cupules exposing their terminal sporangia or bisporangiate synangia (Pl. 3, Fig. 15). A single detached sporangiophore (Pl. 3, Fig. 12) is preserved as a slightly compressed three-dimensional structure with a relatively



Text-fig. 2. *Vitimantha crypta* gen. et sp. nov., a pedicellate flower-like structure

massive axis giving off a few short helical branches that are crowded at the apex. A lower branch facing the observer bears a pair of adpressed or connate sporangia preserved as prominent spherical bodies filled with pollen grains. The next branch to the right terminates in a large, probably four-sporangiate synangium. A few paired sporangia are discernible in the distal branches. Studies with SEM confirm that the sporangial structures are variable, ranging from pairs of distinct sporangia on the forking sporangiophore branches (Pl. 4, Fig. 21) to 2–4-sporangiate synangia (Pl. 4, Figs. 19, 23). Individual sporangia are ovate, shortly stalked, thin-walled, their epidermis consisting of narrow elongate cells with a transverse or oblique ring of tabloid cells apparently forming a stomium (Pl. 4, Fig. 22). The synangia are hemispherical to flabellate, their external lobes corresponding to the laterally connate sporangia. Split synangia reveal a thick central column (Pl. 4, Fig. 24). The locules are filled with pollen grains. In the ripe synangia, the pollen grains could be shed from cracks between the lobes, as seen in Pl. 4, Fig. 19.

Pollen grains are produced in tetrahedral tetrads. An unripe sporangium shows no less than 28 tetrads, all apparently at the same developmental stage (Pl. 4, Fig. 20; Text-fig. 2). The pollen grains are elliptical, rounded at the ends and with one end broader than the other, about 27–30 μm long, 20 μm broad, psilate, with a thick sexine that is irregularly folded, occasionally appearing sac-like (Pl. 5, Fig. 29). While still in tetrads, the pollen grains show a broad sulcus, shorter than grain axis, about $7 \times 18 \mu\text{m}$ covered with a granular membrane. In ripe grains the sulcus gapes widely exposing the nexine (Pl. 5, Fig. 28).

The sexine is separated from the nexinal body by a broad cavity and is perhaps attached at the ends of the sulcus alone, although in a split grain shown in Pl. 5, Fig. 27 there appears to be a few interconnecting filaments in the middle. The nexinal body protrudes through the gaping sulcus and is detachable, sometimes even preserved separately in the pollen mass (Pl. 5, Fig. 25), perhaps squeezed from the sexine under pressure. It is narrowly elliptical, about 11 μm broad, symmetrical or irregularly constricted at one end, without any apertural marks, minutely pitted or, with a more distinct pitting, microfoveolate (Pl. 5, Fig. 26). A few orbicules adhere to the pollen grains (Pl. 5, Fig. 30).

Comparison: Cupulate sporangiophores occur in *Dinophyton* (KRASSILOV & ASH 1988), but in this Triassic genus they are scaly, with adaxial synangia or solitary sporangia at the base, the latter producing bisaccate pollen grains. In the pollen cone *Aegianthus* (KRASSILOV & BUGDAEVA 1988), the sporangiophores are peltate, partly enclosing the sporangia that are distinct and are facing the cone axis. In *Synangispadix*, the supposed pollen cone of the *Sanmiguelia* plant (CORNET 1986), lateral sporangiophores bear paired sporangia that appear free or semisynangiate, but scarcely fused. In both *Aegianthus* and *Synangispadix*, the pollen are anasulcate, a widespread cycadalean type of grain. Three-locular synangia occur in *Piroconites keuspertii* GOTHAN (emend. VAN KONIJNENBURG–VAN CITTERT 1992). However in the latter genus they are born on scaly sporangiophores, and the pollen grains are polylicate.

Branching cupulate sporangiophores are unknown in fossil gymnosperms thus restricting comparisons to the extant gnetalean genera that have a basically similar sporangiophore structure (PEARSON 1929, MAHESHWARI & VASIL 1961, SANWAL 1962, MARTENS 1971, FOSTER & GIFFORD 1974). In *Ephedra*, the pollen organs are produced in spikes bearing 2–3 bracteate whorls of axillar sporangiophores that are enclosed in cupules formed of two bracteoles. The sporangiophores are unbranched or sometimes forked, bearing 6–8 terminal synangia with a porous aperture. The pollen grains are ribbed inaperturate, with a thin tectum that is continuous between the ribs. In *Gnetum*, the sporangiophores are produced in several whorls above the collar formed of connate nodal bracts. They are enveloped in the cupular perianths – occasionally two per perianth – protruding at maturity, bearing apical synangia of four or fewer sporangia. The pollen grains are distally leptomate. In *Welwitschia*, the pollen spikes bear flower-like spikelets axillar to bracts, with two decussate pairs of bracteoles the inner of which are connate to half their length forming an open cupule that contains six sporangiophores arranged radially around a central glandular structure. The sporangiophores are basally connate, each bearing a 3-locular synangium. The pollen grains are ribbed, as in *Ephedra*, but with a single or several sulcate apertures between the ribs.

Thus, in all the extant genera the cupules are formed of a pair, or two pairs, of bracteoles. A homologous derivation can be assumed for the *Baisianthus* cupules, with a pair of bracteoles free and the other pair connate. However the fossil genus differs from the extant genera in the branching mode, the sporangiophores bearing the lateral, as well as the terminal synangia. It differs also in the pollen grain morphology that is peculiar among gymnosperms, although perhaps derivable from a monosaccate form. Caveate pollen grains occur in advanced angiosperms, such as the Compositae (Asteraceae) where the cavity is formed by separation along the infratectum/foot layer boundary (BOLICK 1978) and is probably non-homologous to that of the fossil form. Some closer related forms can perhaps be found among the early angiosperms, such as *Retimonocolpites* with the reticulum loosely attached to the nexinal body (WALKER & WALKER 1984).

Genus *Eoantha* KRASSILOV

Eoantha zberikhinii KRASSILOV

Plates 6, 7

Eoantha zberikhinii: KRASSILOV 1986, p. 10, Plates 1–2.

Previous findings: The genus was based on two specimens of detached flower-like structures with a bracteate perianth and a four-lobed gynoeceium, each cupulate lobe bearing a solitary orthotropous ovule. The floral axis protrudes over the gynoeceium and bears a terminal tuft of linear bracts (KRASSILOV 1986). The structure was interpreted as corresponding to the proximal floral node of a gnetalean spike, with the next node reduced to a tuft of bracts and analogous to the corona of a bennettitalean flower. Polyplicate pollen grains were found in the pollen chambers of two ovules. In one of the specimens, the bracts and gynoeceial lobes were adpressed while in the other they were spread in the bedding plane.

Description of new material: The recently found third specimen (Pl. 6, Fig. 31) is a closed flower, wedge-shaped, 3 mm broad, attached by a stalk 2 mm long to an axis that is broken 3 mm above and 4 mm below the point of attachment. The axis is about 1 mm thick, with a few ribs marking vascular bundles. Fragments of the compressed vascular bundles were studied with SEM revealing tracheary elements about 10 μm across intermingled with the equal or broader fibres (Pl. 7, Fig. 39). The tracheary elements show irregular helical-reticulate thickenings and bordered pits (with the bordering occasionally more distinct than in the figured fragment). The pitting of the radial wall is uniseriate or occasionally biseriate, with the pit spacing typically about 2–3 pit diameters, but sometimes closer. The apertures are circular, about 5 μm in diameters. The fibers show irregularly scattered small and large pits, the latter circular, up to 3 μm in diameter.

The flower-like structure consists of a relatively massive obconical receptacle 1.8 mm long bearing a gynoeceium of four adpressed cupules 2.2 mm long. It is crowned by bracts that extend up to 3 mm over the gynoeceium. The inner walls of the cupules show a characteristic pattern of reticulate ribs. The ovules are

preserved as compressions attached at the base of the cupules, with the rib pattern of the latter imprinted on their coats. One of the ovules (Pl. 6, Fig. 33) was cleared, showing, in addition to the features described by KRASSILOV (1986), a low chalazal platform 300 μm wide, pierced by a number of holes (Pl. 7, Fig. 36) perhaps marking entries of the vascular bundles that might not extend above the chalaza. The megaspore membrane is exceptionally well-preserved, showing distinct or occasionally coalescent granules (Pl. 7, Figs. 37, 38). The pollen chamber is scarcely defined. No pollen grains were found adhering to the nucellar apex.

Remarks: The newly found specimen seems to represent an earlier developmental stage than those described in KRASSILOV (1986), with the nucellar pollen chamber yet not defined. On the other hand, the chalazal platform was not observed in the previously described material. In spite of the widely held opinion that gnetalean ovules lack a megaspore membrane (sometimes even influencing taxonomic assignments, see REYMANÓWNA 1968), it is here confirmed as a constant feature of *Eoantha*. New data on the tracheary elements of the axis bearing an *Eoantha* flower are important as they suggest the possibility of assigning the associated graminoid leaves *Praeherba spathulata* to the *Eoantha* plant.

Genus *Praeherba* KRASSILOV et BUGDAEVA, gen. nov.

Type species: *Praeherba spathulata* KRASSILOV et BUGDAEVA, sp. nov.

Derivation of name: *Prae*, before and *herba*, grass.

Diagnosis: As for the type-species.

Praeherba spathulata KRASSILOV et BUGDAEVA, sp. nov.

Plate 8

Holotype: N° 31-265, Institute of Biology and Pedology, Vladivostok., Pl. 8, Figs. 40–41.

Locality: Left bank of the Vitim River downstream of the mouth of its tributary Sololy Creek, Transbaikalia.

Age: Early Cretaceous, Hauterivian–Barremian.

Derivation of name: *spathulata*, spatulate, spoon-like, referring to the shape of the leaf.

