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Exine ultrastructure of in situ peltasperm pollen from the Rhaetian of Germany and its implications

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ABSTRACT

Morphology and exine ultrastructure of pollen grains of Triassic peltasperms have been studied for the first time. Pollen grains of *Antevsia zeilleri* from the Rhaetian of Germany are of the *Cycadopites*-type and monosulcate; the sculpturing is the same in the apertural and non-apertural areas. The proximal exine includes a row of lacunae covered by a solid, thick tectum and underlined by a foot layer. Pillars are hanging from the tectum between the lacunae. The exine is thinning to a homogeneous layer in the apertural region. The latter is bordered by thicker alveolate areas of the exine, in places resembling a saccus-like ultrastructure. The endexine includes white-line-centred lamellae. The exine ultrastructure is compared with that of pollen of Permian peltasperms. Although pollen types ascribed to Permian peltasperms are completely different in their general morphology, a transformation can be hypothesized by ultrastructural data from Permian *Vesicaspora* into Triassic *Cycadopites* extracted from pollen sacs of *Antevsia*. Comparison with *Cycadopites* of non-peltaspermalean (Ginkgoalean, Cycadophyte) and unknown affinities has been accomplished. The exine ultrastructure is distinctive enough to differentiate among peltaspermalean, cycadalean and bennettitalean *Cycadopites*; some ultrastructural features are shared with pollen of modern *Ginkgo biloba*. More ultrastructural data are needed as well as numerous sections of pollen grains are necessary to reveal original unchanged ultrastructure.

1. Introduction

The Peltaspermales are a group of seed ferns ranging from the Permian to the latest Triassic, showing a great diversity in foliage but are all characterized by their female fructifications of the *Peltaspermum* type. It was an important group during the Permian occurring worldwide, but mainly in Laurasia, with natural genera (e.g., *Autunia* and *Meyenopteris*) and a large number of frond morphogenera (e.g., *Comia* and *Rhachiphyllum*) often associated with the typical *Peltaspermum*-type of female fructifications (Poort and Kerp, 1990; Taylor et al., 2006). The latter consist of a rachis with spirally arranged peltate, umbrella-like megasporophylls bearing a number of ovules in a ring on their lower side. During the Early Triassic the group was not so well-represented; so far only one record is known from Australia (Retallack, 2002). In the Middle and Late Triassic *Lepidopteris* is the main peltasperm frond genus, usually found in close association with *Peltaspermum* female fructifications. A second Triassic frond genus is *Scytophyllum*, also associated with *Peltaspermum* female remains. It occurs from the Middle Triassic onwards and plays in important role in, mainly, Russian Triassic floras (Dobruskina, 1982; Kustatscher et al., 2007; Kustatscher et al., in press).

Peltasperm pollen organs from the Permian (e.g., *Pterispermostrobus* and *Permotheca*) and the Triassic (*Antevsia*) are morphologically rather similar, consisting of either cup-shaped structures bearing elongated pollen-sacs fused only at their base (*Pterispermostrobus, Permotheca*) or pinnately branched axes bearing a large number of peltate heads with free pollen sacs (*Antevsia*) (see e.g., Harris 1932; Townrow 1960; Meyen 1984; Taylor et al., 2006).

The Peltaspermales also show a great diversity of pollen types ascribed to it, either found in situ or dispersed. Among pollen types named for Permian peltasperms (with different degree of certainty) are *Vesicaspora*, *Falcisporites*, *Protohaploxypinus*, *Piceapollenites* and *Vittatina* (Plate VI, 1, 2, 4–6); *Falcisporites* and *Cycadopites* were found in situ in Triassic peltasperms (see the next section). These bisaccate non-striate, bisaccate striate, non-saccate striate and non-saccate, monosulcate pollen are morphologically very different from each other. Moreover, most of these pollen types are not confined to peltasperms alone. Ultrastructural studies are hoped to help in understanding the diversity of peltasperm pollen and in comparing between peltasperm pollen and pollen of the same morphological types that belong to other plant groups. Some data for such

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comparisons have been already accumulated (Meyer, 1977; Zavialova, 1998; Afonin, 1999; Krassilov et al., 1999a,b; Zavialova et al., 2001). As it is often the case, information about in situ material is still sparse.

The aims of the present paper are to document for the first time the exine ultrastructure of Triassic in situ peltasperm pollen and to compare the obtained data with available ultrastructural data on Permian pollen ascribed to peltasperms. Additional comparison will be made with pollen grains of the same morphological type of various geological ages, modern gymnosperms including.

1.1. Pollen types ascribed to peltasperms

Pollen sacs attached to *Pterispermostrobus* microsporophylls from the Early Permian (Germany) contain pollen grains of *Vesicaspora*-type up to 50 μm in size (Barthel, 2006).

Russian Permian deposits are rich in peltasperm macroremains and contain diverse palynological assemblages. Therefore, Russian scientists dealing with Permian plant macroremains and palynological assemblages repeatedly attempted to relate plant macrofossils and dispersed pollen, based on extraction of pollen grains from microsporangia, seed micropyles and coprolites, as well as comparison between dominant taxa from macrofossil and palynomorph assemblages from the same beds (see below).

Pollen of *Vesicaspora* ex gr. *magnalis* (transitional forms from *V. magnalis* to *V. ovata* and *V. potoniei*) dominates the palynological assemblage from a coal layer exclusively composed of *Phylladoderma* cuticles (Upper Permian of the Pechora Basin). On this basis Gomankov (1986) related this pollen with *Phylladoderma* of the peltaspermalean family Cardiolepidiaceae. Esaulova (1986) shared this opinion, based on her study of a plant macrofossil assemblage of the Kazanian age, Tatarstan Republic, Russia. The assemblage includes numerous leaves of *Phylladoderma*, seeds of *Nucicarpus* and pollen organs *Permotheca*, which yielded *Vesicaspora* pollen. Gomankov and Meyen (1986) reported from the Vologda Region, Tatarian stage, *Permotheca vesicasporoides* Meyen, Esaulova et Gomankov (1986) containing in situ *Vesicaspora* pollen.

Krassilov et al. (1999a) reported pollen organs of *Permotheca disparis* (Zalessky) Naugolnykh 1999 from the Lower Permian of the Ural Mountains with in situ *Vesicaspora* pollen grains. These authors underlined that, based on sporangial and pollen grain morphology, the *Permotheca* material that they studied seems related to Carboniferous callistophytes. Meyen (1987) also suspected a phylogenetic relationship between callistophytes and peltasperms.

Gomankov (1986) related the dispersed pollen genus *Protohaploxypinus* to peltasperms with *Tatarina* foliage and female fructifications *Peltaspermopsis*. His evidence is a coprolite with numerous pollen grains of *Protohaploxypinus limpidus* (Balme & Hennelly) Balme & Playford 1967 and fragmentary cuticles of *Tatarina* (it seems unlikely that the animal was eating leaves of one plant and sporangia of another plant); occurrence of such pollen in synangia of *Permotheca striatifera* (illustrated and discussed in Gomankov and Meyen, 1986), in their turn co-occurring with *Tatarina* foliage; and finds of such pollen in micropyles of *Salpingocarpus bicornutus* Meyen and *S. variabilis* Meyen, which probably belong to peltasperms (seeds of *S. variabilis* were found attached to ovuliferous discs of *Peltaspermopsis*). In addition, both *Protohaploxypinus limpidus* and remains of *Tatarina*-*Peltaspermopsis* plants dominate in relevant assemblages. So, it is quite probable that in Angaraland pollen of *Protohaploxypinus* type was produced by peltasperms. Sporangia of *Permotheca striatifera* also contain rare pollen grains attributable to *Striatopodocarpidites*, which is a rare but constant component of palynological assemblages. The rarer type can be an aberrant form of the common type, as for some Gondwana *Protohaploxypinus*/*Striatopodocarpidites* found in glossopterid fructifications (Lindström et al., 1997; Plate VI, 2, 6).

Pollen masses of *Vittatina subsaccata* f. *connectivalis* Samoilovich 1953 were found under peltoids of *Peltaspermopsis buevichiae* Gomankov et Meyen, which is attributed to *Tatarina conspicua* Meyen foliage due to its epidermal characters (Gomankov and Meyen, 1979). This pollen was also found in sporangia of *Permotheca*? *vittatinifera* S. Meyen et Gomankov 1986 and within seeds of *Salpingocarpus variabilis* Meyen (Gomankov and Meyen, 1986). Thus, Gomankov (1986) supposed that *Vittatina* is another type of peltasperm pollen; he also believed that *Protohaploxypinus* and *Vittatina* have intermediate forms (Foster and Gomankov, 1994). Therefore, the pollen types *Vesicaspora*, *Protohaploxypinus*, and *Vittatina* are probably related to Permian peltasperms.

