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Pollen genus *Eucommiidites*: ultrastructure and affinities

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ABSTRACT. Pollen grains of *Eucommiidites* type were produced by Mesozoic gymnosperms of supposedly gnetophytic affinities. Microsporangiate organs and seeds with *Eucommiidites* pollen in situ were recently assigned to an extinct family Erdtmanithecaceae of the order Erdtmanithecales. We studied micromorphology and ultrastructure (SEM, TEM) of in situ *Eucommiidites*-type pollen grains from pollen cones *Bayeritheca hughesii*, recently described from the Late Cretaceous of Bohemia, a putative member of the Erdtmanithecales, and *Hastystrobus muirii* from the Middle Jurassic of Yorkshire), which perhaps has a more conventional cycadophytic microsporophyll morphology. Pollen from both taxa show differences in configuration of lateral furrows and arrangement of infratectal granules. The pollen cones of *Aegianthus* (mid-Jurassic of Siberia) and *Loricanthus* (Early Cretaceous of Transbaikalia), macromorphologically similar to *Erdtmanitheca,* produced monosulcate pollen grains ultrastructurally similar to *Eucommiidites*, but lacking additional furrows, whereas in the trisulcate *Cryptosacciferites* and *Zolerella*, the ultrastructures are alveolate rather than granular, attesting to parallel development of *Eucommiidites* morphology in different groups of Mesozoic gymnosperms.

KEY WORDS: *Eucommiidites*, ultrastructure, pollen, gnetophytes, Mesozoic

INTRODUCTION

The genus *Eucommiidites* Erdman is based on dispersed Mesozoic pollen, and was first described as angiospermous (Erdtman 1948), but actually of a gymnospermous heteropolar morphology (Kuyl et al. 1955, Couper 1956). It has been found *in situ* in the pollen organs of *Erdtmanitheca* Pedersen et al. (1989), *Eucommiitheca* Friis and Pedersen (1996) and *Bayeritheca* Kvaček & Pacltová 2001). Additionally, it has been found repeatedly in the pollen chambers and micropyles of detached ovules (Hughes 1961, Brenner 1963, 1967, Reymanówna 1968, Pedersen et al 1989), which proves a gymnospermous mode of pollination in this plants. Eucommiidites is characterized by a median sulcus and additional sulci (furrows) parallel to it or joined into an encircling furrow. This apertural configuration has no close morphological analogues among extant pollen types, thereby conceivably is representing an extinct plant group (Friis & Pedersen 1996, Pedersen et al. 1989).

Based on morphology of the reproductive organs and the in situ *Eucommiidites* pollen Friis and Pedersen (1996) established a new family and order of seed plants, Erdtmanithecaceae – Erdtmanithecales, characterized by male organs with closely spaced peltate and stalked microsporangiate units bearing numerous radially arranged sporangia producing pollen grains of *Eucommiidites* type.

However, a wide range of variation in pollen ultrastructural characters (e.g.: Osborn 2000), may suggest that the group of Eucommiidites pollen is more diversified or even polyphyletic.

In this paper we describe the ultrastructure of *in situ Eucommiidites*-pollen from two pollen organs *Hastystrobus* from the Middle Jurassic of Yorkshire and *Bayeritheca* from the Late Cretaceous of the Czech Republic. Pollen from these organs is compared with *Cryptosacciferites,* a pollen morphotype with aperture configuration similar to that of *Eucommiidites* from the gut compression of a Cretaceous insect, as well as with the *in situ* pollen, distinct from *Eucommiidites*, but found in pollen organs of *Aegianthus sibiricus* and *Loricanthus resinifer* that are similar to those of *Eucommiidites*-producing plants (*Erdtmanitheca*). We attempt to assess morphological variability of the *Eucommiidites* morphotype and its taxonomic significance.

MATERIAL AND METHODS

Pollen grains of *Hastystrobus muirii* from the Middle Jurassic of Yorkshire, UK, and *Bayeritheca hughesii* from the Late Cretaceous, Cenomanian of Bohemia, Czech Republic, were extracted from fragments of respective pollen organs from the type material studied by van Konijnenburg-van Cittert (1971), and Kvaček and Pacltová (2001). We sectioned also in situ pollen grains of *Aegianthus sibiricus* from the mid-Jurassic of Ust'-Baley, Angara River, East Siberia (Krassilov & Bugdaeva 1988). For comparison, we utilized our ultrastructural data for in situ pollen grains of *Loricanthus resinifer* from the Early Cretaceous of Transbaikalia (Tekleva & Krassilov 2004) and *Cryptosacciferites pabularis* from gut compression of an Early Cretaceous sawfly *Ceroxyela dolichocera* Rasnitsyn (Krassilov et al. 2003).

Pollen of *Gnetum* species was obtained from herbarium specimens of Botanical Institute, St.-Petersburg, Russia (*G. africanum* and *G. funiculare*) and Chiang Mai University, Thailand (*G. leptostachyum*).

Pollen grains selected for transmission electron microscopy (TEM) were fixed with 1% OsO_4, dehydrated in a graded ethanol series, stained with uranyl acetate, dehydrated in acetone, and embedded in Epon mixture (Meyer-Melikian et al. 2004). Ultrathin sections were made with a diamond knife on an ultramicrotome LKB-3. Some sections were post-stained with lead citrate for 15–20 minutes. Both stained and unstained sections were examined under Jeol 100B transmission electron microscope.

DESCRIPTION OF POLLEN WALL ULTRASTRUCTURE IN *EUCOMMIIDITES* AND RELATED FORMS

Hastystrobus muirii

van Konijnenburg-van Cittert 1971

Pl. 1, figs 1–8

1971 *Hastystrobus muirii* sp. n., van Konijnenburg-van Cittert, p. 30–33, pl. 9, figs. 2, 4; text-fig. 5,
1972 *Hastystrobus muirii* van Konijnenburg-van Cittert; p. 95, pl.1, figs. 1, 2

The pollen cone was described (van Konijnenburg-van Cittert 1971) as cylindrical, with spirally arranged microsporophylls probably abaxially covered with sporangia. Based on LM studies the *in situ* pollen grains, were described as "tricolpate", with one colpus more developed than the other two (van Konijnenburg-van Cittert 1971). The pollen are elliptical with longest axis 29–36 (av. 33) µm, asymmetrical, flattened on the apertural face. The median colpus extends for almost the whole length of pollen grain, obtuse on ends; the other two on either face of it are much shorter, slit-like. In optical section the exine clearly consists of two layers, the sexine 0.5–1.5 µm thick and nexine 0.5–1.0 µm thick.

In SEM the median aperture extends the whole length of the grain, gaping or only slightly so in the middle. The lateral sulci are considerably shorter than the median, slightly arcuate, converging, but never joining on ends, often, but not always, expanded at one end. The pollen surface is psilate or, locally, minutely scabrate, occasionally showing an indistinctly foveolate sculpture, probably caused by preservation (Pl. 1, figs 1, 2).

Ultrastructure. In TEM, the sporoderm is of a different thickness on the opposite sides, about 0.4 µm on the apertural side, 0.7 µm on the non-apertural side (Pl. 1, figs 3, 4, 7, 8). The tectum is about 0.16 µm thick throughout, imperforate. The infratectum is granular, of a somewhat different structure with granules about 0.05 µm, arranged in 1–2 tiers and partly merging into columella-like elements on the apertural side (Pl. 1, fig. 8), and in 2–4 tiers on the non-apertural side, attached at both ends and giving the infratectum a spongy appearance (Pl. 1, figs 4, 7). A thin foot layer is sometimes discernible (Pl. 1, fig. 6). Under the sexine, there is an electronically dense homogeneous layer, about 0.21 µm thick interpreted as the nexine.

Towards both the median sulcus and lateral furrows, the ectexine is gradually reduced, and over the apertures the pollen wall consists solely of the supposed endexine (Pl. 1, fig. 5). There are no appreciable ultrastructural differences between the median and lateral apertures.