Diagnosis: Stem articulate with scattered vascular bundles. Tracheary elements of the latter with large bordered pits and with irregular helical-reticulate thickenings. Leaves sheathing, sessile, veins parallel with thin cross-veins, showing an arcuate groove at base and small appendages at the blade–sheath junction. Stomata contiguous in longitudinal intercostal files.

Description: The material consists of two specimens, the better preserved (Pl. 8, Fig. 41) shows a tubular stem bearing an incompletely preserved leaf torn at the apex. The stem is 4 mm thick at base, with internode 70 mm long and the leaf node 2.5 mm thick. It is traversed by five vascular bundles that are partly preserved as compressed xylem. Maceration of the latter revealed tracheary elements intermingled with fibers. The tracheary elements are about 7–8 μm across, with irregular helical-reticulate thickenings and with large bordered pits, the latter are uniseriate or occasionally in two alternate series, with a pit spacing of about two pit diameters. The pit apertures are elliptical, about 3–4 μm long. The fibers show a thin reticulate striation and pits of two sizes.

The leaf blade is 7 mm broad, constricted at the base, plicate and irregularly lacerate distally, with about 14 parallel veins. The blade–sheath junction is marked by a broad arcuate ridge showing large tabloid cells. Two minute reflexed or pending appendages are discernible on the flanks of the arcuate zone. The leaf cuticle is very thin and difficult to separate from the mesophyll. Cleared fragments of the leaf blade show dense cross-veins traversing the intercostal stomatal grooves (Pl. 8, Fig. 42). The stomatal grooves contain longitudinal files of contiguous stomata with elliptical stomatal pits about 30 μm long, bordered by a prominent ridge. The guard cells are poorly preserved and the apertures appear as longitudinal slits or else sealed by a ridge (Pl. 8, Figs. 43–45). The stomata give an impression of being stretched by the continuing intercalary elongation of the blade.

Remarks: Vascular elements are described in the reproductive structures *Baisianthus*, *Vitimantha* and *Eoantha* which are associated with the graminoid foliar organs *Praeherba*. The tracheary elements of the leaves are most similar to those of *Eoantha* in the irregular helical-reticulate secondary thickenings as well as in the shape and disposition of the large bordered pits, although in *Praeherba* the pit apertures are elliptical rather than circular, as in *Eoantha*. These comparisons suggest that *Praeherba* leaves might belong to the plant that produced the *Eoantha* pistillate flower-like structures and polypllicate *Ephedripites*-type pollen grains. This plant would then be reconstructed as herbaceous, with graminoid leaves and perhaps with an apical raceme of declinous flowers.

Comparison: In addition to the general graminoid aspect of the parallelveined leaves, *Praeherba* shows an arcuate ligule-like ridge of large tabloid cells at the base of the leaf blade, lateral appendages resembling auriculae, cross-veins, and intercostal files of contiguous stomata. *Graminophyllum primum* KRASSILOV from the Lower Cretaceous of Mongolia is similar, but anatomical features are not preserved in that species. It differs from the Baisian fossil in the broader leaf blade that is not constricted at the base, as well as in the more prominent auricles. Perhaps the generic name *Graminophyllum* (CONWENTZ 1886) should be reserved for fossil leaves of a graminoid aspect not showing micromorphological features.

Genus *Vitimantha* KRASSILOV et BUGDAEVA, gen. nov.

Type species: *Vitimantha crypta* KRASSILOV et BUGDAEVA, sp. nov.

Derivation of name: From the Vitim River and *anthus*, flower.

Diagnosis: Flower-like organ, having a long pedicel and a perianth of four bracts subtending follicle-like structures. Bracts showing dichotomous-reticulate venation. Follicle-like structures shorter than the bracts, narrow ovate, with attenuate apex and with a prominent adaxial groove. Cuticle of the ridges flanking the adaxial groove with a network of papillate ribs (that may capture polypllicate pollen grains). Vascular traces of the follicular structures consisting of pitted fibres and of tracheary elements with helical and scalariform thickenings.

Vitimantha crypta KRASSILOV et BUGDAEVA, sp. nov.

Plates 9, 10, Text-fig. 2

Holotype: N° 31-243, Institute of Biology and Pedology, Vladivostok, Plate 9, Figs. 49–50.

Locality: Left bank of the Vitim River downstream of the mouth of its tributary Sololy Creek, Transbaikalia.

Age: Early Cretaceous, Hauterivian–Barremian.

Derivation of name: *crypta*, hidden.

Diagnosis: As for the genus.

Description: The material consists of an impression of a flower-like structure showing a pedicel more than 10 mm long (whole length unknown), 1 mm thick, with 7 distinct longitudinal ribs. The pedicel is distally expanded into a broad receptacle bearing four petaloid bracts peripheral to four follicle-like organs. Vascular traces of the latter are partly preserved as a coaly compression consisting of fibers and tracheary elements. The fibers are long thick-walled cells 3–6 μm broad, with large and small unbordered pits on the radial walls (Pl. 9, Fig. 53). The tracheary elements are about 4–5 μm broad, with tightly coiled helical, occasionally reticulate, thickenings (Pl. 9, Fig. 54). Terminations of the tracheary elements (Pl. 9, Figs. 51, 52) show scalariform bars interconnected by vertical bars, perhaps with perforations between the latter, but this feature will have to be confirmed in better preserved material.

The bracts are spread at a wide angle and are irregularly curved and folded. Two of them are exposed on the bedding plane and the other two are partly immersed in the rock matrix below the follicles, suggesting they are soft and flexible laminar structures that might have been originally disposed radially or decussate, but are now flattened by compression. The better preserved bract (left in Pl. 9, Fig. 49) is oblanceolate, about 7 mm long, 4.5 mm broad, constricted and apparently twisted at the base, with a distinct pattern of dichotomous and occasionally anastomosing veins. At least two veins are discernible in the basal part of the

bract. They fork repeatedly and unequally at an acute angle, their branches spreading flabellately, with anastomoses formed of the criss-crossed or steeply converging branches that give rise to a longer vein (Text-fig. 2).

The follicular structures are crowded in the central part of the receptacle and are not exactly in one plane. They are sessile, narrow-ovate, with a long attenuate apex that is preserved in a single follicle only (right in Pl. 9, Fig. 50). This follicle is 5 mm long, 4 mm broad at the base, turned parallel to the bedding plane and thickened at the adaxial margin. A median follicle next to it shows a distinct adaxial groove. Cuticular ridges flanking the groove were macerated and studied with an SEM. The cuticle shows an irregular reticulate pattern of thick anastomosing ribs covered with small papillae (Pl. 10, Figs. 55, 56). A clump of overlapping pollen grains, perhaps of a tetrad that fell apart, was found stuck to the cuticle fragment shown in Pl. 10, Fig. 57. The pollen grains are polyplicate, elliptical, 30 μm long, 15 μm broad, with thickened ends and indistinct auriculae (Pl. 10, Fig. 60). A grain in proximal view (Pl. 10, Fig. 59) shows a thin straight median line and four flat ribs, or taeniae, diverging at an acute angle on each side. Another grain is positioned in an oblique distal view (Pl. 10, Fig. 58) showing a sulcus that extends almost the whole length of the grain and is bordered with thick ridges. The taeniae are parallel to the sulcus, psilate, of unequal width ranging from 1 μm to 1.6 μm , divided by thin shallow furrows that are neither clefted nor gaping or only occasionally so, perhaps due to bending of the taeniae under pressure.

Remarks: Since ovules were not obtained from the follicle-like structures, their interpretation as gynoecial organs remains tentative at the moment. The pollen grains sticking to papillate ridges flanking the adaxial groove may suggest sutural stigmatic crests of a follicular carpel or cupule. Alternatively, the follicle-like organs could be sporangiophore cupules shedding pollen grains. However an attenuate apical beak is quite unusual in a sporangiophore cupule, thus supporting a pistillate, rather than staminate, interpretation of the follicle-like organs.

Comparison: Superficially at least, *Vitimantha* resembles a pistillate flower with a monochlamydeous perianth of bracteate petals and possible gynoecial organs similar to the ascidiform follicles of, e.g., *Sarcandra* and other chloranthacean genera. If actually derived from two decussate pairs of bracteate follicles, this flower-like structure is comparable to the gynoecial pseudanthia of *Cercidiphyllum*, another archaic angiosperm. However, these comparisons may not reflect taxonomic proximity or phylogenetic affinities. Judging by the pollen grain morphology, *Vitimantha* belongs to the plexus of gnetalean proangiosperms that includes *Eoantha*, another pedicellate flower-like structure from the same locality. These two differ, however, in their bract and cupule morphologies. Polyplicate pollen grains found in the pollen chambers of *Eoantha* are inaperturate, with clefts between the ribs rather than being monosulcate and differ from those associated with *Vitimantha* in more spirally oriented ribs and unthickened ends. In spite of these differences, *Vitimantha* is here conceived of as a variation of the *Eoantha* theme, but even closer to a conventional flower.

4. Conclusion

Bearing in mind that fossil gnetophytes are rare and only recently discovered, three genera from a single plant-bed, with a good prospect of additional finds, is a considerable diversity. Moreover, these genera show such morphological features as a diminution of floral parts that are considerably smaller than in both the earlier Mesozoic and extant gnetophytes and, in the case of *Eoantha* and *Vitimantha*, a reduction in the numbers of reproductive nodes to a single floral node as a step in their transformation into flower-like proangiospermous structures. Because of similar tracheary elements and their association, the graminoid foliar organs *Praeherba spathulata* are assigned to the *Eoantha* plant thus increasing its previously postulated (KRASSILOV 1986) phylogenetic significance as a possible link between gnetophytes and angiosperms.