Retallack (2002) reported peltasperm remains from the Sydney Basin of Australia dated to the earliest Triassic. *Permotheca helbyi* Retallack 2002 was found in association with the foliage *Lepidopteris callipteroides* (Carpentier) Retallack 2002 and the female fructification *Peltaspermum townrovii* Retallack 2002. The pollen organ contained poorly preserved pollen attributed to *Falcisporites australis* (de Jersey) Stevens 1981, a pollen genus that is not very distant in general morphology from *Vesicaspora*.

From the Upper Triassic (Carnian or Norian) of Antarctica, Bomfleur et al. (2011) have reconstructed a peltasperm with *Dejerseya lobata* (Jones et de Jersey) Herbst foliage, *Matatiella dejerseyi* ovulate organs and *Townrovia polaris* pollen organs. The micropylar canals of seed cuticles and ovules, and the pollen sacs contained bisaccate, non-striate pollen ascribed to *Falcisporites*.

Triassic *Antevsia extans* (Frenguelli) Townrow 1960 and *A. zeilleri* (Nathorst) Harris 1937 yield in situ *Cycadopites* pollen (Townrow, 1960). Monosulcate pollen grains of the *Cycadopites* type are common in Mesozoic deposits, but are also known from older rocks. For example, *Cycadopites* is reported from dispersed palynological assemblages of the Tatarian of the Russian Platform (Gomankov et al., 1998). There are no Permian in situ finds of this pollen. Gomankov (1986) and Gomankov et al. (1998) pointed out that *Cycadopites* is abundant in a particular Tatarian locality where remains of the presumed leptostrobalean leaves *Sphenarion* are common. It is also possible that this *Cycadopites* was peltasperm pollen associated with *Glossophyllum* foliage and *Stiphorus* polysperms. Gomankov (2011, pers. comm.) named three variants of the affinity of Permian *Cycadopites* that can be conceived by indirect indices in the current absence of in situ data: Leptostrobales with *Sphenarion* leaves; Peltaspermaceae with *Lepidopteris* leaves and *Peltaspermum* female fructifications; and Peltaspermaceae with *Kirjamkenia* leaves and *Stiphorus* female fructifications. *Cycadopites* pollen, however, has also been found in situ in cycadalean, bennettitalean and ginkgoalean inflorescences from younger deposits (see e.g., Balme, 1995).

2. Material and methods

The *Antevsia* specimen used for this study was collected in a quarry near the village of Wüstenwelsberg in the vicinity of Coburg (Bavaria, Germany) (for details of the locality, see Bonis et al., 2010). The specimen was found in Rhaetian clay layers (level 2 in Bonis et al., 2010). It is housed at the Laboratory of Palaeobotany and Palynology, Utrecht, The Netherlands (nr. 23238).

Pollen was extracted from pollen sacs attached to branched axes. These pollen sacs were cleaned with HF followed by maceration in Schulze's solution and KOH. The cleared pollen sacs with adhering pollen grains were used to study the general morphology of pollen grains in transmitted light, with a Zeiss Axioplan-2. Pieces of cleared pollen sac walls with adhering pollen and detached pollen grains were mounted on stubs for Scanning Electron Microscopy (SEM), coated with platinum/palladium and viewed on a Hitachi S-405 SEM (accelerating voltage of 20 kV) at Lomonosov Moscow State University. Fragments of the cleared pollen sac walls with attached pollen grains and several individual pollen grains were taken off light microscopical slides and SEM stubs, and embedded for Transmission Electron Microscopy (after Meyer-Melikian & Telnova, 1991), but without preliminary staining. Ultrathin sections of 50 nm thick were made with an LKB 5 ultra-microtome. Some of them were stained (Gayer, 1973) and others were observed under TEM unstained. The sections were viewed on a Jeol 100 B TEM (accelerating voltage 80 kV) and photographed. Most ultramicrographs were made on films and digitized via an Epson Perfection V700 Photo Scanner; others were recorded with an Olympus CO-770 digital camera. Composite images were made from individual ultramicrographs via Photoshop 7.0.

In total, dozens of pollen grains were observed in transmitted light; about twenty better preserved pollen grains were measured. About twenty pollen grains were studied under SEM. Six specimens were studied with help of TEM, four of which were previously observed under SEM. Numbers were only designated to the pollen grains studied with TEM.

Remains of polymerized resins with embedded pollen grains, grids with ultrathin sections, files of LM, SEM and TEM photos, and TEM film negatives are kept at the Laboratory of Paleobotany, Paleontological Institute, Moscow.

The terminology used in this paper is that of Punt et al. (2007); if a term is not mentioned in there, we refer to the paper from which it was taken.

3. Morphological description

Pollen sacs are elongate, and can be up to 10 mm long and 500 μm wide, although smaller examples also occur. Walls of pollen sacs consist of elongate epidermal cells. The ultrastructure was observed in Specimen 3, which is a fragment of pollen sac wall with pollen grains on its internal surface (Plate III, 1, 4). The wall is about 1.0–1.3 μm thick, composed of fine-grained material. The grains appear to be arranged more densely in areas situated closer to the external and internal surfaces of the wall. Rare large granules occur on the external surface of the wall. They are slightly wider than high, about 0.9 × 1.2 μm in size.

Pollen sacs yielded numerous pollen grains (Plate I, 2). The length of the pollen varies from 41.1 to 52.6 μm; the width ranges from 25.3 to 37.9 μm. The average size is 47.4 × 33.1 μm. The majority of pollen grains are ellipsoidal, being compressed in polar orientation (Plate I, 3, 8, 9, Plate II, 5, 8, 10). However, irregularly folded and partly damaged pollen grains having more irregular outlines are also common (Plate I, 2); some pollen are compressed in lateral-polar position (Plate II, 1, 2, 4; Plate V, 8). The proximal exine can also be folded (Plate II, 7). The sulcus is evident in better preserved specimens (Plate I, 9). Pollen grains with an open sulcus are broadly ellipsoidal with rounded extremities (Plate I, 1, upper pollen; Plate II, 5, 8, 12). Pollen grains with a closed sulcus are narrower and their extremities are very slightly pointed (Plate I, 3; Plate II, 2, 10). In transmitted light, the exine of the sulcus is lighter (= thinner) than the exine of non-apertural areas; the areas bordering the sulcus appear thicker and structured in transmitted light (Plate I, 4). Optical sections show that the exine is not homogeneous (Plate I, 5); they do not exclude the presence of regularly arranged columellae or granules or alveolae.

The surface as observed under SEM is scabrate and occasionally punctured (Plate II, 5, 6, 9). These are mainly pits rather than perforations, as evidenced by ultrathin sections showing uninterrupted tectum (e.g., Plate III, 8; Plate IV, 5). Some specimens show a more or less open sulcus exposing the surface of the aperture; we have not recognised significant differences between the apertural and non-apertural surfaces. However, we have detected several short filaments about 2.0–2.3 μm long and 0.3 μm wide on the surface of the sulcus of one specimen (Plate II, 8, 11).

The exine is two-layered with a thicker and less electron-dense alveolate ectexine, and a much thinner and more electron-dense lamellate endexine (Plate III, 3; Plate IV, 2). The ectexine varies in thickness and ultrastructure depending on the position within the exine (Plate IV, 1, 4; Plate V, 1). The thickest areas are lateral, the thinnest is the apertural area and proximal areas are of intermediate thickness. The endexine is very thin in comparison to the ectexine; some variations in the endexine thickness are probably due to preservation rather than representing an original feature of the pollen wall (Plate III, 7).

Proximal exine is about 0.57–0.73 μm thick. The ectexine is nearly homogeneous in some sections (Plate IV, 3) or with rare lacunae in others (Plate IV, 4). The lacunae, where detected, are arranged in one row and situated deeper in the ectexine, dividing it into three sublayers (Plate III, 8). The uppermost sublayer of the ectexine is a continuous tectum of up to 0.5 μm thick, which is only occasionally pierced with perforations (Plate IV, 6). The intermediate layer, an infratectum, is about 0.08–0.10 μm thick, formed by pillars hanged from the tectum and either reaching or not reaching the lowermost layer (Plate III, 5, 6, 8). The footlayer is about 0.14 μm thick (Plate III, 8), but is not always detected (Plate IV, 2). This organization is evident in some sections, whereas the proximal ectexine is nearly homogeneous in others, where the position of the intermediate layer is only occasionally marked by much rarer lacunae. These variations are from section to section rather than from specimen to specimen.

Laterally, the ectexine is 0.7–1.0 μm thick. A rim surrounding the aperture is apparent (Plate IV, 3; Plate V, 2–6). Numerous alveolae are present in this region and the tectum is thinner than proximally, being about 0.13–0.27 μm thick. In places, the ultrastructure of this area even resembles a saccus-like ultrastructure (Plate V, 10). The rim is also detectable under SEM (Plate II, 8, lower specimen, arrow) and in transmitted light (Plate I, 4). We consider that the rim varies in width and thickness around the margin of the aperture. In case of boat-shaped folding of pollen grains, their extremities are situated in the areas where the rim is less developed and allowed easier folding. Uneven development of the rim is visible in a specimen shown in Plate I, 4. The rim is visible in Specimen A10 over its distal pole (Plate I, 9), but is not detectable over its extremity (Plate I, 8). On the other hand, the rim was detected in many, but not all studied specimens, as evidenced by LM, SEM and TEM.

