



The exine ultrastructure of *Pretricolpipollenites bharadwajii* from the Permian of Jordan

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ABSTRACT

Dispersed trisulcate pollen grains of *Pretricolpipollenites bharadwajii* from the ?latest Permian of Jordan were studied with light, scanning, and transmission electron microscopy. The three sulci are located on the disal side. The median sulcus is usually longer, wider than the other two sulci, and has rounded aperture ends. The exine sculpturing and aperture membrane are scabrate. The ectexine includes a thick tectum, granular infratectum, and thin foot layer. The endexine is lamellate. A comparison with the closest similar genus *Eucommiidites* suggests overlapping characters; though the position of the three sulci on the distal side in *Pretricolpipollenites bharadwajii* and sulci on different sides in *Eucommiidites* indicates a possible distinguishing feature. Studies of exine ultrastructure of the other two *Pretricolpipollenites* species are needed to support or discard the distinction of *Pretricolpipollenites* and *Eucommiidites*.

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1. Introduction

Pre-Cretaceous pollen grains with three furrows are worthy of investigation as possible precursors of true tricolpate angiosperm pollen grains, or as evidence of pre-Cretaceous angiosperms (Maheshwari, 2007). Such pollen grains are mostly accommodated in the genus *Eucommiidites* Erdtman, 1948 (mainly from the Jurassic and Cretaceous) both dispersed and in situ. Other three-furrowed pollen grains from the Permian, Triassic, Jurassic, and Cretaceous are few and poorly studied with electron microscopy and include the genera *Pretricolpipollenites* Danzé-Corsin et Laveine, 1963, *Cryptosacciferites* Krassilov et al., 2003, and *Zolerella* Scheuring, 1978.

In this case, it is important to study the oldest known specimens of such pollen to understand whether Permian and younger pollen grains with three furrows could have been produced by related parent plants or that their similar general morphology resulted from convergence and independent repeated appearance of the same character in non-related plant groups.

So far, the only known species of *Cryptosacciferites*, *Cryptosacciferites papularis* Krassilov et al., 2003, from the Lower Cretaceous of Russia, and a number of *Eucommiidites* type pollen, dispersed, found in pollen chambers and from pollen organs, have been studied in detail by means of light, scanning, and transmission electron microscopy (see review in Tekleva et al., 2006). This allowed accurate comparison of *Eucommiidites* species and the discovery of a great diversity of the

exine ultrastructure, proving the heterogeneity of this evolutionary important group.

In this paper, we study for the first time three-furrowed pollen grains of *Pretricolpipollenites bharadwajii* Balme, 1970 discovered in abundance in the ?latest Permian Umm Irna Formation of Jordan. Light and electron microscopy was used to document exine morphology and ultrastructure, and to understand relationships between *Pretricolpipollenites* and other known pollen with three furrows.

2. Geological setting of the Umm Irna Formation

The Umm Irna Formation, exposed along the eastern shore of the Dead Sea (Fig. 1), consists of a mixed arenaceous–argillaceous clastic succession. The Umm Irna Formation was first described by Bandel and Khoury (1981) who also gave a description of the lithology in the type section in Wadi Himara. They also mentioned the presence of “iron-oxidic pisolites.” Makhlof et al. (1991) recognized an informal Lower Member, about 10 m thick, consisting of sandstones and silty shales in upward-fining sequences, which they attributed to a distal braidplain setting. Their Upper Member comprises five fining-upward cycles with elements of both braided and meandering stream deposits, with silty beds deposited in abandoned channels. Paleosols with ferruginous glauclites are developed in the middle and upper part of the formation (Makhlof et al., 1991; Powell and Moh'd, 1993; Stephenson and Powell, 2013).

Paleontological work in the Umm Irna Formation has mainly focused on the well-preserved plant fossils and their depositional environments (Kerp et al., 2006; Uhl et al., 2007; Abu Hamad et al., 2008). More