Insofar as the Baisian gnetophytes are associated with the proangiospermous *Baisia*, as well as with early angiosperms, we can speak of a strong innovative drive distinguishing this Early Cretaceous assemblage from most contemporaneous fossil floras. There are a few similar assemblages in other parts of the world. Palaeoecological evidence of mass mortalities among aquatic organisms coming from the same strata

suggest environmental events, such as acid rains, with disturbing effect on the wetland vegetation. Frequent disturbance might create a potential niche for herbaceous colonizers that first appeared among gnetophytes as the ecological, and probably also phylogenetic, precursors of angiospermous herbs.

5. Acknowledgements

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7. Explanation of plates

Plate 1

Baisianthus ramosus gen. et sp. nov.

- Figs. 1–5. Reproductive shoot morphology.
Fig. 1. Holotype, shoot with sporangiophore whorls terminal on lateral branches of the lower node and sessile at subsequent nodes, the distal ones crowded and almost contiguous, 7×. Specimen N° 31-309.
Fig. 2. Three fertile shoots, their arrangement suggesting a cluster, 7×. Specimen N° 31-310.
Fig. 3. Shoot bearing two distinct sporangiophore whorls distally, 7×. Specimen N° 31-443.
Fig. 4. A larger shoot showing a candelabrum arrangement of lateral branches; a slender shoot with sterile branches (left) does not actually belong to the larger shoot, 10×. Specimen N° 31-26.
Fig. 5. Part of Fig. 3 enlarged to show bracts and cupules of sporangiophore whorls, 10×.

Plate 2

Baisianthus ramosus gen. et sp. nov.

- Figs. 6–11. Vascular elements of shoot axis, SEM. Specimen N° 31-435, counterpart of the specimen shown in Fig. 3.
Fig. 6. Tracheary elements with helical thickenings and segmented with rhomboid pits, 900×.
Fig. 7. Part of Fig. 6 enlarged to show the pattern of tight helical, occasionally reticulate, thickenings, 2700×.
Fig. 8. Tracheary element showing reticulate secondary thickenings, large pits and a network of thin striation on the tertiary wall, 4000×.
Fig. 9. Part of Fig. 6 enlarged to show a warty surface of the primary wall and pits, 2400×.
Fig. 10. End of a tracheary element (right) with the helical thickenings transformed into scalariform perforation, 2100×.
Fig. 11. Tracheary element with equidistant rhomboid pits and partly preserved secondary wall showing helical-reticulate thickenings, 2400×.

Plate 3

Baisianthus ramosus gen. et sp. nov.

- Figs. 12–18. Sporangioophores and cupules. Specimen N° 31-181.
Fig. 12. Sporangioophore with synangia on short lateral branches and terminal, 40×.
Fig. 13. Sporangioophore node with one cupule split (center) showing immature sporangioophore inside (arrow), 25×.
Fig. 14. Pair of cupules, the left one showing outlines of a branching sporangioophore inside (arrow), 25×.
Fig. 15. Sporangioophore whorl showing terminal synangia, 25×.
Fig. 16. Vascular bundle of a sporangioophore from the whorl shown in Fig. 15, with an oval scar, supposedly of a resin body, in the middle, SEM, 1100×.
Fig. 17. Part of Fig. 16 enlarged to show a junction of tracheary elements with scalariform perforations, SEM, 2600×.
Fig. 18. Bracteole obtained by maceration of the whorl shown in Fig. 15, with adhering pollen grains, SEM, 200×.

Plate 4

Baisianthus ramosus gen. et sp. nov.

- Figs. 19–24. Synangia and sporangia, SEM. Specimen N° 31-181.
Fig. 19. Three-lobed synangium, with pollen grains adhering near the crack at the base, 210×.
Fig. 20. Pollen mass of immature sporangium; tetrads are visible along the left margin, 450×.
Fig. 21. Two sporangia terminal on sporangiophore branches, 130×.
Fig. 22. Part of the left sporangium shown in Fig. 21, stomium of tabloid cells, 500×.
Fig. 23. Synangium showing pollen masses of four sporangia, 300×.
Fig. 24. Split synangium showing central column (arrow), 500×.

Plate 5

Baisianthus ramosus gen. et sp. nov.

- Figs. 25–30. Pollen grains from sporangia shown in Figs. 21 and 24, SEM.
Fig. 25. Several grains and a nexinal body (center) apparently squeezed from the sexine under it, 2500×.
Fig. 26. Nexinal body, 3000×.
Fig. 27. Split pollen grain showing outlines of nexinal body, 3000×.

- Fig. 28. Part of grain shown in Fig. 25 (upper left) with nexinal body protruding from the gaping sulcus, 9000×.
Fig. 29. Sexinal folds of a bisaccate configuration, 2500×.
Fig. 30. Orbicule on a pollen grain (center), 2500×.

Plate 6

Eoantha zherikhinii KRASSILOV

- Fig. 31. Flower-like structure attached to an axis, 15×. Specimen N° 31-511.
Fig. 32. Part of Fig. 31 showing gynoeceium lobes (g) and bracts (b), 18×.
Fig. 33. Part of Fig. 31 showing ovule, 27×.

Plate 7

Eoantha zherikhinii KRASSILOV

- Fig. 34. Nucellus of the ovule shown in Fig. 33, SEM, 50×.
Fig. 35. Nucellar tissue overlapping the megaspore membrane, 100×.
Fig. 36. Nucellar platform with pits, supposedly of chalazal vascular bundles, 800×.
Figs. 37–38. Megaspore membrane, 3000× (Figs. 37) and 650× (Fig. 38).
Fig. 39. Tracheary elements of the axis with helical-reticulate thickenings and pits (arrows), 1000×.

Plate 8

Praeherba spathulata gen. et sp. nov.

- Figs. 40, 41. Holotype, graminoid leaf with plicate parallelnerve blade showing arcuate zone and a minute pendent appendage at base, 1× (Fig. 41) and 8× (Fig. 40). Specimen N° 31-265.
Fig. 42. Cross-vein, SEM, 320×.
Fig. 43. File of stomata longitudinally stretched by elongation of the leaf blade, SEM, 690×.
Figs. 44, 45. Contiguous stomata of an intercostal file, SEM, 750×.
Fig. 46. Vascular bundles of the axis, 15×.
Figs. 47, 48. Tracheary elements of the vascular bundles showing helical-reticulate thickenings and elongate pits; fibres are minutely pitted, 1400× (Fig. 48) and 3000× (Fig. 47).

Plate 9

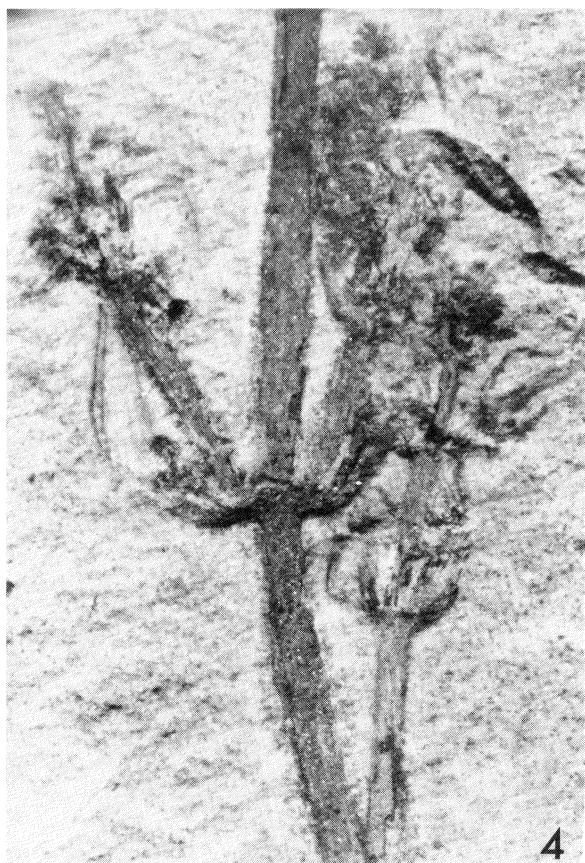
Vitimantha crypta gen. et sp. nov.

- Fig. 49. Holotype, pedicellate flower-like structure showing perianth bracts with dichotomous-reticulate venation (left) and follicle-like structures in the middle, 6×. Specimen N° 31-243.
Fig. 50. Part of Fig. 50 enlarged to show follicle-like structures, the right one with attenuate apex preserved, 10×.
Figs. 51–54. Vascular elements of the traces seen as dark areas on the receptacle in Fig. 51, SEM.
Figs. 51, 52. Fibres and tracheary elements, the latter showing scalariform bars interconnected by vertical bars, 2500×.
Fig. 53. Fibres with large and small pits, 2500×.
Fig. 54. Tracheary elements with tight helical thickenings, 2200×.