Sections in the polar region confirm that the pollen grains have one aperture formed by a considerable thinning of the ectexine (Plate IV, 1, 4, 7; Plate V, 1). The ectexine is homogeneous in this region and allows folding, in accordance with the harmomegathic function that was once carried out. The absence of differences between the surface of apertural and non-apertural regions probably implies that it is the upper sublayer of the ectexine, the tectum that only remains over the apertural area.

The endexine is thin and has suffered from compression to various degrees. White-line-centred lamellae are detectable at places in the endexine under considerable magnification (x 25000 and greater) and in stained sections (Plate III, fig 7; Plate IV, 2; Plate V, 7, 9). There are certain difficulties in accurately measuring the endexine thickness and counting the number of the lamellae. This is because the position of the gametophyte cavity is, as a rule, indicated by the endexine, but the two faces of pollen grain are usually adpressed to each other very tightly. No cavity is visible, and we cannot decide for sure what the proximal and what the distal endexine may be (Plate V, 7). The endexine ultrastructure is best visible in areas of folds, transitions towards extensions, where the sporoderm suffered from compression in a lesser degree (Plate III, 2); however, areas of bending are not suitable for accurate measurements. In some areas, the lamellation of the endexine is clearly visible, whereas elsewhere it appears homogeneous, slightly more electron-dense than the ectexine. Supposedly, the endexine consists of six lamellae. Its thickness varies between 0.04 and 0.09 μm.

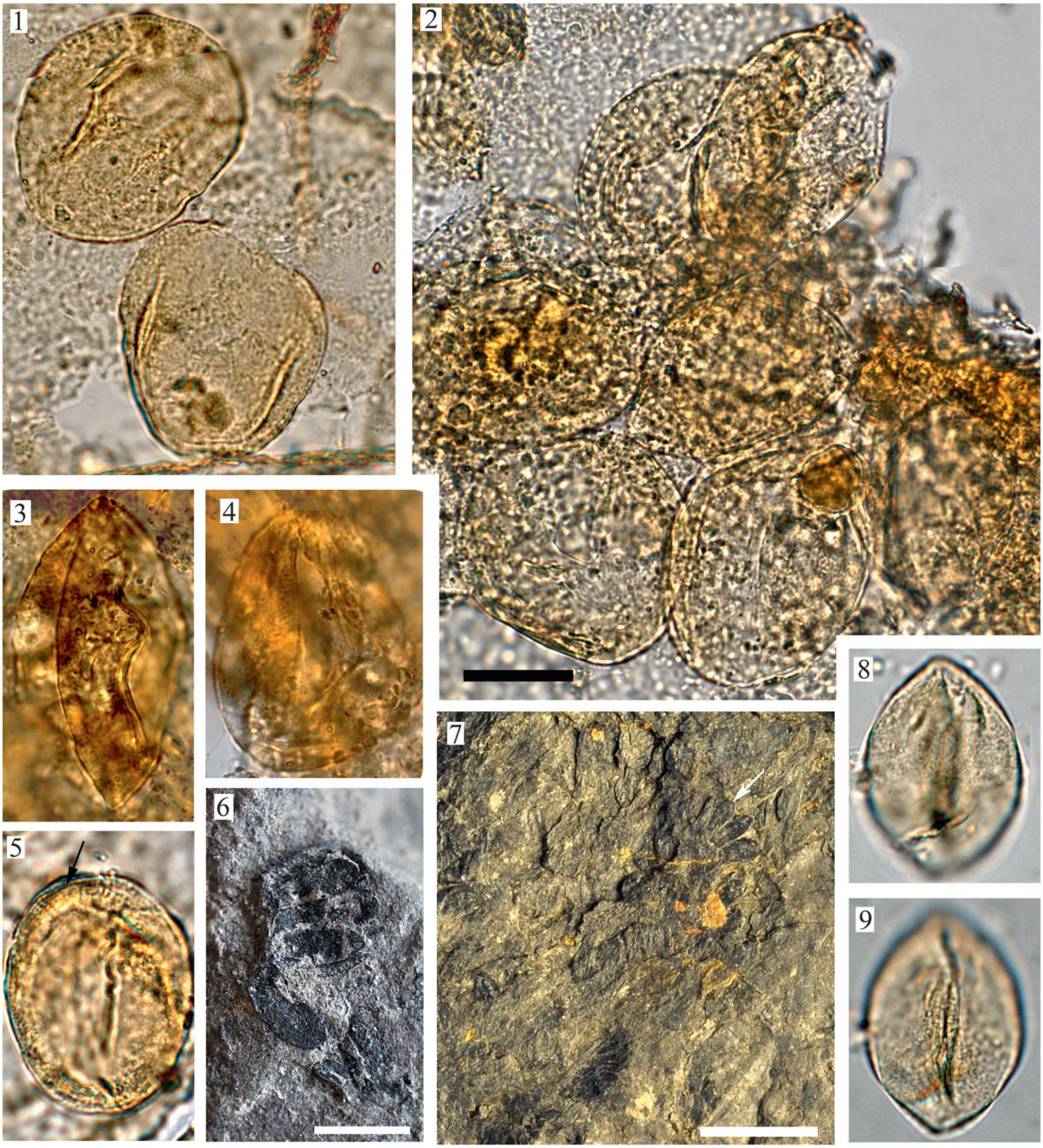

Plate I. General morphology of pollen sacs and pollen grains of *Antevsia zeilleri* from the Rhaetian of Germany.

1. The lower pollen is Specimen A1 (Plate II, 7; Plate IV, 1, 2, 5–7); folds visible on Specimen A1 belong to the proximal face; the upper pollen shows an open sulcus.
2. Group of pollen grains, two upper right pollen grains are shown in Plate II, 8, 11, 12.
3. Pollen is shown in Plate II, 2.
4. Pollen with an open sulcus, exine surrounding the sulcus is thickened.
5. Pollen, the optical section shows that the exine is not homogeneous (arrow).
6. Cluster of pollen sacs; specimen S. 23308, Laboratory of Palaeobotany and Palynology, Utrecht, The Netherlands.
7. Part of specimen S. 23238 (Laboratory of Palaeobotany and Palynology, Utrecht, The Netherlands), showing microsporophyll head with attached pollen sacs (arrow).

8, 9. Specimen A10 (Plate II, 6, 9, 10; Plate V, 1–6, 9).

8. Focus on an extremity.
9. Focus on the sulcus. Scale bars (1–5, 8–9) 20 μm, (6) 5 mm, (7) 10 mm.

3.1. Remarks concerning the presence of filaments

Several threads have been remarked on the apertural surface of one of the studied pollen grains (Plate II, 8, 11), which appear to be original features of the pollen surface rather than contamination. The presence of various filaments on pollen is usually related to pollination ecology and nearly exclusively reported from angiosperms, best known in the Ericaceae and Onagraceae. Functions ascribed to the viscin (acetolysis-resistant, presumably sporopollenin) threads are to form pollen aggregates during pollen transfer by animal vector, to fix pollen at the border of the opened pollen sac, to prevent pollen from falling off prematurely and to play a role in pollen presentation (Hesse et al., 2000). Fossil angiosperm pollen with acetolysis-resistant threads have also been reported (e.g., Zetter and Hesse, 1996). Few reports of filaments in gymnosperm pollen are mostly fossil examples, such as *Dicheiropollis* (Trevisan, 1971), and *Triadispora* and members of Circumpolles (Scheuring, 1976). Various filaments have been repeatedly reported from the most well-known member of the Circumpolles group, *Classopollis* (e.g., Courtinat, 1980; Zavialova et al., 2010, fig. 5A). Kurmann and Zavada (1994, figs. 5, 6) illustrated filaments connecting pollen grains into a tetrad in modern *Ginkgo biloba*.

It should be pointed out that sporopollenin filaments are conventionally thought to be related to animal pollination and they are situated proximally in known fossil examples, unlike distal filaments observed in *Antevsia*. Nothing is so far known or hypothesized about pollination biology of *Antevsia*-bearing plants. In their review of plant/insect interactions in Permian and Mesozoic times, Krassilov et al. (2007) noted that pollen of *Cycadopites* type were never reported from insect guts, that counts on the wind pollination of the plant under study rather than insect pollination. Although *Ginkgo biloba* is a wind-pollinated plant (Tredici, 2007), it was shown to have filaments on pollen grains (Kurmann and Zavada, 1994). In sum, the filaments found in *Antevsia* may be somehow related to pollination adaptation, though not necessarily with insect pollinator.