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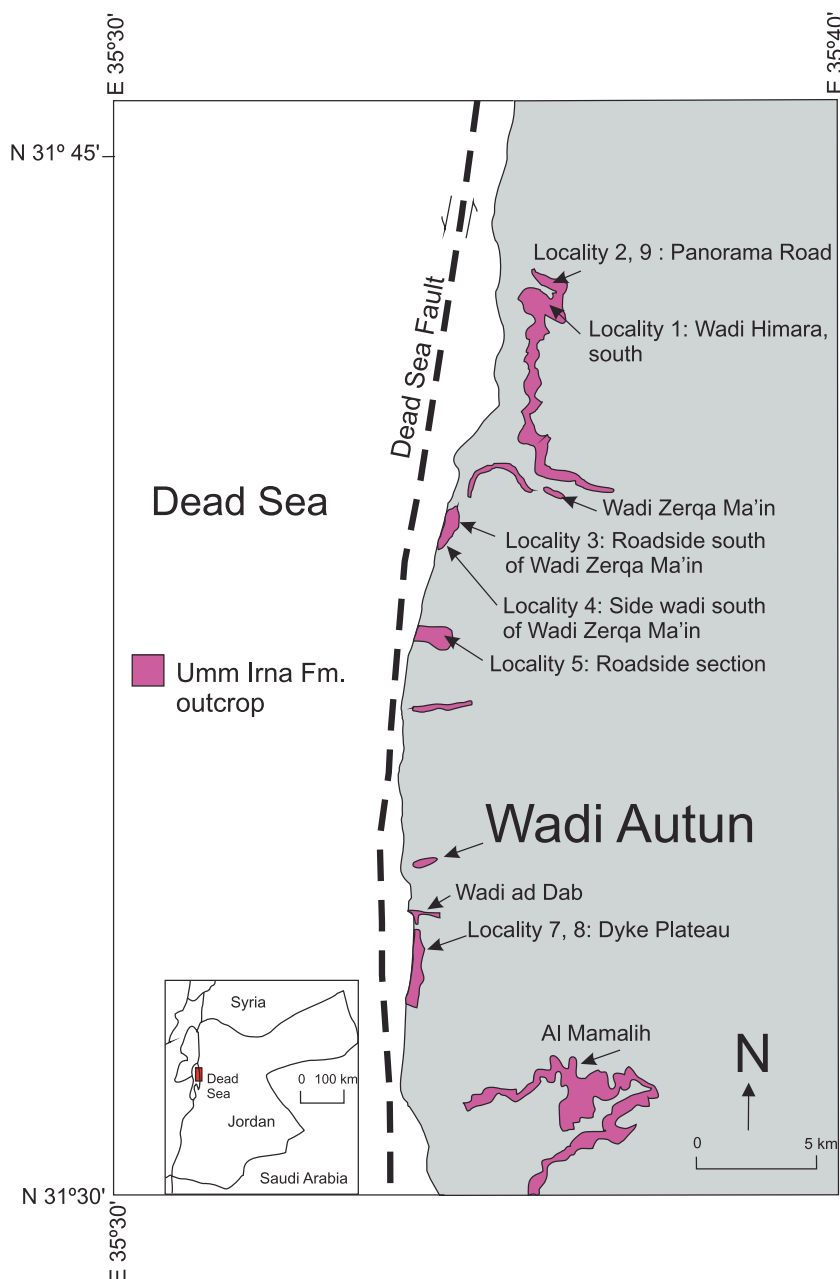


Fig. 1. Location of Wadi Autun, east Dead Sea shore Jordan; inset shows location of Dead Sea. Locality numbers refer to localities of [Stephenson and Powell \(2013\)](#).

recently, [Stephenson and Powell \(2013\)](#) synthesized palynology and sedimentology into a comprehensive depositional model and correlated the Umm Irna Formation with successions elsewhere in the Arabian Peninsula and Israel.

The assemblages are very variable but in general contain common non-taeniate bisaccate pollen (often fragmentary or too poorly preserved to be identified); those that are determinable include *Falcisporites stabilis* [Balme, 1970](#), *Alisporites nuthallensis* [Clarke, 1965](#), *A. indarraensis* [Segroves, 1969](#), and *Cedripites priscus* [Balme, 1970](#). The most common taeniate bisaccate pollen is *Protohaploxypinus uttingii* [Stephenson et Filatoff, 2000](#) and *P. limpidus* ([Balme et Hennelly, 1967](#)). Monosaccate pollen grains are rare, as are spores. Details of the quantitative character of the assemblages and the stratigraphic ranges of taxa are given in [Stephenson and Powell \(2013, 2014\)](#).

Pretricolpitenites bharadwajii occurs throughout the Umm Irna Formation, but is particularly common in a sample at a locality in

Wadi Autun (Locality 6 of [Stephenson and Powell, 2013](#); [Fig. 1](#); N 31° 32'40.1"; E 35° 33'31.7"). The north-facing, measured section in Wadi Autun lies about 15 m below the top of the Umm Irna Formation. It consists of intercalated yellow, pink and gray medium-grained sandstone and gray siltstones with black carbonaceous laminae. The sample with abundant *Pretricolpitenites bharadwajii* was the lower of the two samples (MPA 62257) from Wadi Autun and was taken from a gray siltstone overlain by black carbonaceous, almost coaly, siltstone that is overlain by trough cross-bedded sandstone with an erosive base (see [Stephenson and Powell, 2013](#), their fig. 8).

In the absence of independent paleontological evidence it is difficult to accurately date the Umm Irna Formation, however, its overall palynological character suggests an age from Guadalupian (mid-Permian) to Lopingian (late Permian), most probably within the later part of this range (see [Stephenson and Powell, 2014](#)).