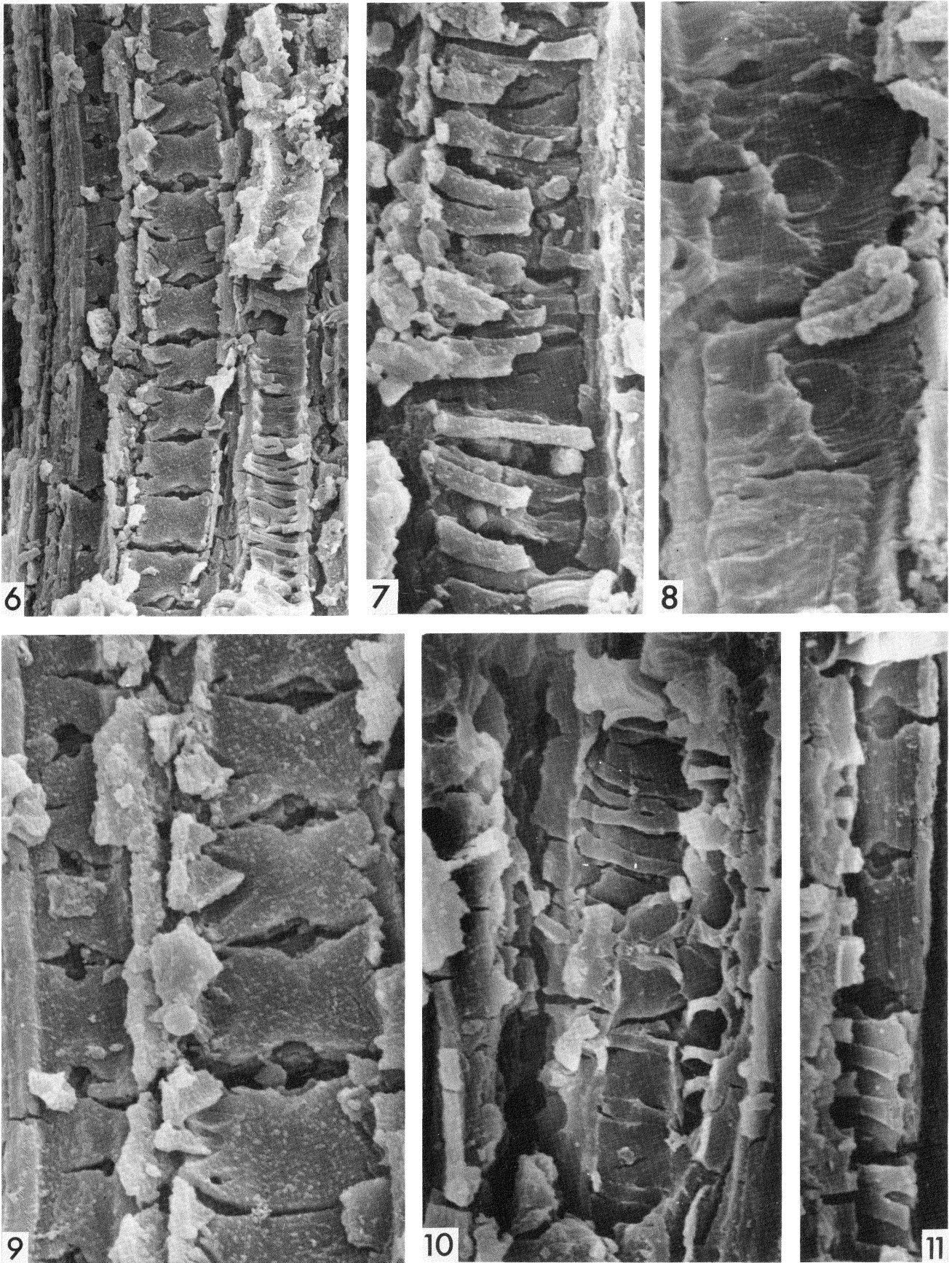
Plate 10

Vitimantha crypta gen. et sp. nov.

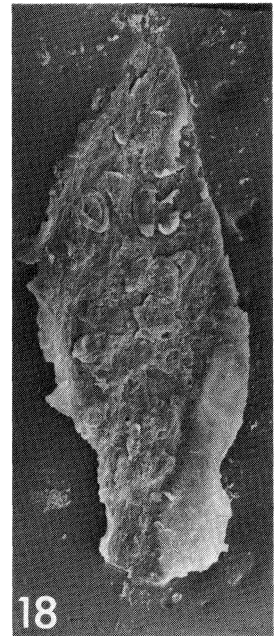
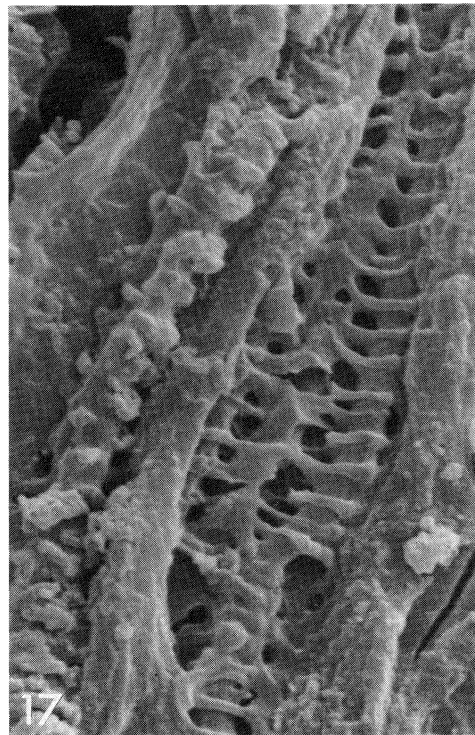
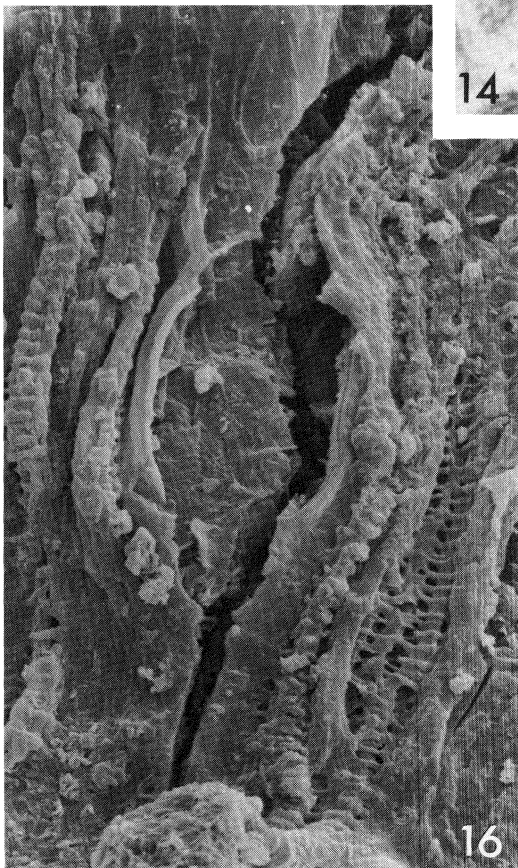
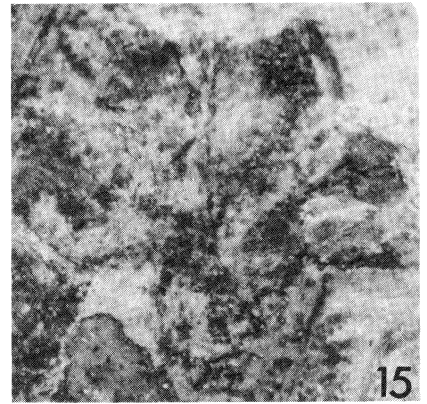
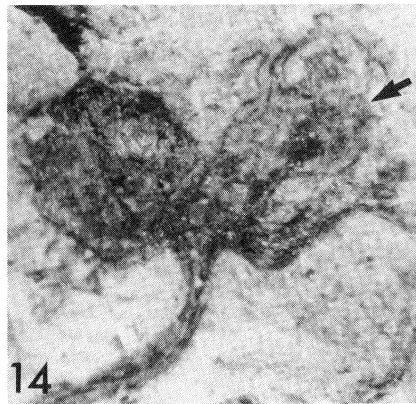
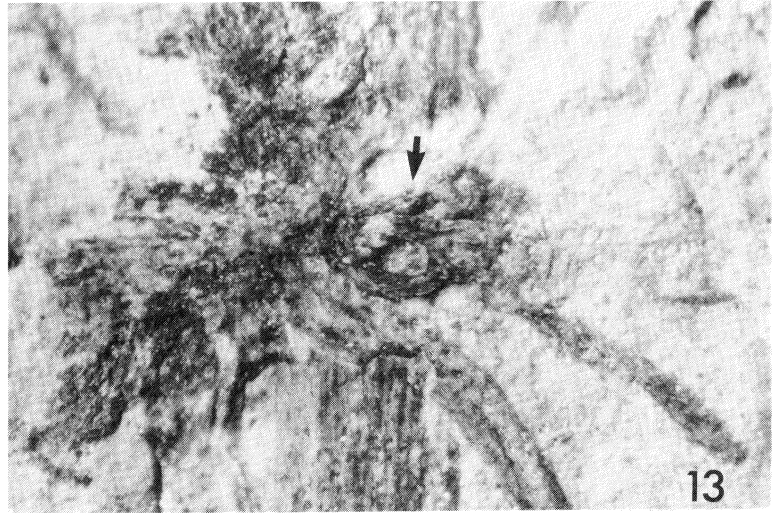
- Figs. 55–60. Cuticle flanking the adaxial groove of a follicle-like structure shown in Fig. 50, with adhering pollen grains, SEM.
Fig. 55. Network of anastomosing ribs on the cuticle, 900×.
Fig. 56. Papillae on the cuticle ribs, 3000×.
Fig. 57. Clump of polylicate pollen grains, 1500×.
Fig. 58. Sulcus and bordering ribs of a pollen grain, 6500×.
Fig. 59. Ribs diverging from the median line on the proximal face of a pollen grain, 2500×.
Fig. 60. Pollen grains showing thickened ends, with indistinct auricule (left), 3000×.