Bayeritheca hughesii J.Kvaček & Pacltová 2001

Pl. 2, figs 1–5

2001 *Bayeritheca hughesii* sp.n., J. Kvaček & Pacltová, p. 696, figs. 1–6

The pollen cone was described by Kvaček and Pacltová (2001) as elongate, consisting of numerous closely spaced and whorled peltate microsporophylls bearing radially arranged sporangia/synangia attached at the stalk insertion.

The pollen grains are circular or subcircular in polar view, elongate-ovate in equatorial view, length 14–16 (av. 15.2) µm, width 10–13 (av. 11.2) µm. Three furrows are present. The median is straight, scarcely reaching the equator, rounded on ends. The other two are curved, approaching each other or meeting before the equator to form a circular furrow. The non-apertural face is convex, the apertural flattened. The exine is 1.0 µm thick; the ectexine thinner than the endexine. In SEM, the exine is finely granular, occasionally showing globular protrusions at the ends of one furrow (Pl. 2, fig. 1, Kvaček & Pacltová 2001).

Ultrastructure. The ectexine of non-apertural region is 0.35–0.45 µm thick. The tectum is about 0.2 µm thick throughout, imperforate. The infratectum is 0.02–0.06 (av. 0.03) µm thick, granular, with granules in a single tier, occasionally attached to the tectum and/or resting on the foot layer. The foot layer is distinct, uniform, about 0.11 µm thick (Pl. 2, figs 3–5).

Under the ectexine, there is a less electronically dense homogeneous layer, which probably represents the endexine.

Towards the median sulcus and lateral furrows the ectexine rapidly decreases; first the tectum and then the foot layer are wedging out. In the apertural region, only the supposed endexine, is left, with few scattered granules of sporopollenin on it (Pl. 2, fig. 2).

The occasionally preserved orbicules are about 0.5 µm in diameter, with a dense core about 0.08 µm in diameter.

Aegianthus sibiricus (Heer) Krassilov 1988

Pl. 3, figs 1–5

1876 *Kaidacarpum sibiricum* Heer, p. 84, pl. 15, figs 9–16

1988 *Aegianthus sibiricus* sp.n., Krassilov & Bugdaeva, p. 369–374, pls 7–9

The pollen organs are large loose strobili of peltate microsporophylls with hexagonal thickly cutinized peltae bearing numerous pendant elongate sporangia. Krassilov and Bugdaeva (1988) described the in situ pollen grains as bilaterally symmetrical, monosulcate, elliptical in polar view (Pl. 3, fig. 1), frequently folded, sometimes split into halves which may indicate equatorial zone of weakness. The longest axis is 30–42.5 (av. 40) µm, transverse equatorial axis is 20–26 (av. 24) µm. Sulcus extends the entire length of the grain, straight or slightly curved, mostly gaping in the middle or at one or both ends. Borders of the sulcus are strongly folded. Exinal folds parallel to the sulcus may be present, but they do not seem to have been a constant feature. The exine is about 1.5 µm thick, smooth in LM, minutely pitted in SEM. Pits are discernible with magnification ca. 10.000×.

Ultrastructure. Stratification of ectexine is discernible in the non-apertural region alone (Pl. 3, figs 2, 4). The tectum is about 0.26 µm thick, undulate, imperforate (Pl. 3, fig. 4). The infratectum consists of large granules, disposed in 2 distinct tiers (Pl. 3, fig. 5) or confluent, forming columella-like elements 0.2–0.6 µm high, 0.2–0.25 µm thick. A thin lamella at the base of the granules may represent foot layer, but it is only locally distinct.

Under the ectexine, there is an electronically less dense homogeneous layer about 0.06 µm thick, probably representing the endexine (Pl. 3, fig. 3).

Towards the apertures, the ectexine decreases rather abruptly and only the supposed endexine, remains (Pl. 3, fig. 3).

Loricanthus resinifer Krassilov & Bugdaeva 1999

Pl. 3, figs 6–7

1999 *Loricanthus resinifer* sp.n., Krassilov & Bugdaeva, p. 115–116, fig. 2, pl. 2, figs 1–8, pl. 3, figs 1–5, 2004 *Loricanthus resinifer* Krassilov & Bugdaeva; Tekleva & Krassilov, p. 98–100, fig. 1a, pl. 10, figs 1–3

Large strobili with peltate sporangiophores, tightly adpressed early in development, becoming more open with maturation. The sporangia are free, pendent, clustered on the adaxial side of the shields. The pollen grains are about several hundreds per sporangium, about 17–19.5 µm in diameter, ellipsoidal or nearly spherical, slightly flattened on the apertural face. In SEM, the aperture is seen as an irregularly elliptical thin area, occasionally crossed with a longitudinal fold and then appearing as two parallel furrows (Pl. 3, fig. 6, Krassilov & Bugdaeva 1999).

Ultrastructure. The non-apertural exine is uniformly 1.25–1.4 µm thick, divided into four structural layers. The tectum is electronically dense, weakly undulate, with occasional narrow perforations, about 0.2 µm thick, abruptly tapering towards the apertural area and disappearing over it. Tapetal remains of variable electronic density are occasionally present. The infratectum is likewise tapering towards the aperture, consisting of large granules 0.2 µm in diameter and columella-like elements 0.4–0.5 µm long, 0.2–0.3 µm thick, attached to the tectum and pending or resting on the foot layer. The latter is thin, about 0.04–0.07 µm, locally up to 0.17 µm, homogeneous and uniform in both apertural and non-apertural regions. The foot layer is either separated from the innermost layer, appearing as a solitary undulate lamella, on which the infratectal elements are resting, or it is coherent with the innermost layer, being only slightly thicker and denser than the lamellae of the latter, which are distinguishable in oblique sections (in Tekleva & Krassilov 2004, pl. 10, fig. 3).

The endexine is slightly less electronically dense than the ectexinal layers, uniformly thick throughout, including the apertural region, lamellate. It comprises five lamellae 0.034 µm thick, divided by irregular slits (Pl. 3, fig. 7; and in Tekleva & Krassilov 2004, pl. 10 figs 2, 3).

Cryptosacciferites pabularis Krassilov & Tekleva 2003

Pl. 4, figs 1–3

2003 *Cryptosacciferites pabularis* sp.n., Krassilov et al., p. 150–154, figs 3–10

Trisulcate pollen grains were extracted from the gut compression of a fossil insect *Ceroxyela dolihocera* Rasnitsyn. They are much larger than the size range of the typical *Eucommiidites* and differ also in rudimentary air bladders discernible in TEM (Pl. 4, fig. 1, Krassilov et al. 2003).

Ultrastructure. The exine is about 1.0 µm thick over the central area increasing to 2.0 µm over the marginal flange (in Krassilov et al. 2003, fig.10A). On the non-apertural side, the tectum is relatively massive, up to 0.53 µm thick, irregular, undulating, with narrow perforations. The infratectum is about the same maximum thickness as the tectum, with alveoli in a single or two, occasionally three, tiers. In the marginal flange, the infratectum is expanded, with the alveoli radially stretched and resembling brochi of protosaccate bladders (Pl. 4, fig. 2). The foot layer is dense, uniformly about 0.1 µm thick. On the apertural side, the tectum is less than 0.26 µm thick, the infratectum is irregularly alveolate vanishing over the furrows (Pl. 4, fig. 3). The foot layer appears as a discontinuous (crumpled) undulate lamella 0.05 µm thick, separated from the somewhat less electronically dense endexine of 3–5 lamellae (in Krassilov et al. 2003, fig. 10B).

DISCUSSION

Sharing the peculiar apertural configuration, *Eucommiidites*-type pollen grains show a considerable diversity of their sporoderm ultrastructure (Osborn 2000 and this study). However, not all the species are adequately studied. Ultrastructural characters have been reported for the following species:

(1) Dispersed pollen grains *Eucommiidites troedsonii* (Scheuring 1978, Batten & Dutta 1997), *Eucommiidites* sp. (Doyle et al. 1975), *Eucommiidites* sp.1 and sp.2 (Trevisan 1980), and *Eucommiidites* sp. (Zavada 1984).