Elsewhere, *Pretricolpitenites bharadwajii* is mainly recorded from the Triassic in the Middle East and North Africa, though it has been

recorded further afield (e.g., Antarctica; Ram Awatar et al., 2014). Mazroui-Kilani et al. (1988), Kilani-Mazraoui et al. (1990), and Kamoun et al. (1994) recorded it spanning the Lower to Upper Triassic in Tunisia; similarly Geleta and Wille (1998) recorded it from the Middle Triassic (Ladinian) of west-central Ethiopia. It was first described from the “upper 12 feet or so of the Chhidru Formation” (Balme, 1970, p. 406) of the Salt Range of Pakistan (reportedly Changhsingian, see Wardlaw and Pogue, 1995). Hermann et al. (2012) in a recent survey of the Salt Range of Pakistan recorded *P. bharadwajii* and *Pretricolpipothenites* spp. between their units PTR1 and PTR2 (lowest Triassic). Venkatachala and Kar (1968) reported a specimen from the Triassic “Kathwai Shales” of the Salt Range which they assigned to *Ginkgocycadophytus* sp. cf. *G. cymbatus* (Balme et Hennelly) Potonie et Lele, 1961, but which is similar to *P. bharadwajii*.

Pretricolpipothenites bharadwajii occurs widely in Israel (e.g. Zuk Tamrur-1 and -2; Zohar-8; Pleshet-1 boreholes) as reported by Eshet (1990), from cuttings rather than core. The key cored well Makhtesh Qatan-2 does not appear to contain *P. bharadwajii* according to Eshet and Cousminer (1986).

3. Material and methods

The sample from Wadi Autun was extracted by deep excavation of the siltstone using a pick-axe to avoid near-surface contamination or the present-day oxidation of palynomorphs. The preparation of strewn mounts for palynological analysis comprised crushing, followed by hydrochloric and hydrofluoric acid treatments (Wood et al., 1996). The post-hydrofluoric acid organic residues were oxidized using Schulze's solution. The palynological slides bear the British Geological Survey code prefix “MPA” and are curated in the BGS collections in Keyworth, Nottingham.

Pollen grains of *Pretricolpipothenites bharadwajii* were picked up from the residue and transferred to a drop of water or glycerin on a slide. They were photographed with a Carl Zeiss Axioplan 2 transmitted light microscope equipped with an AxioCam 105 digital camera at the A.A. Borissiak Paleontological Institute of the Russian Academy of Sciences (PIN). For SEM, each pollen grain was cleaned with alcohol, mounted on a SEM stub, sputtered with gold and palladium, and observed with a Tescan, 20 kV, at PIN. For TEM, pollen grains were embedded in a mixture of epoxy resins (unstained or first stained with osmium tetroxide) for 48 h at 62 °C. Sections of 70 nm thick were prepared using a Leica EMUC6 ultramicrotome equipped with a diamond knife at PIN. They were viewed and photographed with the help of a JEM-1011 TEM (accelerating voltage 80 kV), at the Electron Microscope Laboratory, Lomonosov Moscow State University. The TEM is equipped with a side mounted digital camera Orius SC1000W (11 Megapixels, effective 8.5 Megapixels); Digital Micrograph v. 2.0 (Gatan) software was used. Composite images were made from individual ultramicrographs using Photoshop 7.0. For detailed methods see Zavialova et al. (2018).

The studied sample and remains of polymerized resins with embedded pollen grains, grids with ultrathin sections, files of LM, SEM and TEM images are housed in the Laboratory of Paleobotany, PIN. In total, we have studied 82 pollen grains in LM and SEM and 7 pollen grains in TEM.

Pollen terminology follows Hesse et al. (2009). Here we assume that all three furrows are situated on the distal side therefore representing sulci (elongated apertures located distally) and the pollen is trisulcate.

4. Results

4.1. LM (Plate I, 1–10)

Pollen grains are trisulcate, oblate, psilate, with an oval amb. The apertures are situated parallel to each other and located on the distal pollen surface, with a median one which is usually longer and wider. Aperture margins are usually rounded in the median sulcus and pointed

in the lateral ones. The long pollen axis is 29.4 (23.8–34.6) μm , the short one is 21.5 (16.9–27.9) μm , the median sulcus is 26.3 (20.0–32.3) μm long, the lateral ones 23.0 (16.0–31.5) μm long. The polar axis to equatorial diameter ratio (P/E) is 0.7 (0.6–0.9) μm .

4.2. SEM (Plate II, 1–9; Plate III, 1–5)

The exine is scabrate and solid, rare perforations occur in some specimens. The aperture membrane is scabrate in median and lateral sulci. The long pollen axis is 27.4 (22.0–32.3) μm , and the short is 19.8 (14.7–27.7) μm ; the median sulcus is 23.8 (16.0–29.3) μm long, and the lateral 20.9 (10.9–26.5) μm long. The polar axis to equatorial diameter ratio (P/E) is 0.7 (0.5–0.9) μm .