4. Discussion and comparisons

4.1. Comparison with the exine ultrastructure of presumed peltaspermalean pollen

The exine ultrastructure of pollen of *Vesicaspora* has been studied several times, in specimens of different presumed or proved botanical affinities (Millay and Taylor, 1974; Zavialova, 1998; Krassilov et al., 1999a; Zavialova et al, 2001). Millay and Taylor (1974) studied in situ callistophytalean *Vesicaspora* from the Pennsylvanian of the United States. Zavialova (1998) and Zavialova et al. (2001) dealt with dispersed Upper Permian *Vesicaspora,* supposedly produced by the Cardiolepidiaceae (Peltaspermales). Krassilov et al. (1999a) published ultrathin sections of in situ *Vesicaspora* from Lower Permian *Permotheca*, which they thought most similar to callistophytes.

The Carboniferous and Permian pollen belong to the same dispersed pollen genus and show several ultrastructural similarities, but also some differences. Some Middle Pennsylvanian pollen show a proximal scar (Millay & Taylor, 1974) which was not detected in Late Pennsylvanian and Permian pollen. Carboniferous pollen grains are unequivocally eusaccate, Lower Permian pollen were interpreted as protosaccate (terms after Scheuring, 1974), and Upper Permian pollen also appear protosaccate or intermediate proto/eusaccate, although it can be a preservational feature, since the dispersed pollen grains were strongly flattened (Plate VII, 1). Carboniferous pollen show fine, but distinct, sculpturing that was not detected in Permian pollen grains. Lamellae were found in the endexine of the Carboniferous and Lower Permian pollen grains, but were not detected in the Upper Permian dispersed pollen. Both Lower and Upper Permian pollen have a thicker proximal ectexine, with upper and lower homogeneous layer, and a row of alveolae between them. The distal aperture is formed by a considerable thinning of the ectexine. Proximal areas in the exine of pollen of *Antevsia* are usually more homogeneous than in the cappa of Permian *Vesicaspora* (Plate VII, 7, 10); however, some sections of *Antevsia* pollen appears very similar (e.g., Plate III, 8; Plate IV, 4). One can imagine the following transformation which would allow the dissimilar pollen of Permian and Triassic peltasperms to be related: the proximal exine of *Vesicaspora* became less alveolate; sacci disappeared, leaving as remnants lateral extensions that were observed in *Antevsia* pollen; and the ultrastructure of the distal area did not change appreciably.

Another pollen type ascribed to peltasperms is *Protohaploxypinus* (Plate VI, 2), which also have been repeatedly studied with TEM. Glossopterid *Protohaploxypinus* was reported by Foster (1979) and Zavada (1991); peltaspermalean *Protohaploxypinus* by Zavialova (1998), Krassilov et al. (1999b) and Zavialova et al. (2001). The morphology of the cappa in *Protohaploxypinus* has something in common with that of *Vesicaspora*; upper and lower homogeneous layers and intermediate alveolate layer are present in both pollen types. *Protohaploxypinus* differs by strong variations in thickness and presence of the upper and intermediate layers due to the striations (Plate VII, 2). In sum, it shows fewer similarities to *Antevsia* pollen than *Vesicaspora*.

The ultrastructure of *Vittatina* was studied by Meyer (1977) and Afonin (1999). Having granular infratectum, *Vittatina* is very different ultrastructurally from the above-discussed saccate pollen of peltasperms (Plate VII, 8). The idea by Foster and Gomankov (1994) about relations between *Protohaploxypinus* and *Vittatina* is not supported by their exine ultrastructure (compare Plate VII, 2 and Plate VII, 8). The granular infratectum also differentiates *Vittatina* from pollen of *Antevsia*. Therefore, although by the general morphology (non-saccate state) *Vittatina* seems closer to pollen of *Antevsia* than *Vesicaspora* or *Protohaploxypinus*, the analysis of the exine ultrastructure shows more shared features in pollen under study to *Vesicaspora*.

Ultrastructural information about peltaspermalean *Falcisporites* is so far lacking. Several corystospermaceous pollen organs were studied in terms of the exine ultrastructure of their bisaccate pollen (Taylor et al., 1984; Zavada and Crepet, 1985; Osborn and Taylor, 1993), which were originally attributed to either *Alisporites* or *Pteruchipollenites*, but reinterpreted by Balme (1995) as *Falcisporites*. The three studies revealed quite different ultrastructures, that is most probably explained by insufficient preservation of the materials, as shown by Osborn and Taylor (1993). This way or another, the proximal ultrastructure of these pollen differs from that in *Vesicaspora* or *Antevsia*: either an extremely thinned exine layer or a homogeneous exine was described in the cappa region. We suppose that the exine ultrastructure of peltaspermalean *Falcisporites* can differ from that of corystospermaceous *Falcisporites*. In this relation, an ultrastructural study of pollen of *Dejerseya lobata* would be pertinent; unfortunately, the illustrated pollen grains do not appear very well preserved (Bomfleur et al., 2011).

4.2. Comparison with the exine ultrastructure of Cycadopites type pollen grains of different age and affinity

The pollen grains under study show significant similarities with the ultrastructure of modern *Ginkgo biloba* pollen grains (Zavialova et al., 2011). Proximal areas in *G. biloba* exine show a thick solid tectum and an infratectum formed of variable pillars, the majority of which hang from the inner surface of the tectum into the infratectal cavity, reaching or not reaching the foot layer; some pillars rise from the foot layer, not reaching the tectum (Plate VII, 3). Though the proximal exine of the *Antevsia* pollen grains is much denser and in several sections nearly homogeneous, there are also sections, which show an analogous ultrastructure of the ectexine. One more significant similarity concerns the ultrastructure of the areas surrounding the aperture. Sahashi and Ueno (1986) hypothesized that a rim surrounding the aperture of pollen of *Ginkgo* (Plate VI, 3), occasionally developing into auricular projections (Sahashi and Ueno, 1986, figs. 1e, 1f), might be degraded sacci, retained as an atavism of saccate ancestors. Our idea about lateral extensions of *Antevsia* pollen is the same.

Zavada and Dilcher (1988) studied the morphology and ultrastructure of dispersed monosulcate pollen grains from the Cenomanian of the Dakota Formation (USA), with variously developed saccate-like structures flanking the distal aperture. Among the seven pollen types that they studied, *Monosulcites* sp. appears very suitable for our comparison. Apart from several dissimilarities (such as the rounded outline, more distinct sculpture, homogeneous proximal exine and the absence of the endexine), it shares some common features with pollen of both *Antevsia* and *Ginkgo*. These are a distal sulcus formed by a thinned ectexine and ectexine swelling bordering it. Among dispersed monosulcate pollen grains from the Jurassic of Siberia studied with SEM and TEM by Meyer-Melikian and Zavialova (1996), several groups were subdivided that differ by the exine ultrastructure; pollen grains of group 3 (defined as *Monoletes* in that paper, but *Cycadopites* is a more appropriate taxon) have a more or less homogeneous proximal exine, a considerably thinned exine of the distal aperture and lateral extensions with narrow small alveolae surrounding the aperture (Plate VII, 5).

Ultrastructural data of dispersed *Cycadopites* of unknown botanical affinity from the Permian of the Russian Platform are available (Zavialova et al., 2001). So far, conceivable parent plants are either the Leptostrobales or Peltaspermales (see section 1.1). Peltaspermalean affinity of this Permian pollen would be very suitable because of the similarity of their general morphology to that of Triassic members of the group, but the exine ultrastructure does not seem to support this idea. Although some sections of pollen grains of both taxa are quite similar, these are poorly preserved areas of nearly homogeneous exine. In better preserved areas, the

Plate II. Surface morphology of pollen grains of *Antevsia zeilleri* from the Rhaetian of Germany.

1. Two pollen grains; the better exposed pollen is Specimen A2, compressed in lateral-polar position (Plate III, 5–8).
2. Pollen is shown in Plate I, 3.
3. Pollen in proximal view.
4. Partly damaged pollen grain, compressed in lateral-polar position.
5. Specimen 7 (Plate IV, 3, 4).
6, 9. Enlargement of Fig. 10.
10. Specimen A10 (see Plate I, 8, 9; Plate V, 1–6, 9). Polar position, sulcus is closed at the pole and slightly opened at the extremities.
7. Specimen A1 (see Plate I, 1, lower pollen; Plate IV, 1, 2, 5–7)); proximal surface shows folds.
8. Two pollen in distal view (Plate I, 2, two upper right pollen grains).
11. Enlargement of Fig. 8, note filaments on the sulcus surface.
12. Enlargement of Fig. 8, surface of the sulcus is visible.Scale bars (1–5, 7, 8, 10) 10 μm, (6) 2 μm, (9, 12) 5 μm, (11) 2 μm.