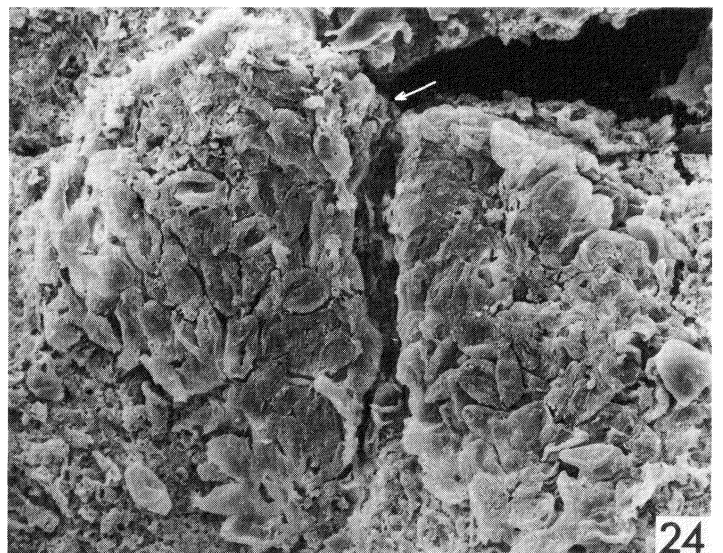
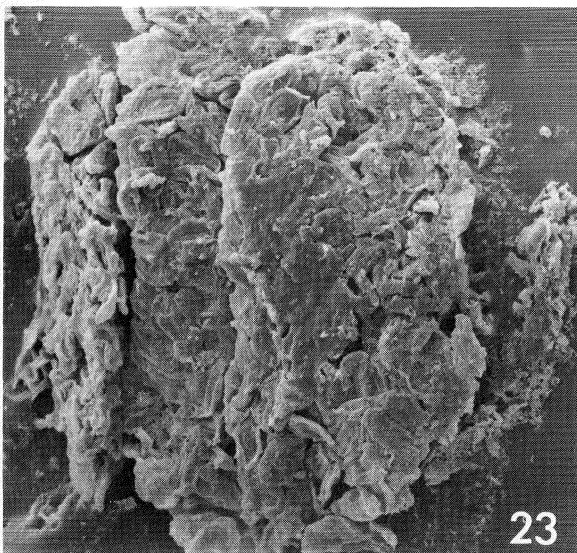
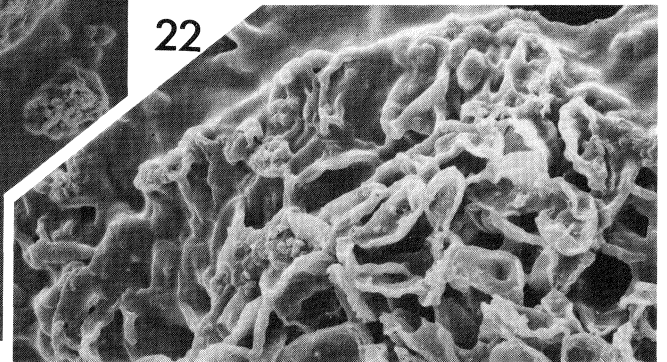
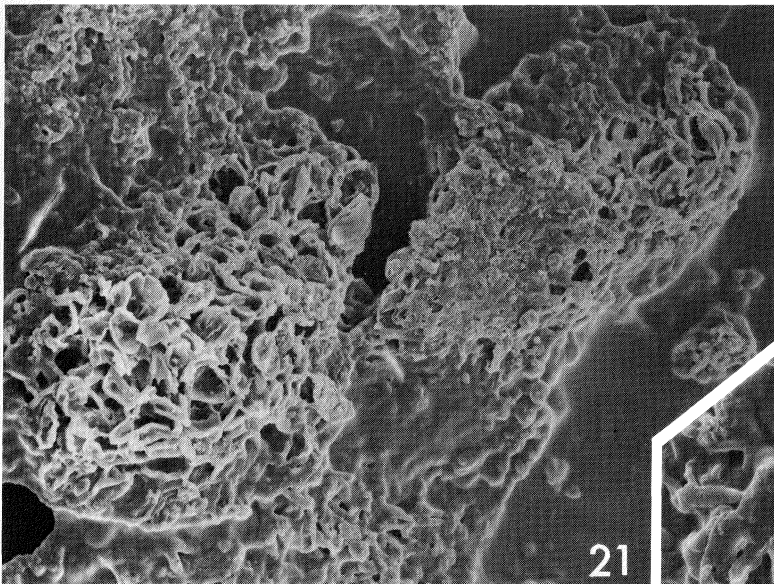
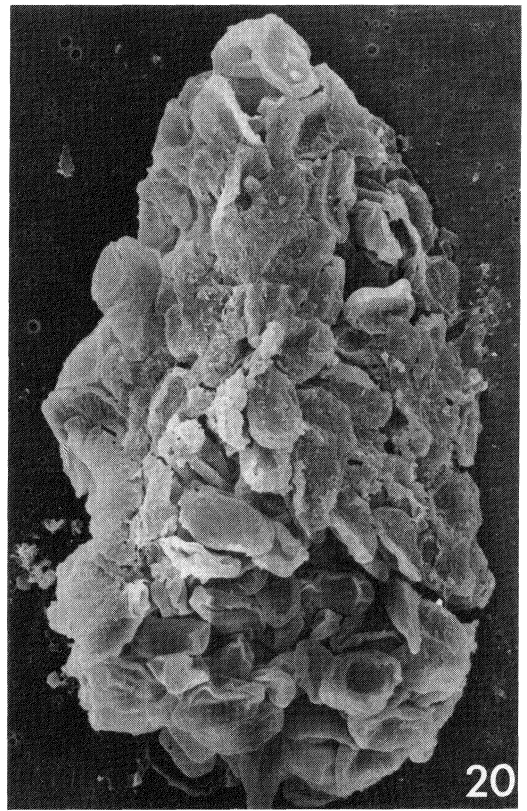
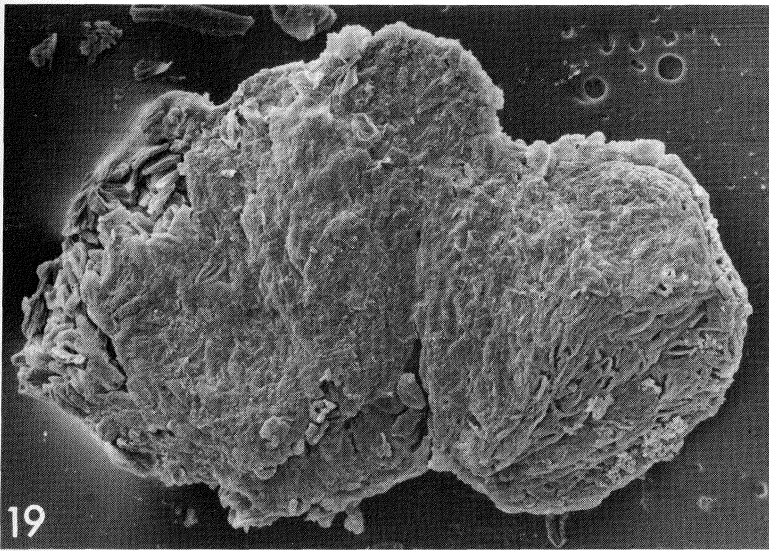
Krassilov, V. A. & Bugdaeva, E. V.: Early Cretaceous gnetophyte assemblage.