(2) *Eucommiidites*-type pollen grains, found in the micropyles and pollen chambers of ovules *Erdtmanispermum balticum* (Pedersen et al. 1989);

(3) In situ *Eucommiidites*-type pollen grains of *Hastystrobus muirii* van Konijnenburg-van Cittert, (this study), *Erdtmanitheca texensis* (Pedersen et al. 1989), *Eucommiitheca hirsuta* (Friis & Pedersen 1996), and *Bayeritheca hughesii* (this study).

We also discuss in situ pollen grains of *Aegianthus sibiricus* and *Loricanthus resinifer*, two pollen cones resembling the *Eucommiidites*-producing organ *Erdtmanitheca*. Further, we discuss the trisulcate *Cryptosacciferites pabularis* from the gut compression of *Ceroxyela dolichocera*.

Variation. *Eucommiidites*-type pollen grains vary in their dimensions, in the configuration and relative development of the apertures, as well as in the sculptural and ultrastructural characters. Consistency of the genus has to be assessed in respect to the ranges of variation and correlation of these characters.

Dimensions. The smallest pollen grains come from *Eucommiitheca hirsuta* (Friis & Pedersen 1996), 10–12×15–20 µm, and *Bayeritheca hughesii* (Kvaček & Pacltova 2001), 10–13×14–16 µm. Pollen grains from *Erdtmanitheca texensis*, and *Erdtmanispermum balticum* (Pedersen et al. 1989) are about 15×25 µm, those of *Hastystrobus muirii* (van Konijnenburg-van Cittert 1971) and dispersed *Eucommiidites troedsonii* (Scheuring 1978, Batten & Dutta 1997), *Eucommiidites* sp. (Doyle et al. 1975), *Eucomjmidiites* sp. 1 and sp. 2 (Trevisan 1980) are about 25×36 µm. *Eucommiidites* sp. (Zavada 1984) is rather large, about 40×45 µm, and the lateral furrows are scarcely discernible in the published LM image, which casts some doubt on the generic assignment (Pedersen et al. 1989, Batten & Dutta 1997, Osborn 2000). However, the lateral furrows are distinguishable in the TEM sections.

Apertures. The additional apertures are either linear, roughly parallel to the median sulcus, or curved, converging and joined into an encircling subequatorial furrow. The latter condition was described by Hughes (1961) for the type species *Eucommiidites troedsonii*, but doubted by other researchers (van Konijnenburg-van Cittert 1971, Friis & Pedersen 1996). However, it has been confirmed for dispersed *Eucommiidites* sp. (Doyle et al. 1975) and recently for *Bayeritheca hughesii* (Kvaček & Pacltová 2001).

Typically, in the forms with three separate furrows, the median one is relatively broad, with obtuse or rounded ends, whereas the lateral ones are slit-like, with pointed ends, but in the pollen from *Erdtmanispermum balticum* (Pedersen et al. 1989) the furrows are only slightly unequal. The median aperture is longer than the lateral ones in *Hastystrobus muirii* and *Erdtmanitheca texensis*, nearly of the same length in *Eucommiidites* sp.1 and sp.2 (Trevisan 1980) and *Eucommiitheca hirsuta.* For *Hastystrobus muirii* van Konijnenburg-van Cittert (1971) noted aberrant grains lacking lateral furrows, or with only one developed.

Sculpture. The pollen surface is typically psilate or indistinctly scabrate, sometimes with irregular granules or pits, except in *Erdtmanispermum balticum* (Pedersen et al. 1989), where it is described as regularly foveolate. The apertural membrane is granulate in *Bayeritheca hughesii* (Kvaček & Pacltová 2001), but apparently smooth in *Erdtmanitheca texensis* (Pedersen et al. 1989), *Erdtmanispermum balticum* (Pedersen et al. 1989), *Eucommiidites* sp.1 and sp.2 (Trevisan 1980).

Ultrastructure. Ectexine stratification is well-developed in all *Eucommiidites* and allied pollen grains, whereas the presence of endexine is problematic in some of them. The distribution of ultrastructural characters among the considered taxa is presented in Table 1. The tectum is thick, coarsely perforate in *E. troedsonii* as described in Scheuring (1978) and Batten and Dutta (1997) and *Eucommiidites* sp. (Doyle et al. 1975), thick, but imperforate in *Bayeritheca hughesii* and *Erdtmanitheca texensis*, as well as in dispersed *Eucommiidites* sp. 2 (Trevisan 1980). In contrast, in *Hastystrobus muirii*, *Eucommiidites* sp. 1 (Trevisan 1980), *Eucommiidites* sp. (Zavada 1984), *Erdtmanispermum balticum* and *Eucommiitheca hirsuta* the tectum is relatively thin, no more than half of ectexine, imperforate.

The infratectum varies in thickness from a narrow slit-like layer to about half of ectexine, consisting of small granules in *Erdtmanitheca texensis*, dispersed *E. troedsonii* (Scheuring 1978, Batten & Dutta 1997), and *Eucommiidites* sp. (Doyle et al. 1975), of middle-sized granules in *Hastystrobus muirii*, *Bayeritheca hughesii*, *Erdtmanispermum balticum* and in dispersed *Eucommiidites* sp. 2 (Trevisan 1980), but of large partly coalescent granules forming columella-like elements in ?*Eucommiitheca hirsuta*, *Eucommiidites* sp. 1 (Trevisan 1980) and *Eucommiidites* sp. (Zavada 1984). In *Hastystrobus muirii,*

Table 1. Distribution of ultrastructural characters among known *Eucommiidites* pollen

Ultrastructural details	Taxon
Thick tectum, infratectum of small granules, indistinct or absent foot layer	*Eucommiidites troedsonii* (Scheuring 1978, Batten & Dutta 1997), *Eucommiidites* sp. (Doyle et al. 1975), *Erdtmanitheca texensis* (Pedersen et al. 1989)
Thin tectum, infratectum of large or partly coalescent granules, indistinct or absent foot layer	*Eucommiidites* sp.1 (Trevisan 1980), *Eucommiidites* sp. (Zavada 1984), *Eucommiitheca hirsuta* (Friis & Pedersen 1996)
Thick tectum, infratectum of medium-sized granules, thin, distinct foot layer	*Eucommiidites* sp.2 (Trevisan 1980), *Bayeritheca hughesii*
Thin tectum, infratectum of medium-sized and/or partly coalescent granules, indistinct or absent foot layer	*Hastystrobus muirii* (van Konijnenburg-van Cittert 1971)
Thin tectum, infratectum of medium-sized granules, thick foot layer	*Erdtmanispermum balticum* (Pedersen et al. 1989)

local fusion of granules results in the spongy infrastructure.

The foot layer is thick in *Erdtmanispermum balticum*, thin, but distinct in *Bayeritheca hughesii*, *Eucommiidites* sp. 2 (Trevisan 1980), vanishingly thin and scarcely discernible in *Hastystrobus muirii*, *Eucommiitheca hirsuta*, *Erdtmanitheca texensis*, *Eucommiidites troedsonii* (Scheuring 1978, Batten & Dutta 1997), *Eucommiidites* sp. 1 (Trevisan 1980), *Eucommiidites* sp. (Zavada 1984), and *Eucommiidites* sp. (Doyle et al. 1975).

The endexine is well-developed, uniformly thick and lamellate in *Eucommiidites troedsonii* (Sheuring 1978, Batten & Dutta 1997), *Eucommiidites* sp. 1 and 2 (Trevisan 1980), *Eucommiidites* sp. (Zavada 1984), *Eucommiidites* sp. (Doyle et al. 1975), *Erdtmanispermum balticum*, being vaguely discernible in *Hastystrobus muirii*, *Bayeritheca hughesii*, and *Eucommiitheca hirsuta.*

In all the adequately studied species, the ectexine is reduced at both the median and lateral furrows, although *Erdtmanitheca* stands apart in the outer layer rather gradually tapering towards the lateral furrows (Pedersen et al. 1989).