4.3. TEM (Plate IV, 1–5; Plate V, 1–7)

The proximal ectexine is 0.65 (0.26–1.4) μm thick, and the distal ectexine in the non-aperture region is 0.47 (0.33–0.76) μm thick. The ectexine consists of a thicker tectum, granular infratectum and thin foot layer. The tectum is more-or-less uniform in thickness throughout the pollen grain in non-aperture regions, 0.35 (0.27–0.44) μm on the proximal and 0.30 (0.15–0.56) μm on the distal side. The infratectum is 0.17 (0.09–0.56) μm thick on the proximal and 0.25 (0.12–0.57) μm thick on the distal side, with granules of about 0.10 (0.05–0.15) μm in diameter, forming several rows. They are usually better discernable in the regions between the sulci (Plate IV, 1, 4, 5; Plate V, 1, 4–6); in some grains, they are only discernable in these regions (Plate IV, 1, 4, 5). The foot layer varies in thickness throughout the pollen grain, being the thinnest in the regions between the sulci (Plate V, 4–6); it is 0.11 (0.06–0.17) μm thick proximally and 0.05 (0.03–0.09) μm thick distally (Plate V, 5). The ectexine reduces abruptly towards aperture regions, first the infratectum and foot layer disappear and the tectum reduces considerably. The endexine is more electron-dense than the ectexine, lamellate (Plate V, 3, 6, 7). In some grains, the endexine is poorly preserved or not preserved (Plate IV, 1–5). The endexine is 0.18 (0.05–0.41) μm thick, becoming thicker towards the aperture regions. The central area of the aperture is formed by the endexine and a thin ectexine layer (Plate V, 3, 6, 7).

5. Discussion

5.1. *Pretricolpipothenites bharadwajii* pollen structure

The studied pollen grains are consistent in morphology in LM, SEM, and TEM. The only exception is a pollen grain (Plate IV) which lacks an endexine (in which case the endexine was not preserved) and another specimen with a somewhat poorer preserved endexine. The infratectum structure can be distinguished to a different extent in different pollen grains too; it is always best recognized in the areas between the sulci, and more indistinct on the proximal side. The proximal exine looks homogeneous in some grains (Plate IV). The homogenization of the whole or part of a pollen exine was shown for some material, probably caused by preservation conditions (e.g., see Tekleva and Roghi, 2018). Better preserved grains show a rather thick tectum, a granular infratectum, often composed of granules in several rows, and a thin foot layer that varies in thickness. The endexine is lamellate.

5.2. Comparison with *Eucommiidites* group and other trisulcate forms

The genus *Pretricolpipothenites* was established for fusiform psilate pollen grains with three furrows, where the median furrow extends to the whole length of the grain and is bordered by folds and there are two lateral furrows which are less distinct and shorter (Briche et al., 1963). So far, three species of *Pretricolpipothenites* have been described: the type species *P. ovalis* Danz  -Corsin et Laveine, 1963 from the Lower Jurassic of France, *P. bharadwajii* from the Upper Permian of



Plate I. Light microscopy, pollen grains. 1. Distal view, all three sulci are open. 2–4. Distal view, with open median sulcus. 5. 7. Distal view, with closed sulci. 6, 8–10. Lateral view, with closed sulci. Scale bar: 10 μ m.

Pakistan, and *P. microgranulatus* Scheuring, 1970 from the Upper Triassic of Germany (Briche et al., 1963; Balme, 1970; Scheuring, 1970). Pollen grains of *P. ovalis* are oval, with a median sulcus extending to the whole pollen length bordered by two folds, and with widenings in the center and ends of the sulcus. The long pollen axis in pollen grains of *P. ovalis* is about 25–35 μ m, and the lateral sulci are shorter than the median one. *P. bharadwajii* differs from *P. ovalis* in “its broadly oval amb, narrow slit-like subsidiary sulci, and the general absence of longitudinal folds bordering the median sulcus” (Balme, 1970). The pollen size for *P. bharadwajii* is 25 (28) 31 \times 17 (20) 24 μ m. Scheuring (1970) described *Eucommiidites microgranulatus* Scheuring, 1970 with the three furrows on the same pollen side, oval to rounded amb, microgranular to micropunctate ornamentation, and with a long pollen axis 35–45 μ m. Later, Bharadwaj (1974) transferred this species to the genus *Pretricolpipollenites* introducing the combination *Pretricolpipollenites microgranulatus*. Pollen grains of *P. microgranulatus* have an oval amb and seem to differ from *P. bharadwajii* only in their somewhat larger size (with the long axis about 35–45 μ m versus 25–31 μ m in *P. bharadwajii*) and shorter lateral sulci. Also, the lateral sulci are located closer to the equator than in *P. bharadwajii*. Unfortunately, neither Scheuring (1970) nor Bharadwaj (1974) mentioned any differences between *P. microgranulatus* and other *Pretricolpipollenites* species.

Danzé-Corsin and Laveine (in Briche et al., 1963) distinguished the type species, *Pretricolpipollenites ovalis* from a similar trisulcate form, *Eucommiidites troedsonii* Erdtman, 1948, by its fusiform amb, longer median sulcus, and exine folds in *Pretricolpipollenites* versus exine thickenings along the sulcus in *Eucommiidites* species (Briche et al., 1963). Balme (1970) added that considering the description of *Eucommiidites troedsonii* by Hughes (1961), *Pretricolpipollenites ovalis* also differs in having all three furrows on the same face of the pollen grain.