Plate III. Ultrastructure of pollen sac wall and exine of *Antevsia zeilleri* from the Rhaetian of Germany. (see on page 14)

1. Ultrastructure of pollen sac wall and pollen attached to its internal surface. Exine (to the right of the figure) is more electron-dense than pollen sac wall (to the left). The orientation of the section is uncertain. No lateral extension is present in this section. Specimen 3.
2. Enlargement of Fig. 1. Two faces of pollen exine are adpressed to each other. Alveolate ectexine and lamellate endexine are evident. Specimen 3.
3. Two faces of pollen exine are adpressed to each other. Ectexine is much thinner than in Fig. 2. Lamellate endexine is less evident. Specimen 3.
4. Enlargement of Fig. 1. Pollen sac wall (to the left of the figure, under black contour) is heterogeneous, composed of fine grains; occasional big granules are scattered over the external surface of pollen sac wall. Specimen 3.
5. Section through one of the extremities, Specimen A2 (Plate II, 1), variable alveolae of proximo-equatorial regions are visible.
6. Section through one of the extremities, Specimen A2; more electron-dense endexine indicates a fold of the exine. Ectexine alveolae have different outlines in comparison to Fig. 5 showing another section of the same series.
7. Enlargement of Fig. 6, showing indistinct lamellations of the endexine. Specimen A2.
8. Enlargement of Fig. 5 showing solid thick tectum, alveolae, and a foot layer. Specimen A2.Black outer layer visible in Figs. 1, 4–8 is remnants of metal coating for SEM study. Numbers in white ovals indicate the position of relevant enlargements; (w) pollen sac wall, (e) exine, (ect) ectexine, (end) endexine, Figs. 2, 6, 7 show stained sections, and Figs.1, 3, 4, 5, 8, unstained sections. Scale bar (1, 5, 6) 1 μm, (2, 3, 8) 0.5 μm, (4) 0.667 μm, (7) 0.25 μm.

Plate IV. Ultrastructure of exine of *Antevsia zeilleri* from the Rhaetian of Germany. (see on page 15)

1. Specimen A1 (Plate I, 1, Plate II, 7). Section shows thinned ectexine of the apertural region and extensions bordering the aperture.
2. Enlargement of fig. 5, white-line-centred lamellae are clearly visible.
3. Enlargement of another section of Specimen 7 than shown in fig. 4. Extensions bordering the aperture are visible; proximal exine is predominantly homogeneous unlike Fig. 4.
4. Section of Specimen 7 (Plate II, 5), proximal exine shows regular alveolae, distal-equatorial extensions surround the aperture.
5. Enlargement of Fig. 1, lamellate endexine can be detected.
6. Enlargement of Fig. 1 showing alveolate ectexine of the extension surrounding the aperture. Arrow indicates a perforation through the tectum, which is usually continuous.
7. Extremely thinned ectexine in the apertural area. Black outer layer visible in Figs. 1, 3, 4, 6, 7 is remnants of metal coating for SEM study. Numbers in white ovals indicate the position of relevant enlargements; intermittent line indicates the position of extensions surrounding the aperture; (p) proximal area; (d) distal area; (a) apertural area; (ect) ectexine, (end) endexine. Scale bar (1, 3) 0.667 μm, (2) 0.25 μm, (4) 1 μm, (5–7) 0.5 μm. Fig. 1, 3, 4, 6, 7 show unstained sections, Fig. 2, 5 show stained sections.

Plate V. Ultrastructure of exine of *Antevsia zeilleri* from the Rhaetian of Germany. (see on page 16)

1. Specimen A10 (Plate I, 8, 9, Plate II, 6, 9, 10).
2–6. Specimen A10. Same areas of serial sections are shown, note changing outlines of elements forming alveolae in the area bordering the aperture. Section shown in full in Fig. 1 was (in the ribbon of sections) after the section shown in Fig. 4.
7. Specimen K1, lamellate endexine.
8. Section of pollen compressed in lateral position (in similar way as, for example, pollen shown in Plate II, 4), Specimen K1.
9. Enlargement of Fig. 1 showing lamellations.
10. Enlargement of Fig. 8 shows saccus-like appearance of extensions bordering aperture. Specimen K1. Black outer layer visible in Figs. 1–8, 10 is remnants of metal coating for SEM study. Numbers in white ovals indicate the position of relevant enlargements; (p) proximal area, (d) distal area, (a) apertural area, (ect) ectexine, (end) endexine, (*) position of supposed contact between internal surfaces of endexines. Scale bar (1–6) 0.667 μm, (7, 9) 0.25 μm, (8) 1 μm, (10) 0.4 μm. Sections shown in Figs. 1–7, 9 are stained; in Figs. 8, 10, unstained.

proximal ectexine of the Permian *Cycadopites* is composed of a thick solid tectum, a much thinner foot layer and merely a row of horizontal slit-like alveolae (Plate VII, 11, 12), whereas the proximal ectexine of pollen of *Antevsia* shows a developed infratectum in better preserved areas. Further, in the Permian *Cycadopites* no extensions surrounding the aperture were revealed, which we consider as an important characteristic feature of *Antevsia* pollen.

4.3. Differentiation between pollen of Antevsia and Cycadopites pollen grains produced by contemporaneous plant groups

This study was in part stimulated by our desire to amass enough electron-microscopical data to be able to differentiate by the exine ultrastructure between dispersed *Cycadopites* pollen grains of various origins. With accumulation of these new data, it seems to us that this aim has be-

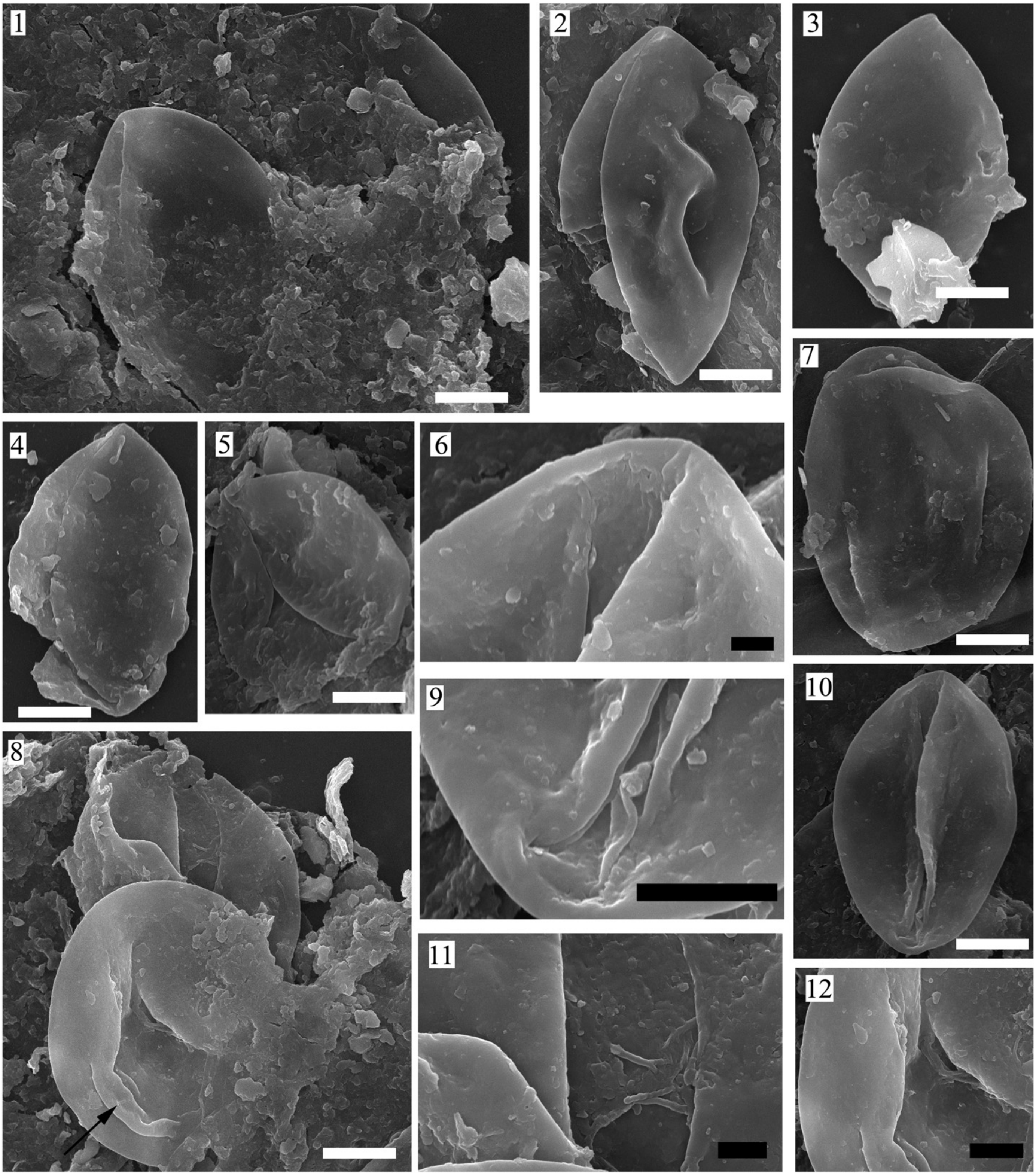

Plate II.