Eucommiidites shares its trisulcate apertural type with *Cryptosacciferites*, which is much larger and differs also in its alveolate infratectum. Another trisulcate pollen, *Zolerella tricolpata* Scheuring (Scheuring 1978), is similar to *Cryptosacciferites* in size and has presumably an alveolate ultrastructure. Lateral sulci are longer than the median one in both these species unlike known *Eucommiidites* species. The monosulcate pollen of *Aegianthus sibiricus* and *Loricanthus resinifer*, the pollen cones similar to those producing *Eucommiidites*-type pollen, are similar to the latter in many characters except the apertures. The dimensions of *Aegianthus sibiricus* (10–13 × 20–26 μm) and *Loricanthus resinifer* (17–19.5 μm) are within the size range of *Eucommiidites.* The ectexine of *Loricanthus resinifer* consists of a relatively thin irregularly perforate tectum, granular infratectum with large granules or columella-like elements and thin, but readily distinguishable foot layer; the endexine is lamellate, of equal thickness all over the perimeter. In *Aegianthus sibiricus*, the ectexine, although poorly preserved, shows a rather thin tectum and infratectum of large granules or, occasionally, the columella-like elements; the foot layer is feebly developed (or poorly preserved). Thus, in the pollen grains from macromorphologically similar pollen cones, the infratectal structures are uniformly granular, varying in the dimensions of the granules alone, whereas the development of additional furrows is inconstant. On the other hand, *Eucommiidites*-like furrows occur in the pollen grains that are unlike the main group in their ultrastructural characters.

The development of infratectum relative to the other ectexinal layers, as well as the arrangement and dimensions of infratectal granules seem to have been the most significant distinguishing features within the group. The larger granules show a tendency of coalescing into columellate elements that are lacking in the minutely granulate forms. Moreover, the infratectum of a single tier of small to medium sized granules tend to correlate with a thick, sometimes perforate, tectum, whereas the forms with a relatively thin tectum usually have a better developed infratectum of larger, partly coalescent granules.

OUTGROUP COMPARISONS

In *Hastystrobus muirii*, the infratectum of the supposed proximal side has a spongy appearance, like in *Monosulcites* sp. (Trevisan 1980). *Bayeritheca hughesii* and *Eucommiidites* sp. 2 (Trevisan 1980), the most closely related members of the group, share their ectexine characters (thick tectum, densely packed granules) with the monosulcate pollen of *Leguminanthus siliquosus*, a pollen organ of the Bennettitales (Ward et al. 1989).

Forms with infratectum of small granules, such as *Eucommiidites troedsonii* (Scheuring 1978; Batten & Dutta 1997), *Erdtmanitheca texensis*, and *Eucommiidites* sp. (Doyle et al. 1975), especially the latter, are comparable with *Equisetosporites* sp. (Osborn et al. 1993), *Ephedripites* sp. (Trevisan 1980), *Cycadeoidea dacotensis* (Osborn & Taylor 1995) and *Lethomasites fossulatus* (Ward et al. 1989), a questionable angiosperm pollen showing certain bennettitalean characters (Crepet & Nixon 1994). *Ephedripites* sp. and *Cycadeoidea dacotensis* are polyplicate, assigned to the Gnetales, *Lethomasites fossulatus* is monosulcate, belonging to the Bennettitales, and the last one is very large (90 µm) foveolate, supposedly angiospermous.

The forms with large and partly coalescent granules (?*Eucommiitheca hirsuta*, *Eucommiidites* sp. 1 (Trevisan 1980), *Eucommiidites* sp. (Zavada 1984), *Aegianthus sibiricus*, *Loricanthus resinifer* are similar in this character to *Sahnia laxiphora*, an Early Cretaceous member of the Pentoxylales. (Osborn et al. 1993) and to *Monosulcites* sp. recovered from Jurassic of Afghanistan (Zavada 2004).

Among the rimulate pollen morphotypes of the *Circumpollis* group, commonly assigned to conifers (the Cheirolepidiaceae), but placed among gnetophytes by Krassilov (1982), *Classopollis* (Pettitt & Chaloner 1964, Taylor & Alvin 1984, Rowley & Srivastava 1986, Pocock et al. 1990) and *Circulina* (Médus 1977), the infratectum is formed of large granules and/or columellate elements, whereas in *Duplicisporites* it consists of profuse, closely packed small and medium-sized granules (Zavialova & Roghi 2005) as in *Hastystrobus* muirii, *Bayeritheca hughesii* (above) and *Eucommiidites* sp. 2 (Trevisan 1980).

Affinities. The taxonomic affinities of *Eucommiidites* type pollen grains were discussed by Friis and Pedersen (1996), who established order Erdtmanithecales based on several intact pollen organs and seeds with in situ *Eucommiidites* pollen. Our deduction has two sources of inference: (1) the intrinsic features of pollen grains themselves and (2) the morphology of macrofossils from which they were extracted. Hughes (1961) suggested a gnetalean affinity for *Eucommiidites* plant and was followed in this by the majority of subsequent researchers. The above comparisons included gnetalean, bennettitalean and pentoxylean forms as possibly related on account of similar infratectal structures.

In situ *Eucommiidites*-type pollen grains have been first described in *Hastystrobus muirii* (van Konijnenburg-van Cittert 1971) from the Middle Jurassic of Yorkshire. Their attribution to *Eucommiidites* was sometimes doubted (Pedersen et al. 1989), but our SEM study of the type material fully confirms the slit-like lateral furrows, typical of *Eucommiidites*. Van Konijnenburg-van Cittert (1971) compared *Hastystrobus* to *Androstrobus* implying a cycadalean affinity because of the microsporangia covering the abaxial surface of the microsporophylls. However, unlike *Hastystrobus*, pollen of extant and fossil cycads has an alveolar, rather than granular, infratectum.

Erdtmanitheca, a Cretaceous pollen organ similar to *Aegianthus*, was placed in the extinct family Erdtmanithecaceae of the order Erdtmanithecales (Pedersen et al. 1989, Friis & Pedersen 1996), including also *Eucommiitheca, Spermatites pattensis* Hughes (1961), *Spermatites patuxensis* Brenner (1963), *Allicospermum retemirum* Harris (Reymanówna 1968), *Erdtmanispermum balticum* (Pedersen et al. (1989). Another Cretaceous pollen cone, *Bayeritheca* J. Kvaček & Pacltová, was assigned to Erdtmanithecales primarily on account of *Eucommiidites* pollen and pollen cone morphology.

Possible relatives: *Loricanthus resinifer* (Krassilov & Bugdaeva 1999) belongs to the same pollen cone morphotype as members of Erdtmanithecales, but its pollen grains, though similar to *Eucommiidites* in shape, dimensions, sculpture and ultrastructure, appear mono- or disulcate.

Large pollen cones with hexagonal shields of peltate sporangiophores were described from the mid-Jurassic Ust' Baley locality, East Siberia, as *Kaidocarpum sibiricum* Heer

(Heer 1876), re-assigned to *Aegianthus sibiricus* by Krassilov and Bugdaeva (1988). Pollen grains from these cones do not show additional furrows, at least not as a constant feature. The gnetalean affinities of *Aegianthus* were inferred from its association with samaroid seed-scale structures resembling the samaras of extant *Welwitschia* (Krassilov & Bugdaeva 1988).

Eucommiidites pollen morphology was considered as a major diagnostic feature of the Erdtmanithecales, the extinct order based on pollen cones and dispersed seeds of a rather generalized gymnospermous morphology. The Erdtmanithecales is placed close to the Gnetales (Friis & Pedersen 1996), three extant genera of which, *Welwitschia*, *Gnetum* and *Ephedra*, produce psilate polyplicate (*Welwitschia*, *Ephedra*) or spinulose (*Gnetum*) pollen of different apertural types, monosulcate or inaperturate, but comparable to *Eucommiidites* on account of granular infratectal ultrastucture, commonly of small granules (Ueno 1960, Gullvåg 1966, Bernard & Meyer 1972, Van Campo & Lugardon 1973, Kedves 1987, Kurmann 1992, El-Ghazaly & Rowley 1997, El-Ghazaly et al. 1998, Zavada & Gabaraeva 1991, Hesse et al. 2000, Yao et al. 2004, *Gnetum leptostachyum* Plume, Pl. 4, fig. 4), but of large granules in *G. africanum* Welwitsch (Oryol et al. 1986, Pl. 4, fig. 5) and extremely small ones in *G. funiculare* Wight (Pl. 4, fig. 6).