The shorter and less developed sulci in *E. troedsonii* are indeed located on the opposite face to the face in which the median sulcus is situated, or there may be one ring furrow instead of two shorter ones. However, the aperture state is more diverse in *Eucommiidites*

pollen grains, which were described in later literature (e.g. Van Konijnenburg-van Cittert, 1971; Pedersen et al., 1989). The furrows can be located laterally, almost symmetrical with the median sulcus, or on the same face as the median sulcus (Scheuring, 1970; Pedersen et al., 1989; Tekleva et al., 2006). One or both lateral sulci can be lacking in pollen grains extracted from pollen organs of *Hastystrobus muirii* Van Konijnenburg-van Cittert, 1971 (Van Konijnenburg-van Cittert, 1971). In *Eucommiidites* pollen the median sulcus is usually with rounded ends and wider than the lateral ones like in *Pretricolpipollenites* pollen; the only exception is *Eucommiidites* pollen associated with seeds of *Erdtmanispermum balticum* Pedersen et al., 1989 (Pedersen et al., 1989) with three almost symmetrical and similarly developed sulci. The median sulcus is usually longer in *Eucommiidites*-type pollen from pollen organs *Hastystrobus muirii* and *Erdtmanitheca texensis* Pedersen et al., 1989, and almost of the same length as the lateral sulci in *Eucommiidites* sp. 1 and sp. 2 (Trevisan, 1980), and in *Eucommiidites*-type pollen from pollen organs of *Eucommitheca hirsuta* Friis et Pedersen, 1996. In *Cryptosacciferites pabularis* (Krassilov et al., 2003) and *Zolerella tricolpata* Scheuring, 1978 (Scheuring, 1978), two other pollen taxa with three asymmetrical sulci, the median sulcus is shorter than the lateral ones; all three sulci in these two taxa are located on the same face of the pollen grain though the angle between the median and lateral sulci is about 90°. In *Pretricolpipollenites* species the three sulci are more or less equal in length, or the lateral ones are somewhat shorter.

The amb is a somewhat difficult character to deal with in fossil pollen. Here, a fusiform amb is mentioned among diagnostic characters of the genus *Pretricolpipollenites* (and the type species *P. ovalis*), but the other two later described species of *Pretricolpipollenites* have an oval amb and therefore this invalidates amb character as diagnostic for the genus.

The size for different *Eucommiidites* pollen varies from 10–12 \times 15–20 μ m in pollen from pollen organs of *Eucommitheca hirsuta* (Friis and Pedersen, 1996) and 10–13 \times 14–16 μ m in pollen from pollen organs of *Bayeritheca hughesii* J. Kvaček et Pačtová, 2001 (Kvaček and