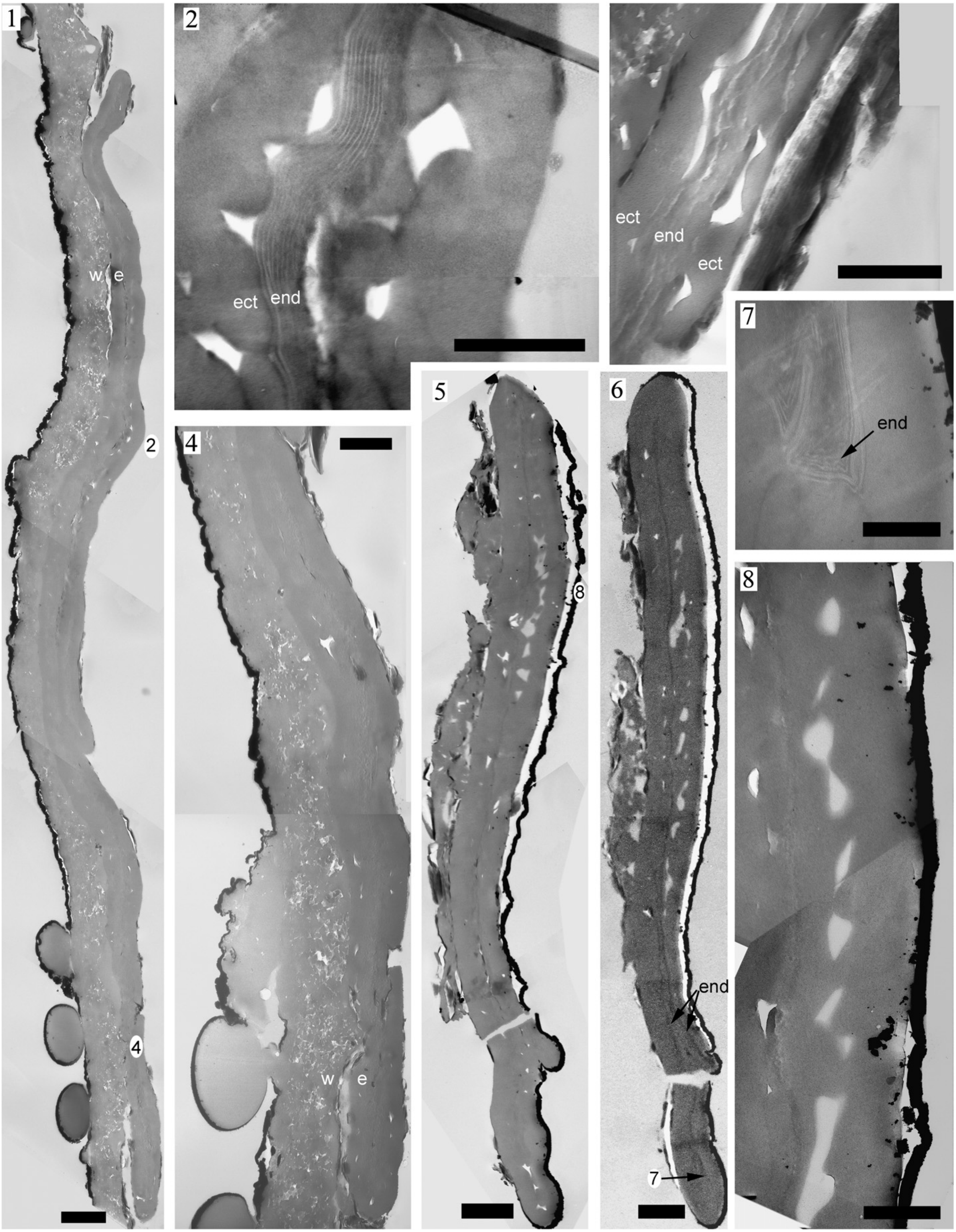

Plate III (*caption on page 12*).

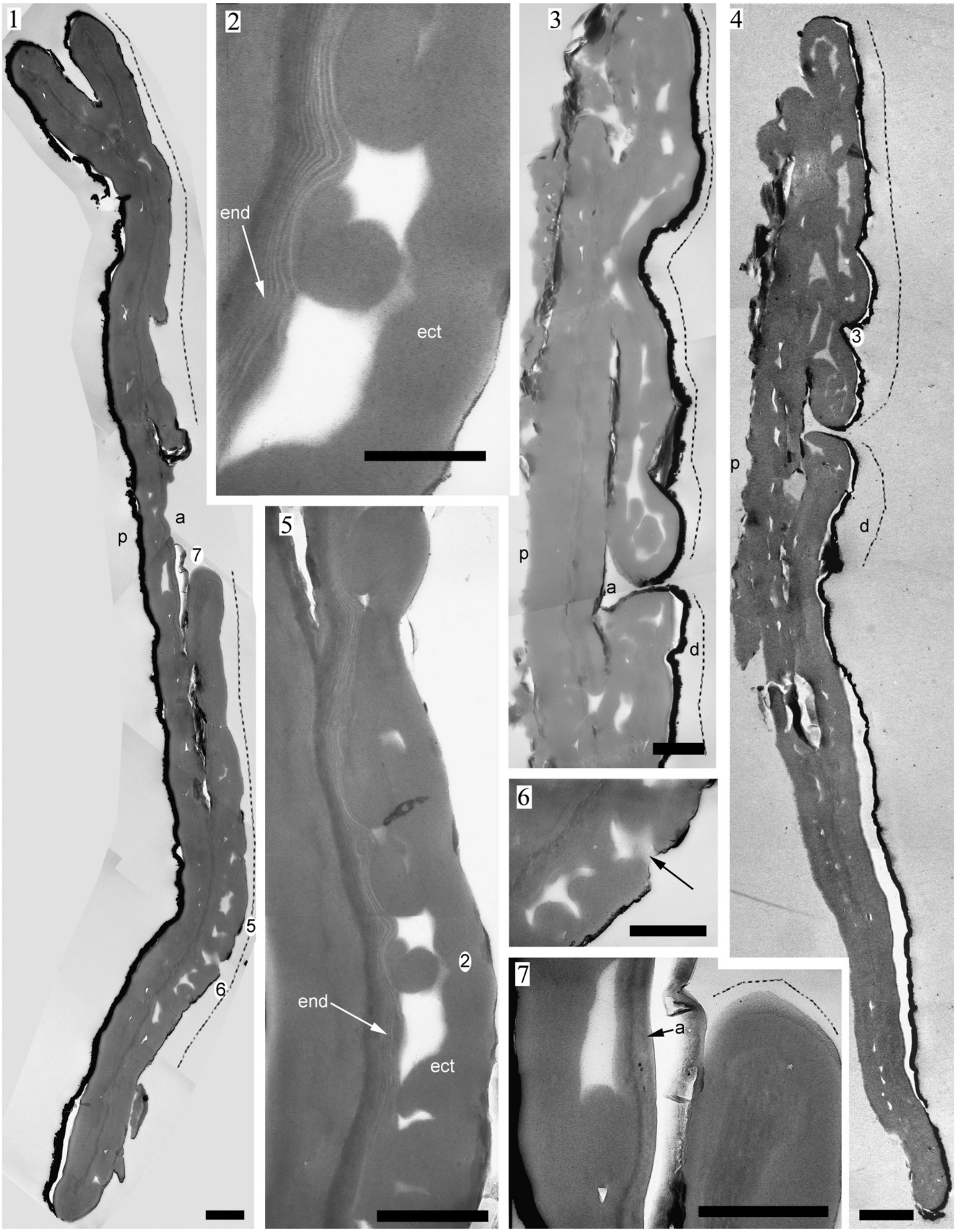

Plate IV (*caption on page 12*).