CONCLUSIONS

Our ultrastructural study of *Eucommiidites* and allied pollen grains of *Hastystrobus muirii, Bayeritheca hughesii, Aegianthus sibiricus, Loricanthus resinifer, Cryptosacciferites pabularis* shows that:

(a) In all ultrastructurally studied *Eucommiidites*, the median and additional furrows are cutting through all the layers of ectexine; the infratectum is granular or granular-columella-like;

(b) At the same time, the pollen genus *Eucommiidites* shows high variability in terms of apertural configurations (subparallel sulci or a median sulcus and encircling furrow) and in such ultrastructural features as a thick or thin, perforate or imperforate tectum; a broad or constricted infratectum of large partly coalescent granules or of small to medium-sized granules arranged in a single or two – three tiers; a well-developed or obscure foot-layer; as well as in the distinct or inconspicuous lamellation of endexine;

(c) The pollen cones of typical Ertdmanithecaceae produced *Eucommiidites*-type pollen grains with subparallel sulci and with an infratectum of large or small tiered granules. Pollen grains from the pollen chamber of *Erdtmanispermum balticum* differ from all the conventional *Eucommiidites* in the almost equally developed median and lateral sulci, massive exine, foveolate sculpture and a relatively thick foot layer.

(d) A trisulcate apertural type occurs in the pollen grains *Cryptosacciferites* and *Zolerella* with an alveolate, rather than granular, infratectum, evidently representing a distinct group of Early Cretaceous gymnosperms.

(e) *Hastystrobus* from the Middle Jurassic of Yorkshire, not included in the Ertdmanithecaceae, produced pollen of *Eucommiidites* type with converging lateral sulci and a granulate-columella-like infratectum;

(f) The pollen cones *Aegianthus* from the mid-Jurassic of Siberia and *Loricanthus* from the Early Cretaceous of Transbaikalia, are similar to *Erdtmanitheca* in general habit, peltate sporangiophores with polygonal apophyses, and sporangial clusters, but their pollen grains are not assignable to, although ultrastructurally comparable with, *Eucommiidites*. In this morphological group, the gnetalean affinities are so far substantiated for *Aegianthus* alone on account of its association with *Welwitschia*-like seed scales *Heerala*.

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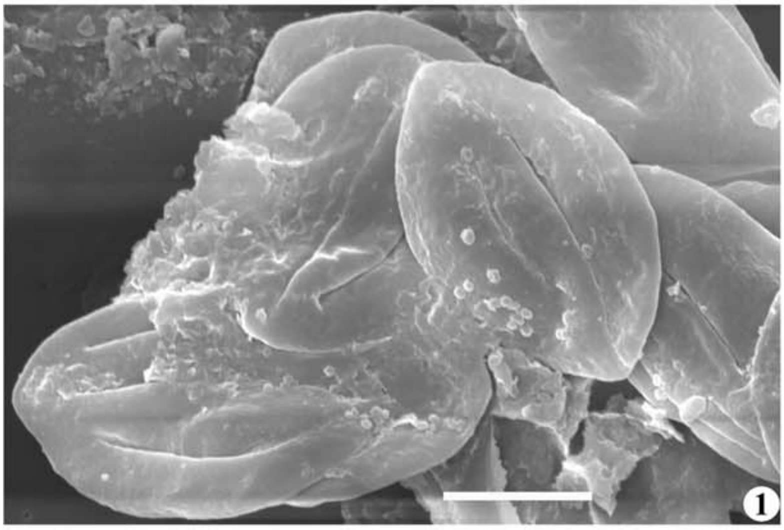
PLATES

Plate 1

Hastystrobus muirii van Konijnenburg-van Cittert, SEM, TEM

1. Group of pollen grains, SEM. Scale bar = 10 µm
2. Single pollen grain, distal view, SEM. Scale bar = 10 µm
3. TEM image of the whole pollen grain, arrows indicate three apertures. Scale bar = 1 µm
4. TEM image of pollen wall, proximal side. Scale bar = 1 µm
5. TEM image of pollen wall, towards apertural region. Scale bar = 0.5 µm
6. TEM image of pollen wall, apertural side, arrow indicates foot layer. Scale bar = 0.25 µm
7. TEM image of pollen wall, proximal side. Scale bar = 0.5 µm
8. TEM image of pollen wall, apertural side. Scale bar = 1 µm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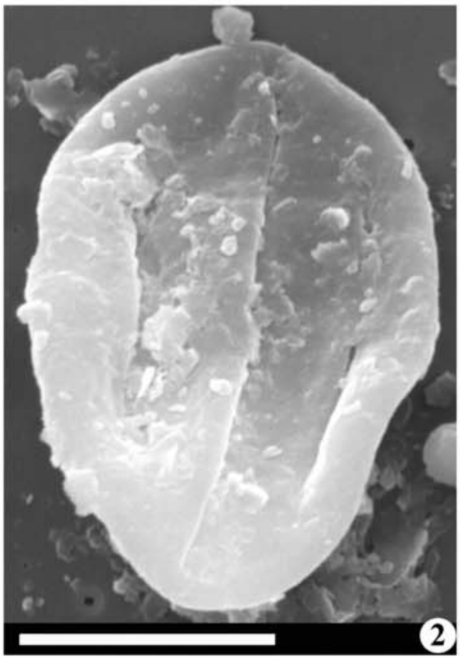
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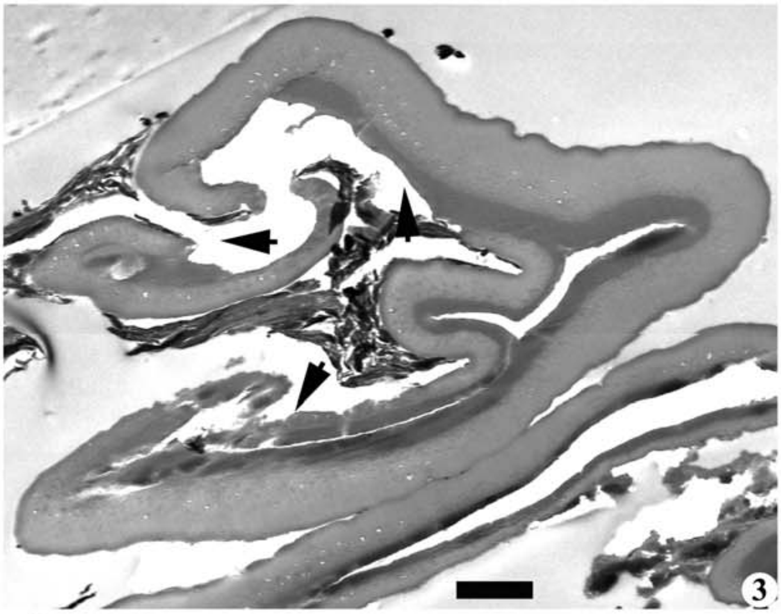
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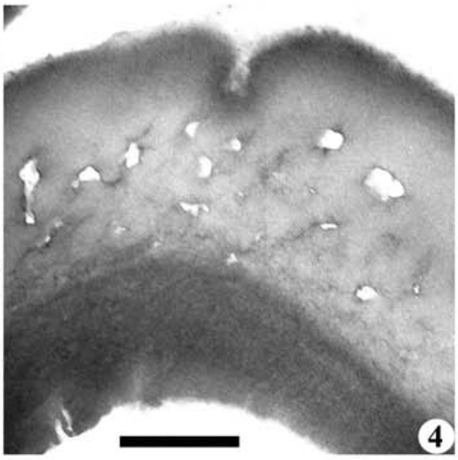
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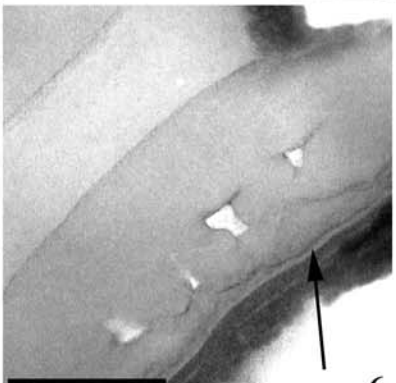
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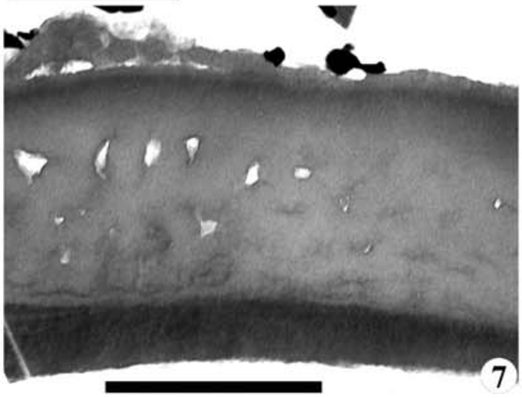
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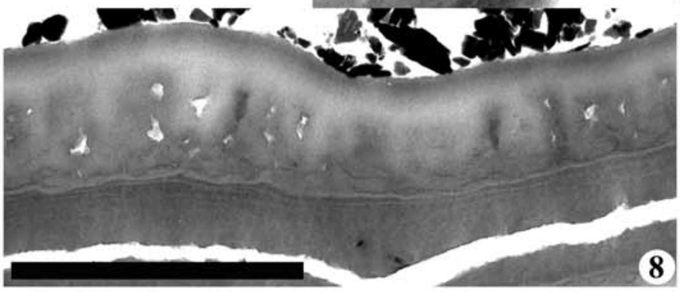
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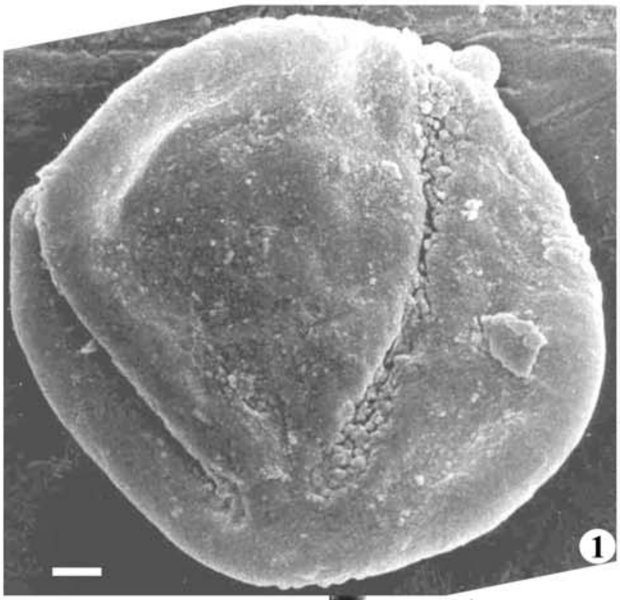
Plate 2