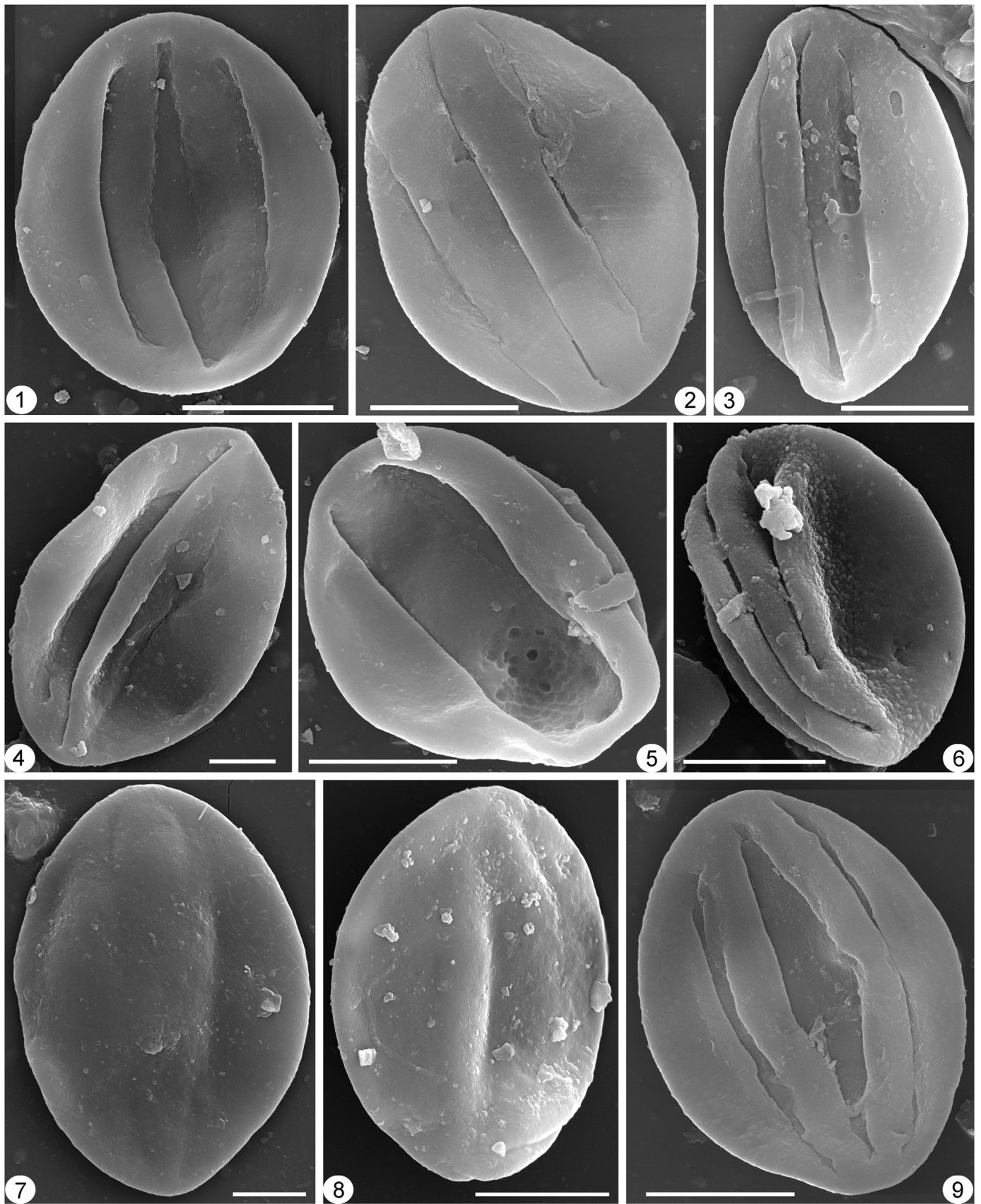


Plate II. Scanning electron microscopy, pollen grains. 1, 9. Distal view, all three sulci are open. 2–4. Distal view, with closed sulci. 5. Distal view, widely open sulcus. 6. Lateral view, with closed sulci. 7, 8. Proximal view. Scale bar: (1–3, 5, 6, 8, 9) 10 μm ; (4, 7) 5 μm .

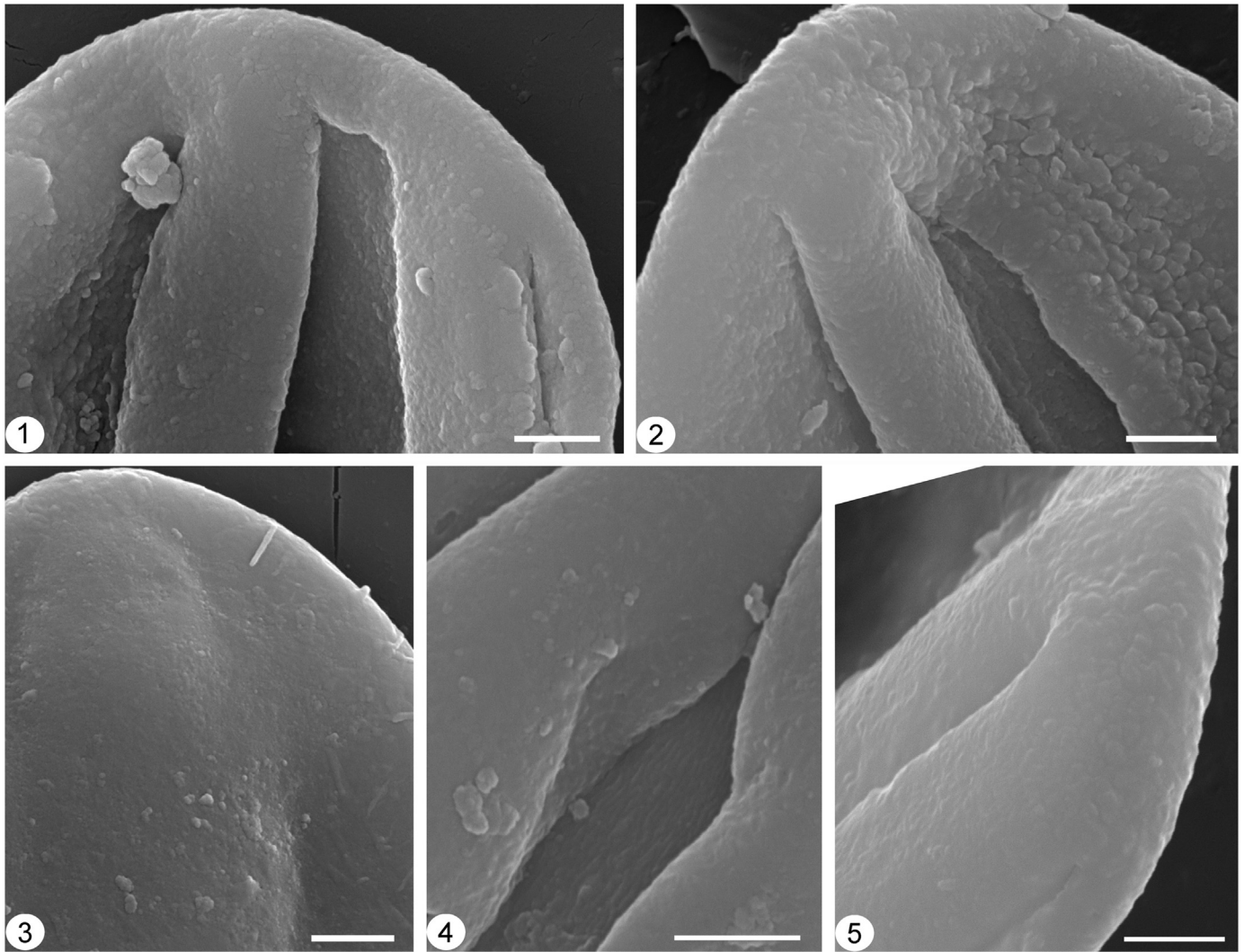


Plate III. Scanning electron microscopy, magnified regions of pollen surface. 1, 2. Ends of sulci and aperture membrane of the median sulcus. 3. Proximal surface. 4. Aperture membrane of the median sulcus. 5. Exine surface in the equatorial region. Scale bar: 2 μm .