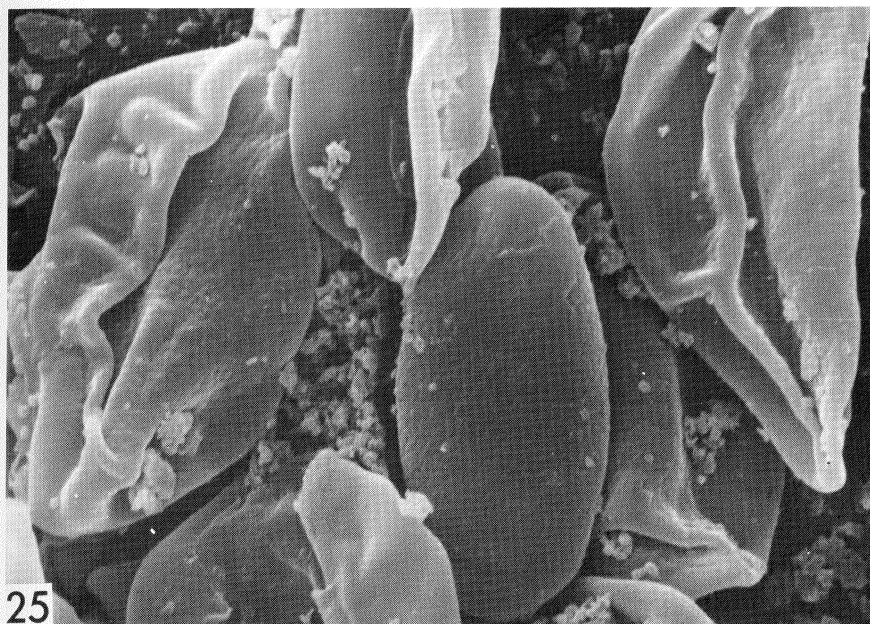
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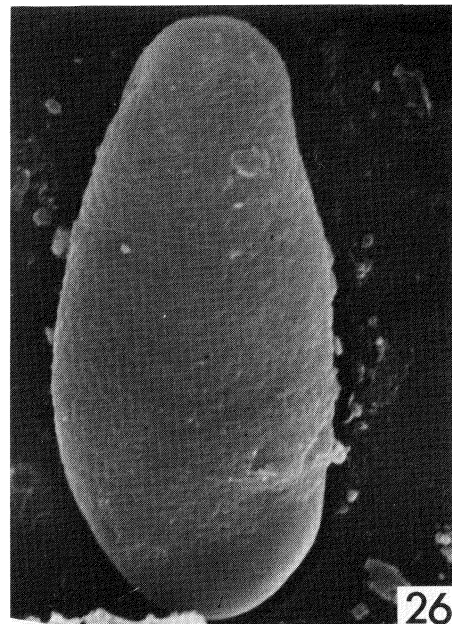
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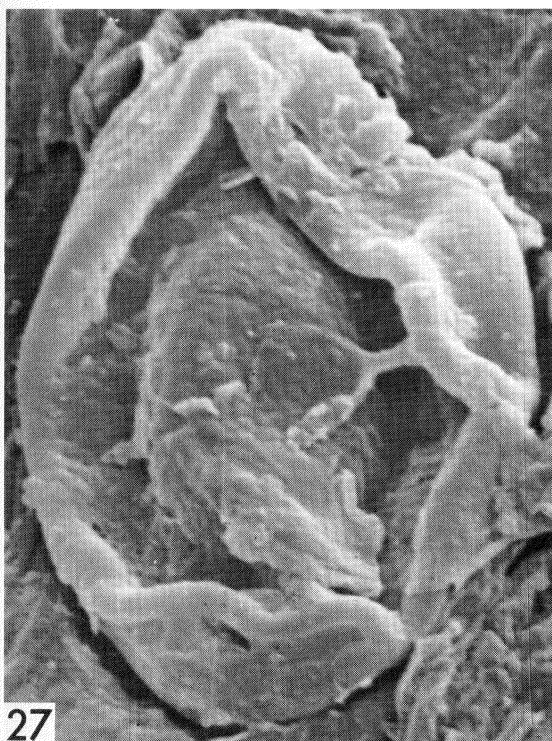
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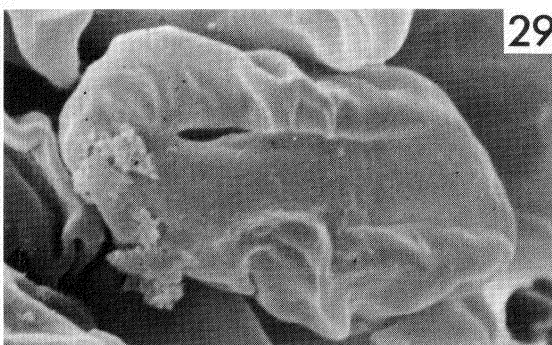
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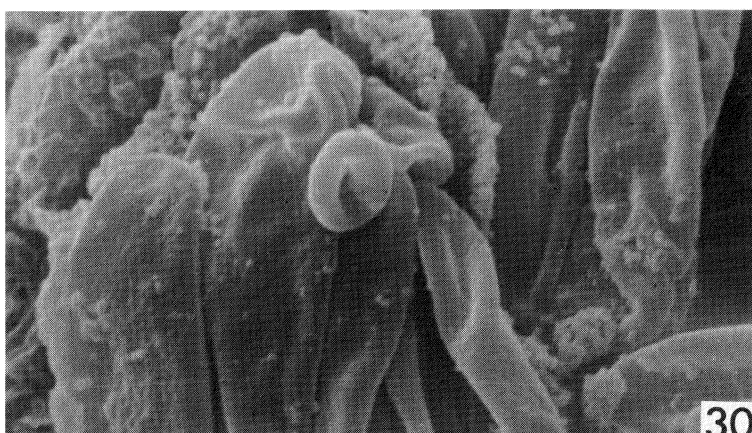
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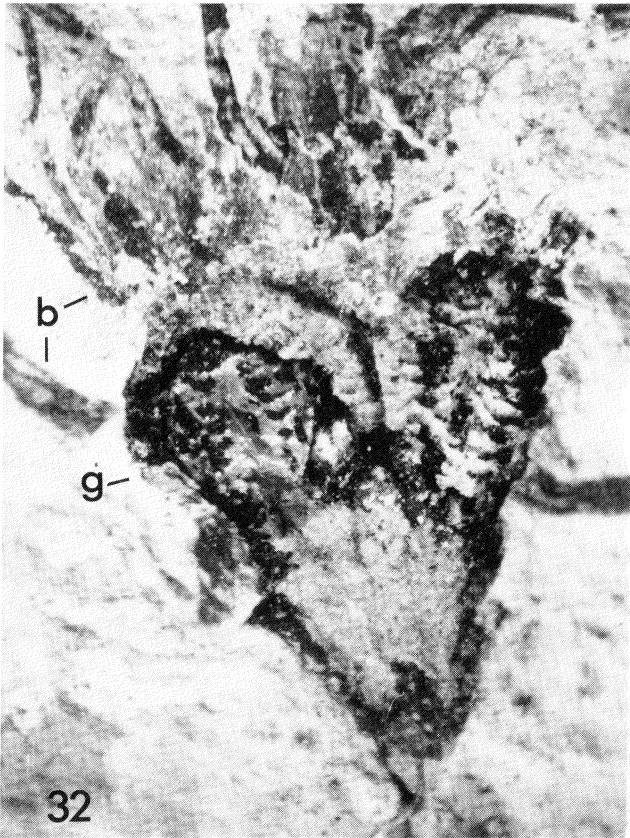
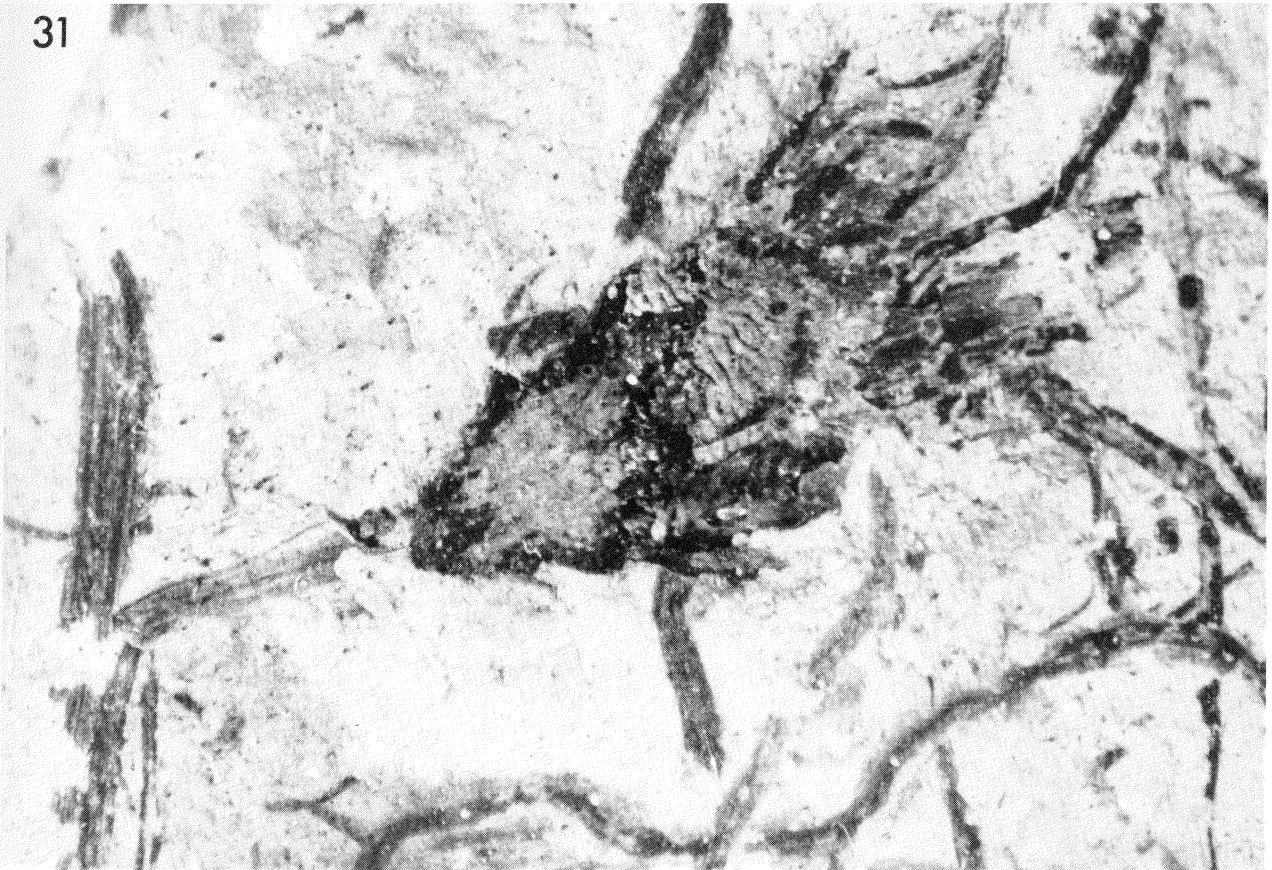
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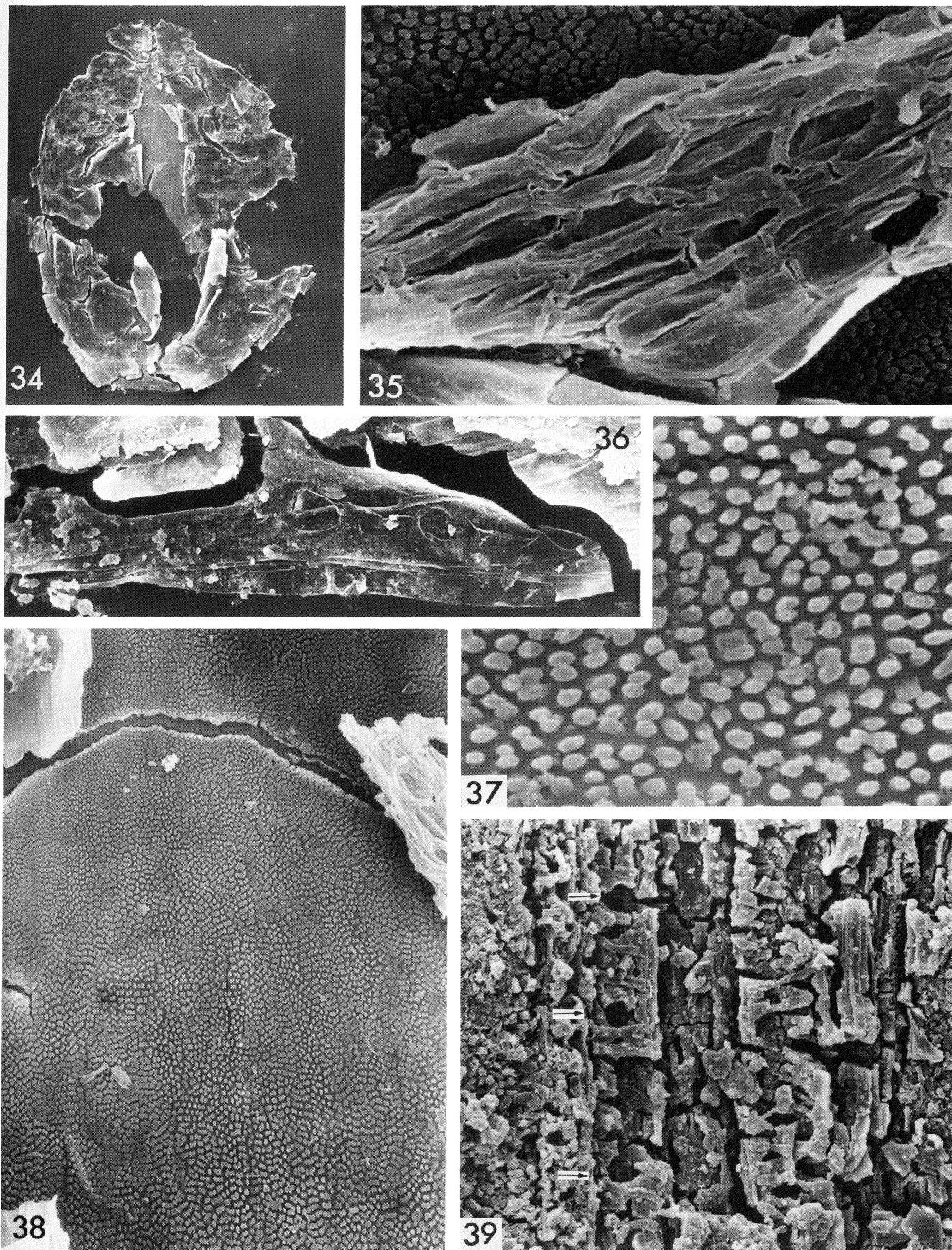
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Krassilov, V. A. & Bugdaeva, E. V.: Early Cretaceous gnetophyte assemblage.