Bayeritheca hughesii J.Kvaček & Pacltová, SEM, TEM

1. Single pollen grain, SEM. Scale bar = 1 µm
2. TEM image of pollen wall, apertural region. Arrow heads show inner border of foot layer. Scale bar = 0.5 µm.
3. TEM image of the whole pollen grain, arrows indicate three apertures. Scale bar = 0.5 µm

4–5. TEM image of pollen wall, non-apertural region. Arrows show inner border of foot layer. Scale bar = 0.5 µm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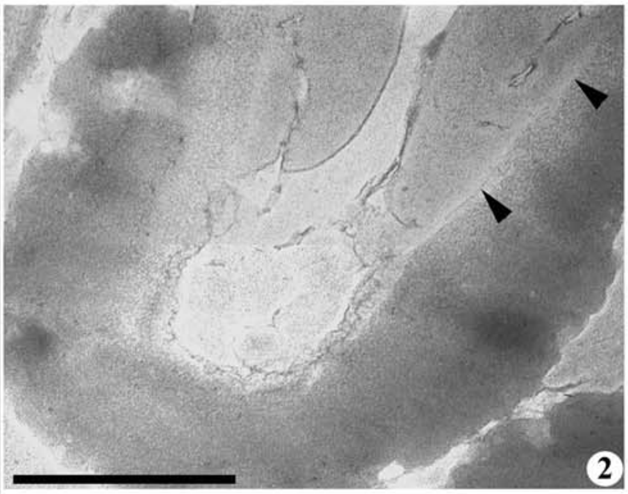
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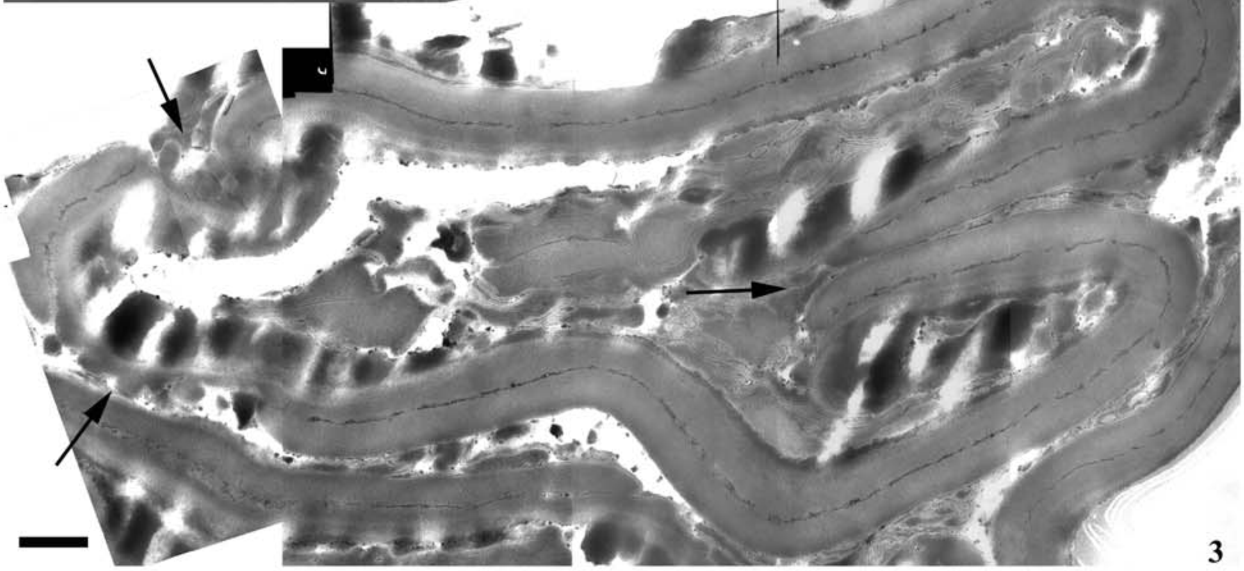
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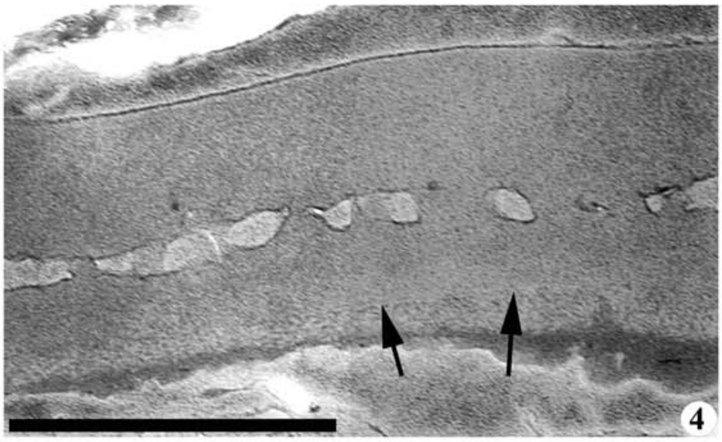
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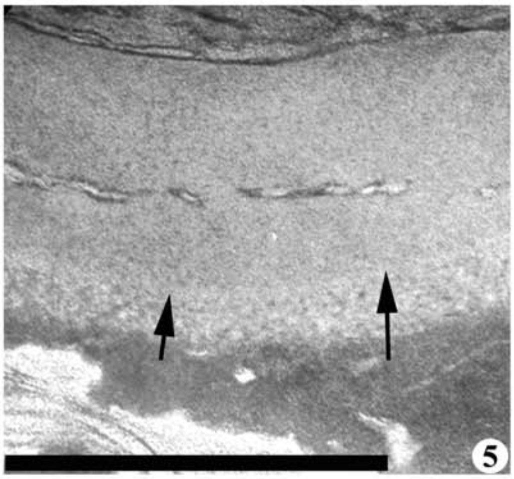
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Plate 3