Pacltová, 2001) to $25 \times 36 \mu\text{m}$ in *Eucommiidites* pollen described by Batten and Dutta (1997), Doyle et al. (1975), and Trevisan (1980). The exception are *Eucommiidites* pollen grains described by Zavada (1984) which are about $40 \times 45 \mu\text{m}$. Some authors (Pedersen et al., 1989; Batten and Dutta, 1997; Osborn, 2000) doubt their attribution to *Eucommiidites*, although the TEM sections clearly show three apertures. Pollen grains of *Cryptosacciferites pabularis* ($55 \times 70 \mu\text{m}$) and *Zolerella tricolpata* ($70\text{--}80 \mu\text{m}$) are considerably larger. The long pollen axis of *Pretricolpipoollenites* species is within the range $24\text{--}45 \mu\text{m}$, similar to that of most *Eucommiidites* pollen. Modie (2007) reported a somewhat larger range for *Pretricolpipoollenites* pollen, with a long pollen axis of $39 \mu\text{m}$ (50) $56 \mu\text{m}$.

Both *Eucommiidites* and *Pretricolpipoollenites* pollen grains have weakly expressed exine surface, which mostly appears psilate in LM and psilate to scabrate, sometimes with irregularly distributed small foveolae or granules, in SEM. According to Scheuring (1970), pollen grains of *Pretricolpipoollenites microgranulatus* show a microgranulate to micropunctate sculpture in LM, but he did not perform SEM analyses. Another exception is *Eucommiidites* pollen from the seeds *Erdtmanispermum balticum* (Pedersen et al., 1989) with foveolate sculpture. Among pollen grains studied with SEM, the aperture membrane is scabrate in those of *Pretricolpipoollenites bharadwajii*, and granular or smooth in *Eucommiidites* pollen.

This study presents the first data on the exine ultrastructure of *Pretricolpipoollenites bharadwajii*; thus so far we do not know whether *Pretricolpipoollenites* species differed in their exine structure or had the same type of sporoderm. Therefore, we compare the exine structure of the genus *Pretricolpipoollenites* with other similar genera based solely on observations of *P. bharadwajii*. The exine structure is similar in *Eucommiidites* and *Pretricolpipoollenites* in having a granular infratectum, while *Cryptosacciferites* and, most probably, *Zolerella* shows an alveolate one. Pollen grains of *Eucommiidites*-type pollen found dispersed and in situ show a considerable diversity of the sporoderm ultrastructure. This includes different ratio of the tectum, infratectum, and foot layer to the total exine thickness as well as various granular structure of the infratectum (see details in Tekleva et al., 2006). Among known *Eucommiidites* pollen grains, the most similar are those of *Hastystrobus muirii* in the relative ratio of the ectexine sublayers and infratectum structure. However, in contrast to the pollen under study, pollen grains of *Hastystrobus muirii* have a thicker ectexine (and infratectum) on the proximal surface and a columella-like infratectum on the distal one. Pollen grains from pollen organs of *Hastystrobus muirii* are also characterized by three sulci on the same pollen side.

Thus, the two genera *Pretricolpipoollenites* and *Eucommiidites* are quite similar in general morphology and pollen size, making the distinction difficult. The outline is not a crucial character for either, and the