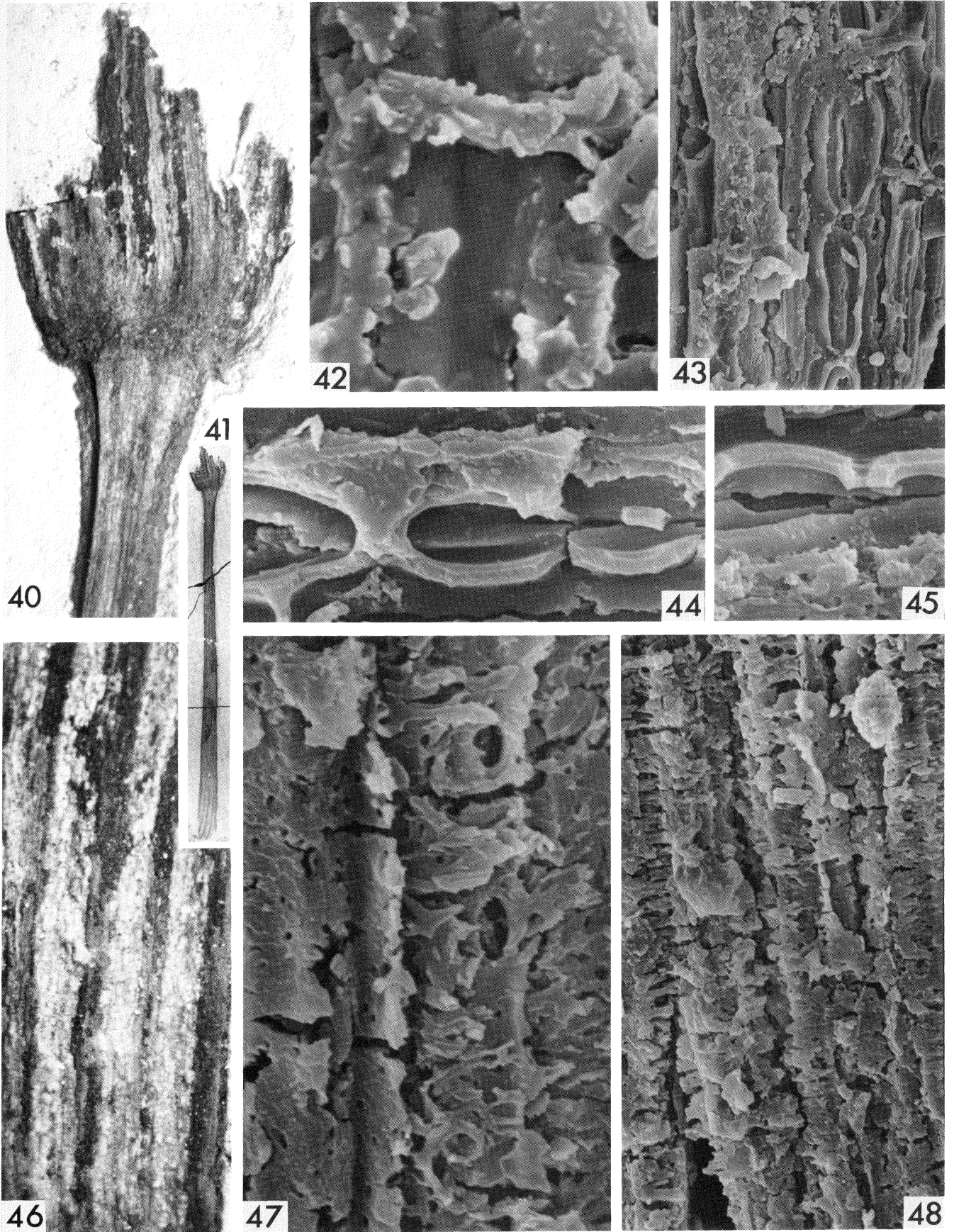
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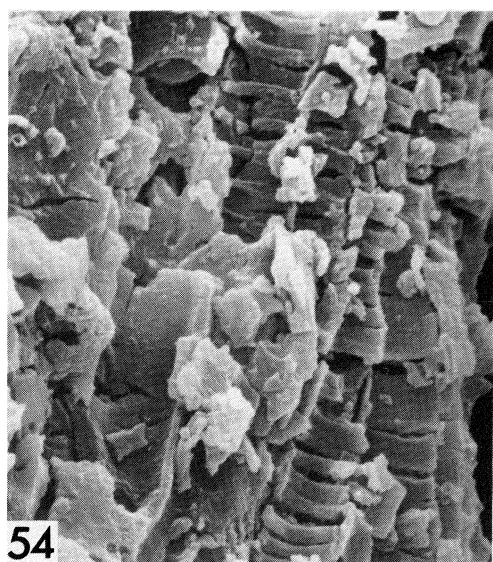
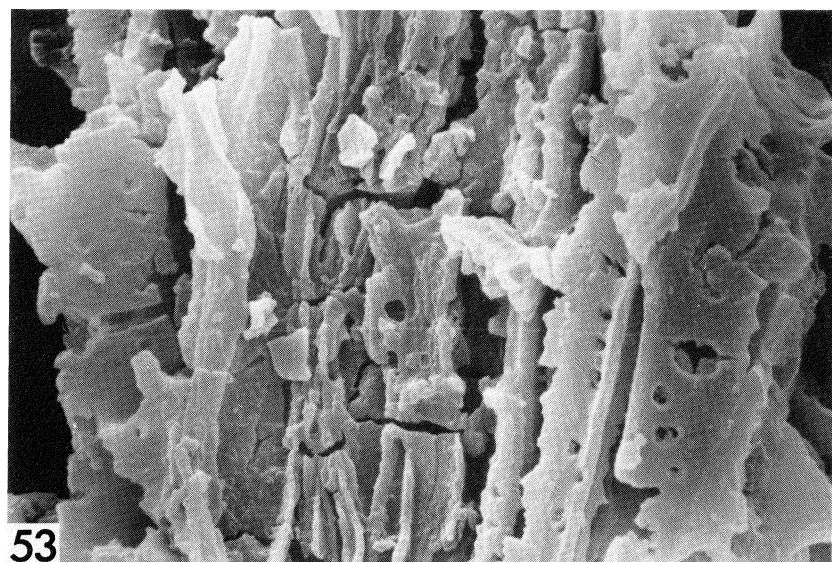
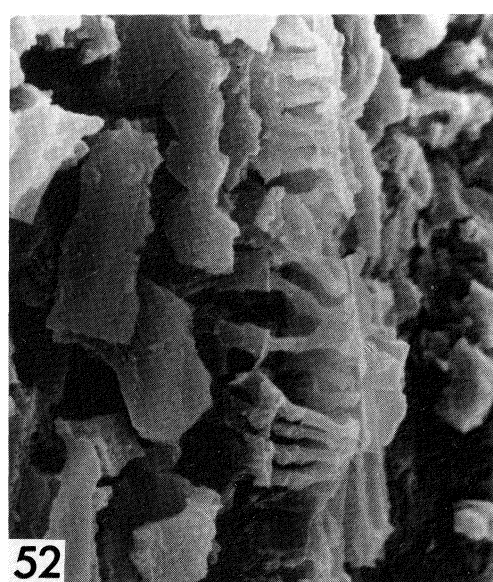
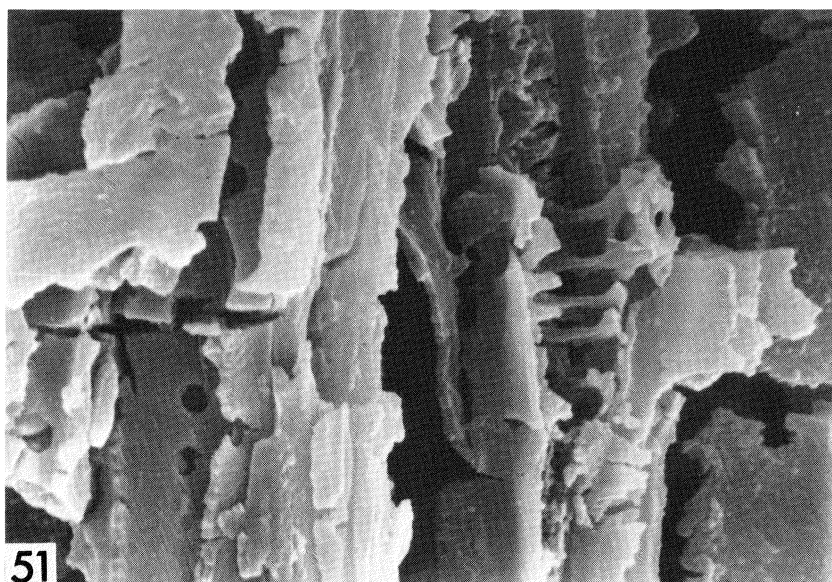
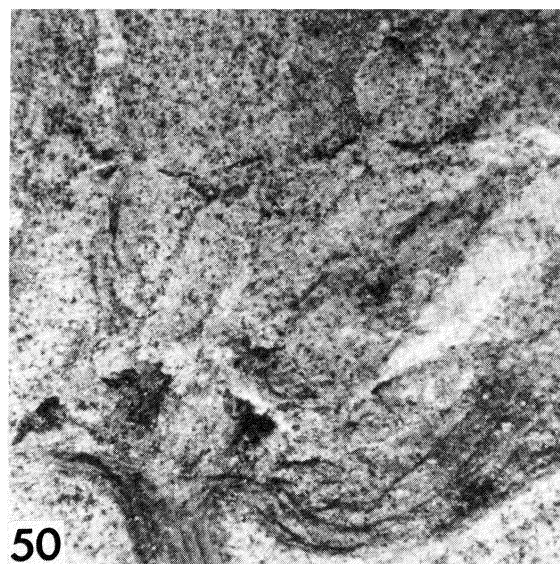
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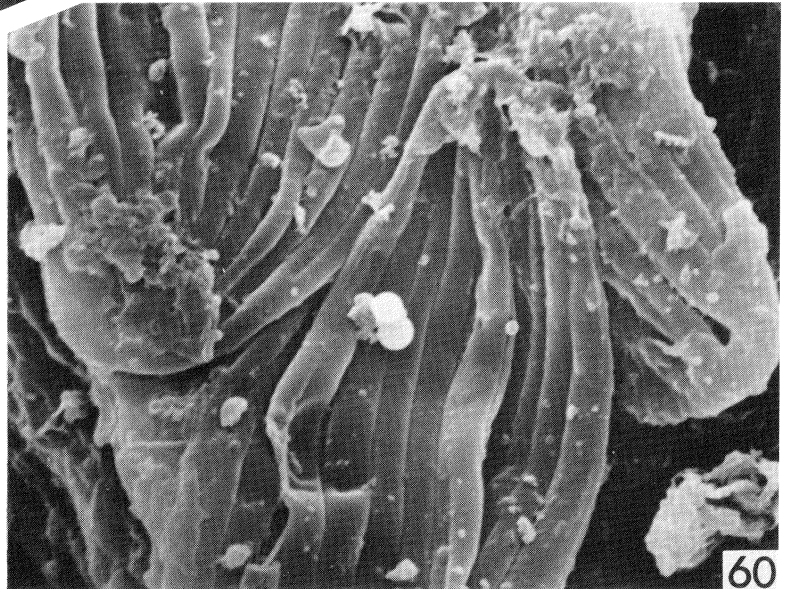