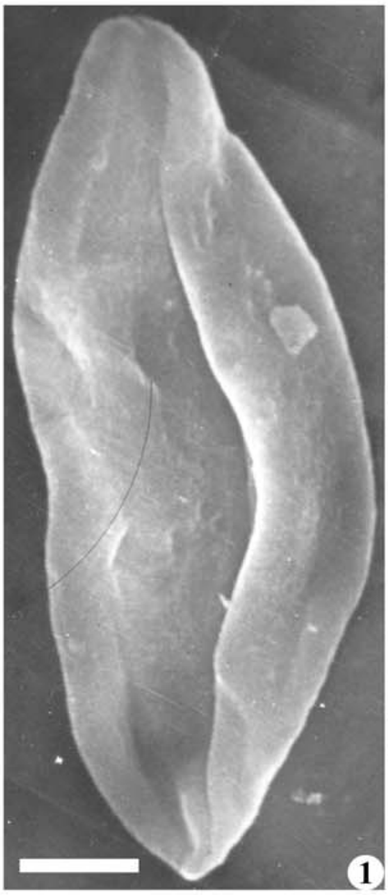
Aegianthus sibiricus (Heer) Krassilov, *Loricanthus resinifer* Krassilov & Bugdaeva, SEM, TEM

1–5. *Aegianthus sibiricus* (Heer) Krassilov

1. Single pollen grain, SEM. Scale bar = 6 µm
2. TEM image of the whole pollen grain, arrow indicates apertural region. Scale bar = 2 µm
3. TEM image of pollen wall; arrow head indicates apertural region, arrow points at a layer, which probably represents endexine. Scale bar = 0.5 µm
4. TEM image of pollen wall, non-apertural region. Scale bar = 2 µm
5. TEM image of pollen wall, non-apertural region, infratectum consists of large granules. Scale bar = 0.5 µm

6–7. *Loricanthus resinifer* Krassilov & Bugdaeva

6. Group of pollen grains, SEM. Scale bar = 10 µm
7. TEM image of pollen wall, non-apertural region, arrow indicates foot layer. Scale bar = 0.5 µm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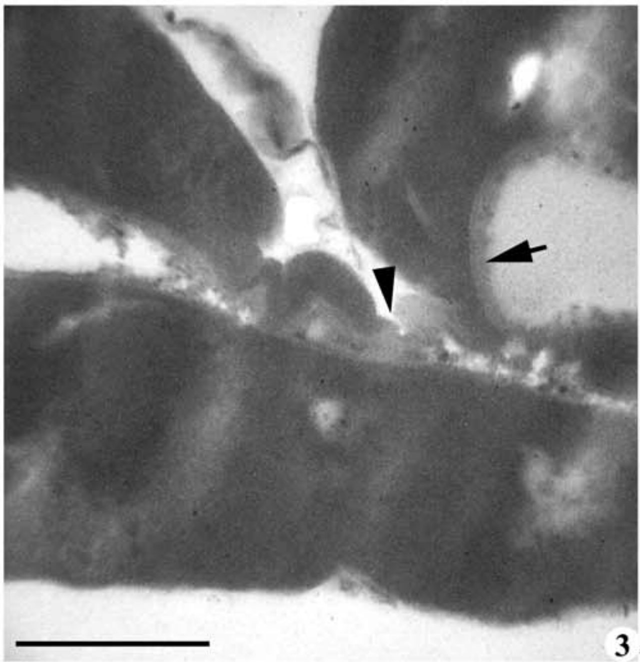
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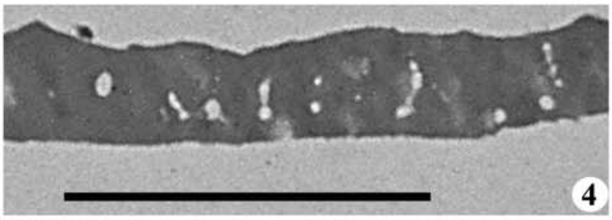
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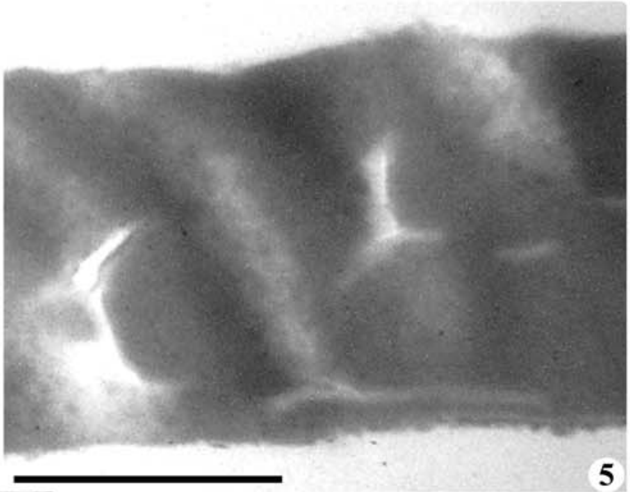
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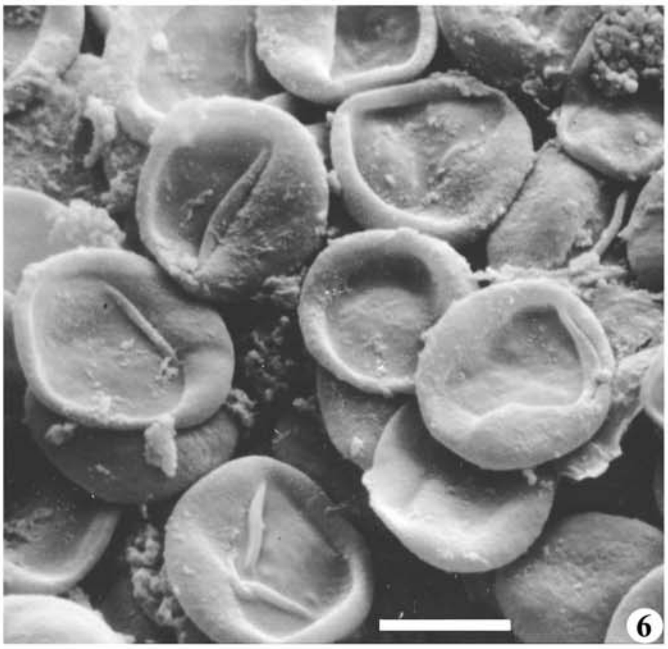
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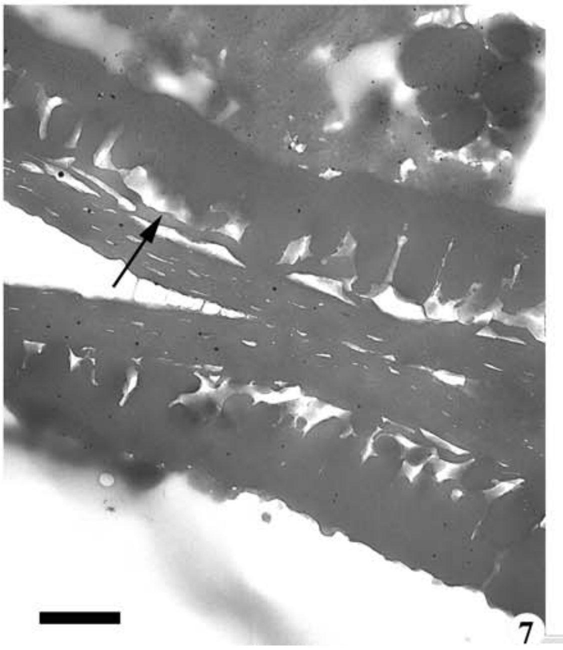
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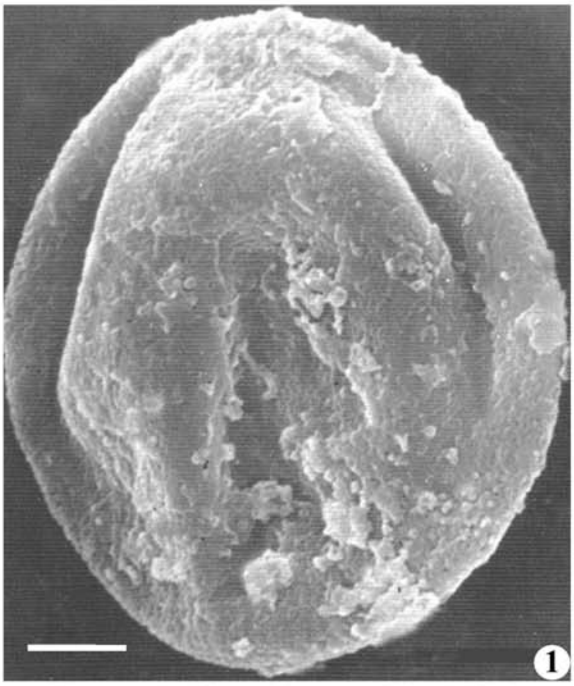
Plate 4