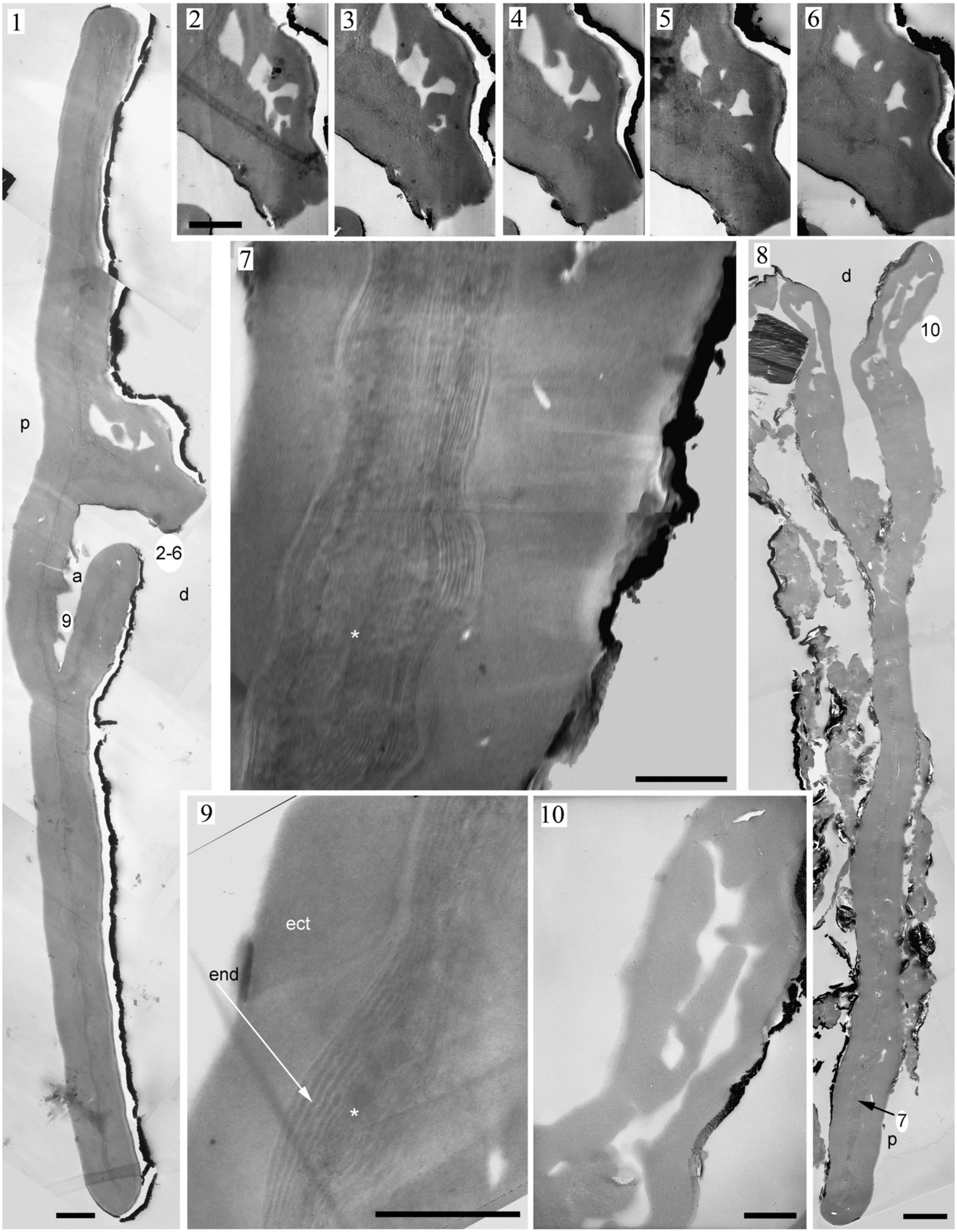

Plate V (*caption on page 12*).

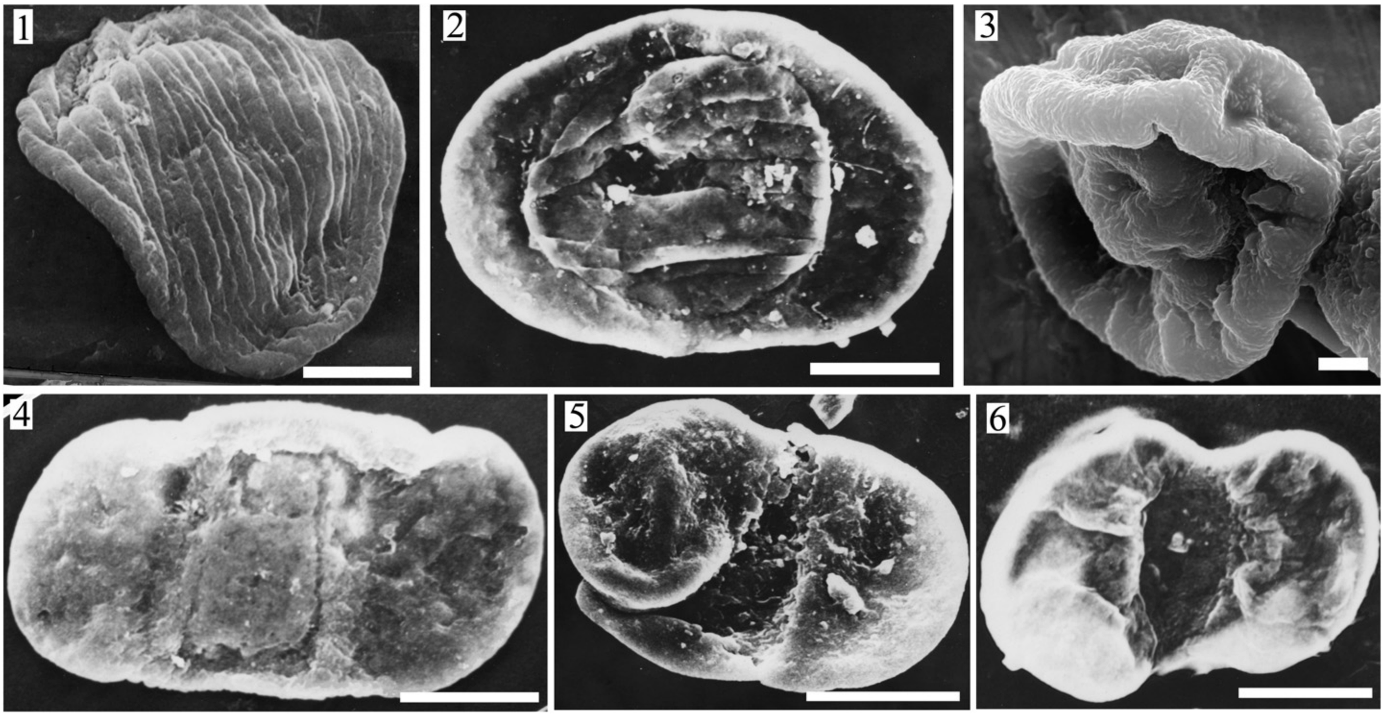

Plate VI. Surface morphology of some Permian dispersed pollen grains of supposed peltaspermalean affinity and modern *Ginkgo biloba*.

1. *Vittatina* sp., striations are evident (Meyer, 1977, plate 171, fig. 5).
2. *Protohaploxypinus* sp., proximal view showing a striated body (Zavialova, 1998, plate 3.6(1)).
3. *Ginkgo biloba*, distal-lateral view of a pollen grain showing a swollen rim surrounding the distal aperture (illustration provided by Svetlana Polevova).
4. *Falcisporites* sp. (Zavialova, 1998, plate 2.1(1))
5. *Piceapollenites* sp. (Zavialova, 1998, plate 5.1(1)).
6. *Striatopodocarpidites* sp., distal view (striations are situated at the opposite, proximal, face) (Zavialova, 1998, plate 9.1(1)).The illustrated pollen grains come from the Permian deposits, Tunguska River Basin, Russia (1), Upper Permian, Viatka River basin, Russia (2, 4–6), and Recent, Krasnodar Region, Russia (3). Scale bar (1) 10 μm, (2, 4–6) 20 μm, (3) 3 μm.

come slightly closer. The material under study is of Triassic age that means that other possible variants of *Cycadopites*-producing contemporaneous plants are cycads, bennettites and ginkgophytes.

Cycads are quite characteristic. The infratectum in pollen of modern cycads is very distinctive, being composed of elongated alveolae, situated perpendicular to the exine surface (Plate VII, 9). Pollen of fossil cycads, in our opinion, had the same infratectum. However, such ultrastructure has a relatively low preservational potential, alveolae become extremely narrowed and the sporoderm often appears nearly completely homogeneous. By tracing serial sections, one can detect areas in predominantly homogeneous exine where alveolae are preserved and the cycad infratectum shows its original structure (Tekleva et al., 2007; Plate VII, 4)). The exine ultrastructure in cycad pollen is different from that in the Triassic peltasperm pollen under study. In addition, pollen of some cycads lack a definite aperture, unlike pollen grains of *Antevsia*, clearly showing an aperture under LM, SEM, and TEM.

Bennettites are more difficult to compare. Pollen of some of them show granular infratectum (Ward et al., 1989; Osborn and Taylor, 1995; Osborn and Taylor, 2010), whereas others have a homogeneous exine (Zavialova et al., 2009; Plate VII, 6). So far, it is not possible to

Plate VII. Exine ultrastructure of pollen grains of some fossil and recent gymnosperms.