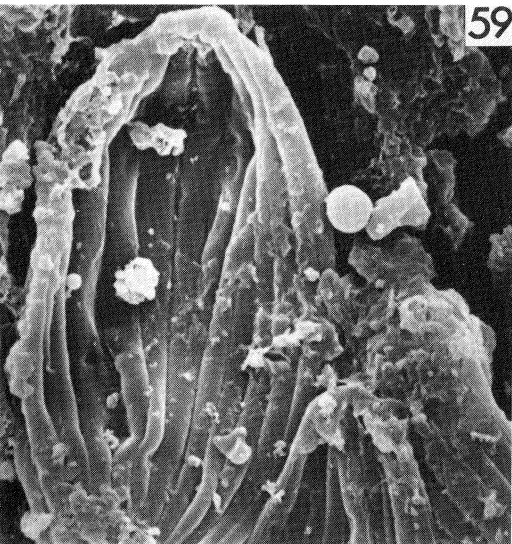
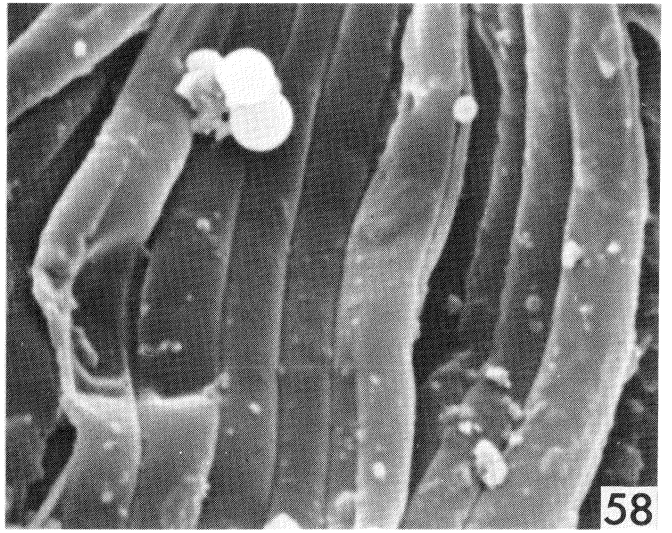
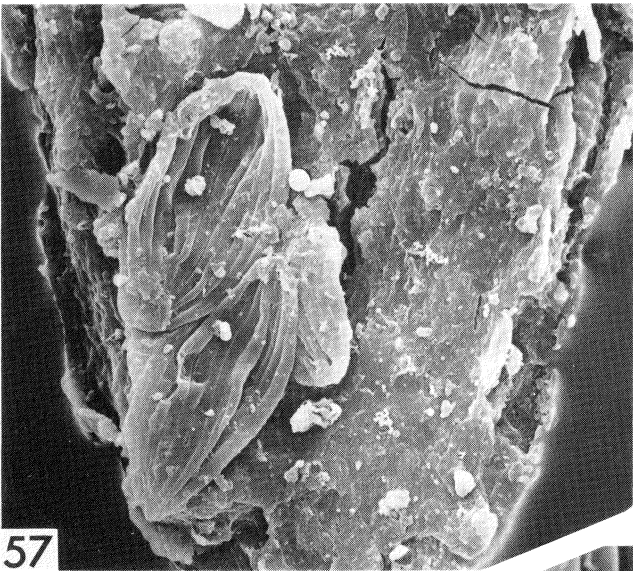
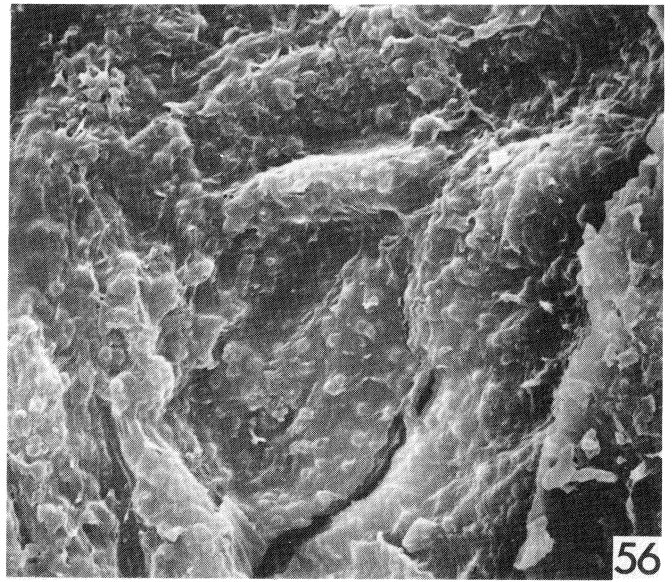
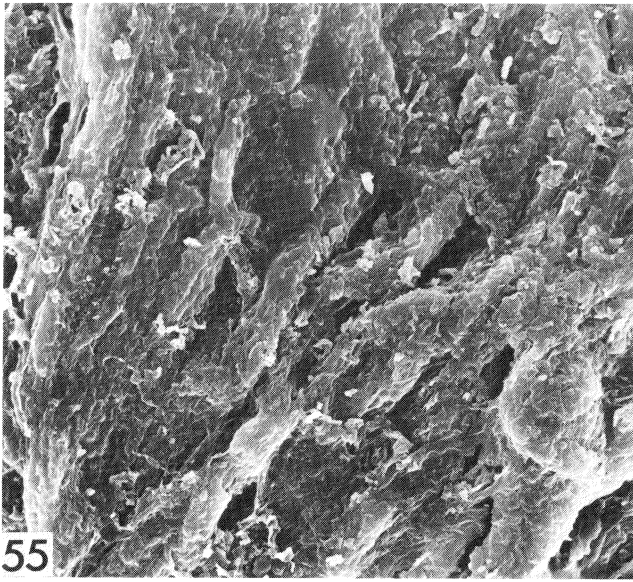
Krassilov, V. A. & Bugdaeva, E. V.: Early Cretaceous gnetophyte assemblage.



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