Cryptosacciferites pabularis Krassilov & Tekleva, SEM, TEM, *Gnetum leptostachyum* Plume, *Gnetum africanum* Welwitsch, *Gnetum funiculare* Wight, TEM.

1–3. *Cryptosacciferites pabularis* Krassilov & Tekleva
1. Single pollen grain, SEM. Scale bar = 10 μm
2. TEM image of pollen wall, marginal flange, where infratectum is expanded. Scale bar = 1 μm
3. TEM image of pollen wall, apertural region; arrow indicates foot layer. Scale bar = 1.84 μm
4. *Gnetum leptostachyum* Plume, TEM image of pollen wall, plicate region; arrow points at infratectal granules. Scale bar = 0.5 μm
5. *Gnetum africanum* Welwitsch, TEM image of pollen wall, plicate region; arrow points at infratectal granule. Scale bar = 0.5 μm
6. *Gnetum funiculare* Wight, TEM image of pollen wall, plicate region; arrow points at infratectal granules. Scale bar = 0.4 μm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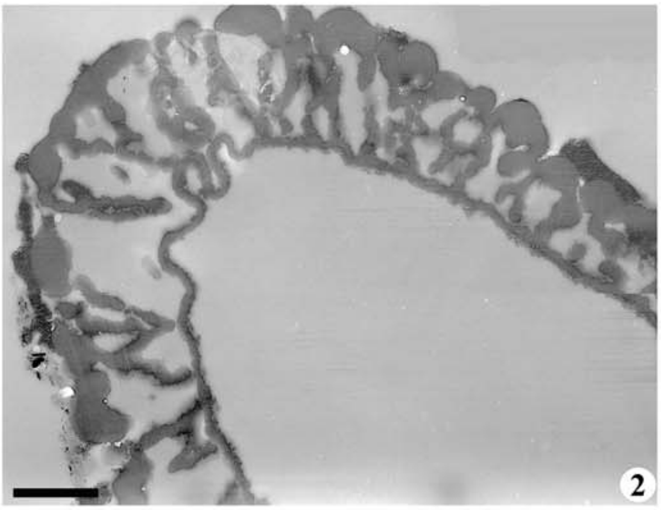
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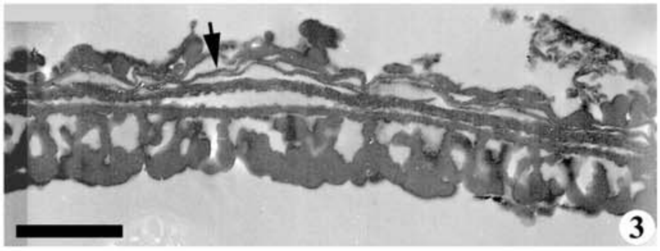
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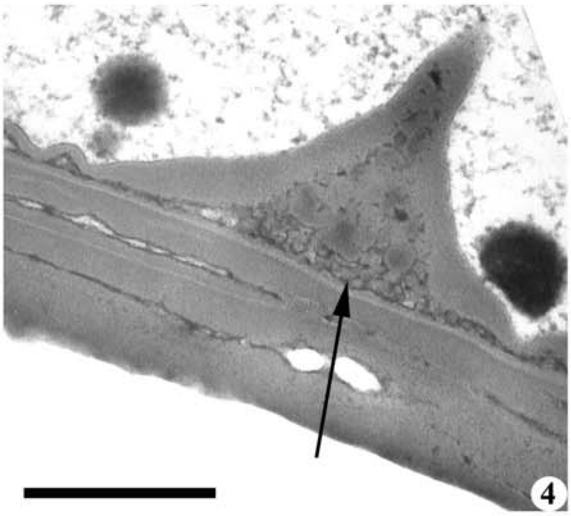
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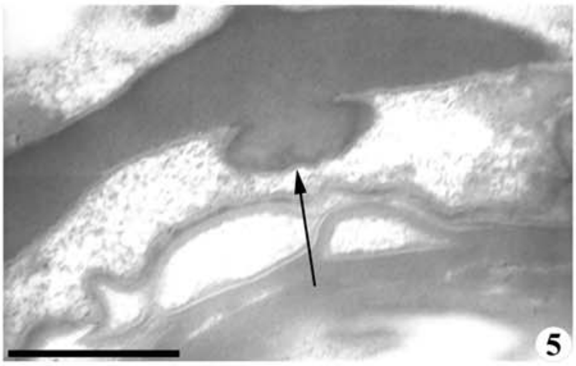
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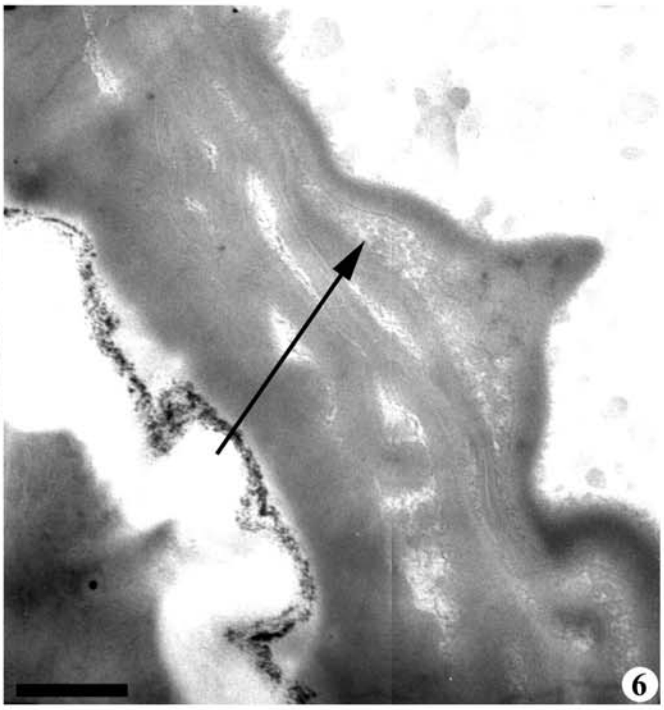
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