1. *Vesicaspora* sp., composite longitudinal section through the body and sacci, proximal face to the left, the approximate position of enlargements (Plate VII, 7, 10) is shown with figures in white ovals (Zavialova, 1998, plate 1.5(5)).
2. *Protohaploxypinus* sp., area of an oblique section, proximal face to the left, the position of the strongly compressed inner hollow is marked by presence of a thin fine-grained endexine (Zavialova, 1998, plate 3.16(2))
3. *Ginkgo biloba*, modern species, area of the section (illustration provided by Svetlana Polevova).
4. *Cycandra profusa*, area of a section through two sporoderms, white arrows indicate the boundary between the two compressed pollen coats, arrowheads point on some of compressed alveolae.
5. *Cycadopites* sp., composite section, proximal face to the left (Meyer-Melikian, Zavialova, 1996, this section is drawn in their text-Fig. 4 and its area is shown in their pl. 1(4)).
6. *Williamsoniella coronata*, exine of two homogeneous layers differing in electron density.
7. *Vesicaspora* sp., cappa, the position of the strongly compressed inner hollow is marked by presence of a thin fine-grained endexine (Zavialova, 1998, plate 1.3(3)).
8. *Vittatina* sp., area of the section showing granular ectexine over a thick endexine (Meyer, 1977, plate 173, fig. 4).
9. *Cycas micholitzii* Dyer, modern species, area of sporoderm showing the characteristic cycadalean elongated alveolae (illustration provided by Maria Tekleva).
10. *Vesicaspora*, cappa (Zavialova et al., 2001, plate 2, fig. 3). Area of transverse section, a region of the cappa. Sporoderm becomes thinner at the distal side of the pollen; a thin membrane between proximal and distal sides indicates the position of the compressed cavity of the pollen.
11. *Cycadopites* sp., area of a transverse section, distal exine is mostly missing (Zavialova et al., 2001, plate 5, fig. 6).
12. *Cycadopites* sp., area of a longitudinal section (Zavialova et al., 2001, plate 6, fig. 1).

The illustrated material comes from the Upper Permian, Viatka River basin, Russia (1, 2, 7, 10-12), Recent, Krasnodar Region, Russia (3), Jurassic, Georgia (4), Jurassic, Siberia, Russia (5), Jurassic, England (6), Permian, Tunguska River Basin, Russia (8), Recent, glasshouse, Moscow, Russia (9). Long black arrow indicates the position of the inner hollow, which is as a rule strongly flattened in fossil pollen, asterix (*) points on striae between ribs in striate pollen of *Protohaploxypinus* sp. and *Vittatina* sp., p — proximal, d — distal, s — saccus, l.e. — lateral extension, a — aperture, t — tectum, i — infratectum, g — granule, end — endexine. Scale bar (1–3, 6, 8) 1 μm, (4, 5) 1.25 μm, (7, 10, 11) 0.67 μm, (9) 0.5 μm, (12) 0.4 μm.

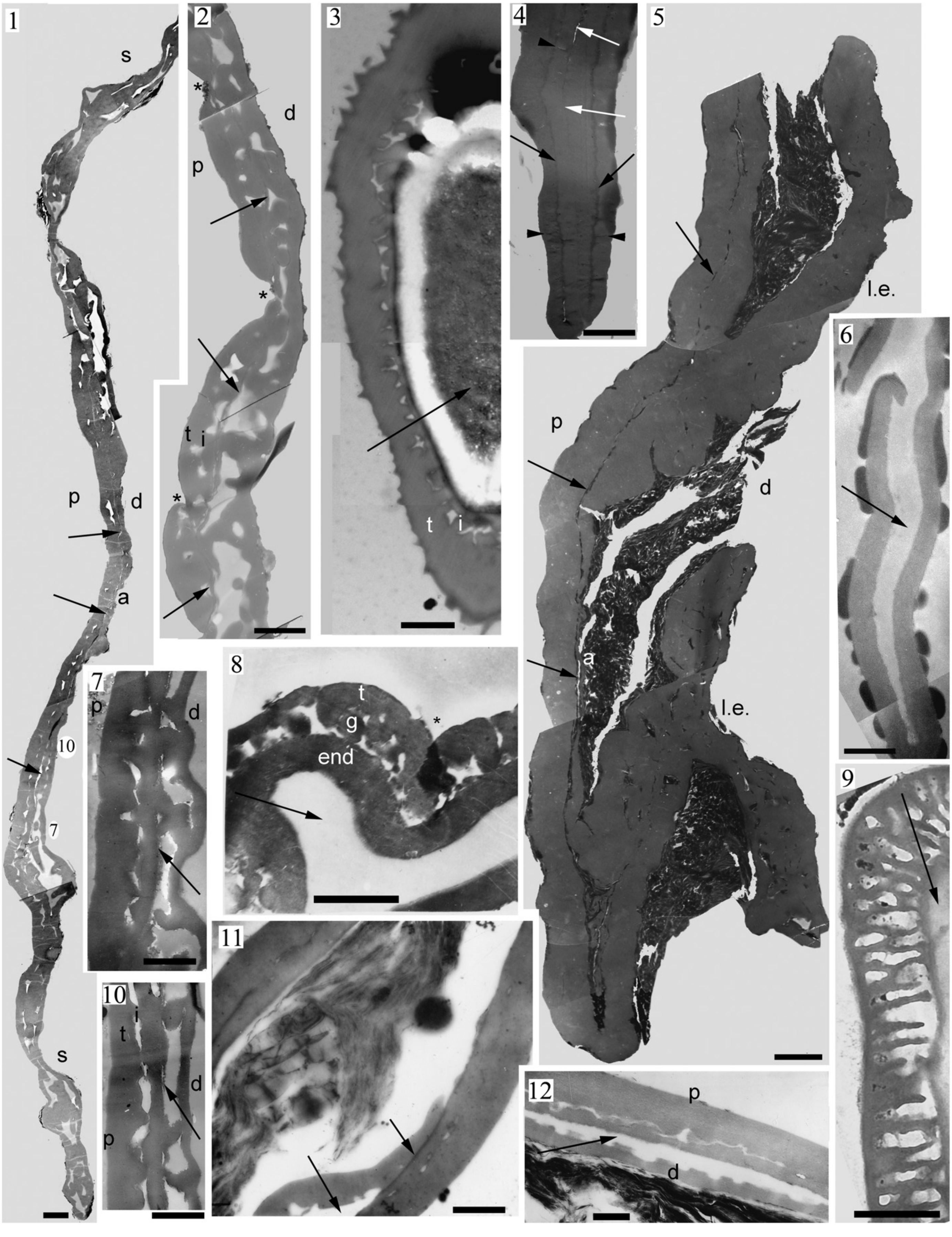

Plate VII. (*caption on page 17*).

formulate the ultrastructural characteristics of pollen of bennettites as a whole group. Nonetheless, the pollen under study easily differs from pollen of bennettites so far studied by the presence of lateral extensions surrounding the aperture. In addition, some hints (supposing differentiating features) can also be drawn from LM and SEM data. Thus, the structure of the exine of pollen of *Antevsia* allows several variants of folding of pollen grains (e.g., with an open and closed sulcus), in contrast to those of *Cycadeoidea dacotensis* (McBride) Ward, which are always preserved with a closed sulcus (Osborn and Taylor, 1995). Pollen grains of *Williamsoniella coronata* Thomas show an open sulcus under SEM which shows that the apertural and non-apertural surfaces are different (Zavialova et al., 2009), which is not the case in pollen grains of *Antevsia.*

No pollen ultrastructure of any early ginkgophyte has been studied. Recently, dispersed pollen of supposed ginkgoalean affinity have been studied with the help of SEM and TEM from Cretaceous deposits (Zavialova et al., 2011). Their ultrastructure shows several significant similarities to that of pollen grains of *Ginkgo biloba*, but some differences were also revealed. Extensions surrounding the aperture in pollen of *Antevsia* seem more similar to corresponding areas in pollen of *G. biloba* than lateral areas in the Cretaceous *Ginkgocycadophytus*. The ginkgoaleans were once a very diverse group with a long geological history. It would be wrong to judge the exine ultrastructure of the entire group merely on the basis of the only modern survivor or to believe that it is the most typical member of the group just because it is more easily available for study than its extinct relatives.

In general, pollen grains of *Cycadopites* of different botanical affinities often show a virtually homogeneous exine. Single sections can be misleading, but numerous sections of as many specimens as possible usually provide enough raw data and allow the investigator to find areas of better preserved and less changed exine and, therefore, to reveal the original ultrastructure.

5. Conclusions

In situ *Cycadopites*-type pollen grains of *Antevsia* show a distinctive exine ultrastructure, by which the pollen of Triassic peltasperms is more similar to *Vesicaspora* than *Protohaploxypinus* and dissimilar to *Vittatina* (among pollen types of Permian peltasperms). Transformation from the proximal exine of *Vesicaspora* to the proximal exine of *Antevsia* pollen grains is conceivable, as well as the reduction of the sacci of *Vesicaspora* into a rim surrounding the aperture of pollen grains of *Antevsia*. Gymnosperm pollen grains with similar, slightly thickened alveolate exine extensions surrounding the aperture are also known from later epochs such as the Jurassic, Cretaceous and today. *Cycadopites* pollen produced by Triassic peltasperms can be differentiated by their exine ultrastructure from pollen of the same type, produced by cycads and bennettites, although additional data on the exine ultrastructure of these groups are necessary.

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