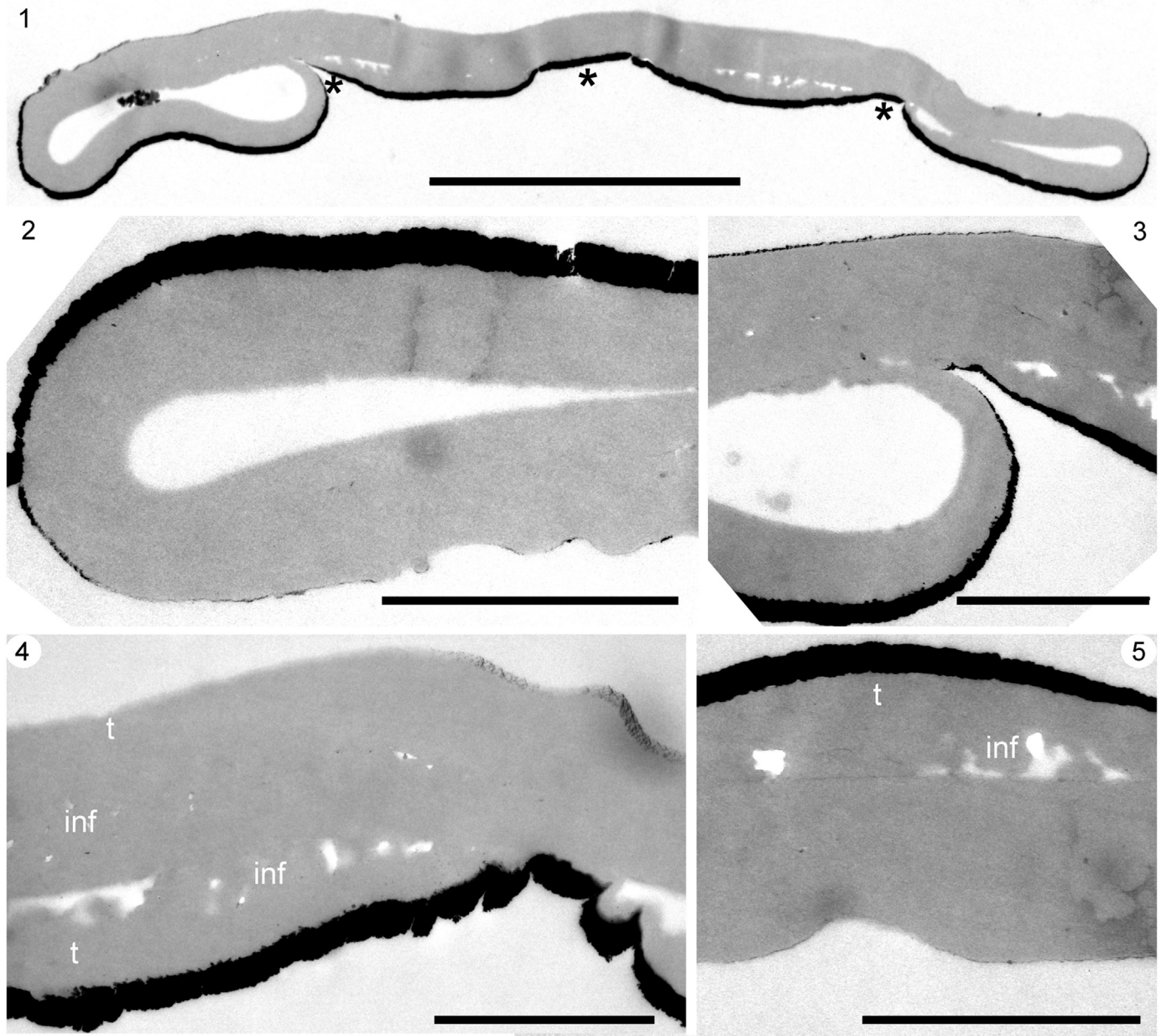


Plate IV. Transmission electron microscopy, pollen grain where the endexine is lacking. 1. Section through the whole pollen grain. 2. Lateral region. 3, 4. Aperture region. 5. Non-aperture region, granular infratectum is seen in the region between two sulci. Asterisks indicate aperture regions, t – tectum, inf – infratectum. Scale bar: (1) 5 μ m; (2–5) 1 μ m.

exine thickening or folds are not always reported; we believe that they are more probably related to the preservation rather than an innate feature of this pollen grain. The length of the median sulcus varies among *Eucommiidites* and *Pretricolpipoollenites* species and so this character also cannot be used for distinction. Location of the three sulci could have been a clear character, but can be also an artificial one. The interlocation of a median sulcus and lateral ones varies among *Eucommiidites* species. One can take this character as diagnostic for the genera distinguishing with the three sulci located on the same side exclusively in *Pretricolpipoollenites* pollen. In this case, we would have to classify pollen grains from pollen organs of *Hastystrobus muirii* as *Pretricolpipoollenites*-type pollen. However, the distinction of the genera based on a sole character does not seem reliable. We think that more generally, distinction should be supported primarily by the characters of the exine ultrastructure which are less variable than those of the general morphology. To understand whether trisulcate pollen grains are adequately incorporated in species of *Pretricolpipoollenites* and

Eucommiidites, a detailed study of the exine ultrastructure of the other two *Pretricolpipoollenites* species is needed. Until then, the question remains whether *Pretricolpipoollenites* and *Eucommiidites* should be considered as separate genera.

5.3. Available data on the exine ultrastructure of similar Permian and Triassic sulcate pollen

Genera of pollen similar to *Pretricolpipoollenites bharadwajii* but with one or several furrows (sulci) described from the Permian and Triassic include *Cycadopites* Wodehouse, 1933 ex Wilson et Webster, 1946, *Sverdrupollenites* Utting, 1994, *Kingiacolpites* Tiwari et Moiz, 1972, *Marsupipollenites* Balme et Hennelly, 1956 emend. Balme, 1970, *Praecolpatites* (Balme et Hennelly, 1956) Bharadwaj et Srivastava, 1969 and *Mulinopollenites* Gomankov, 1998. Among them, the exine ultrastructure has been studied for *Marsupipollenites triradiatus* Balme et Hennelly, 1956 and *Praecolpatites sinuosus* (Balme et Hennelly, 1956)

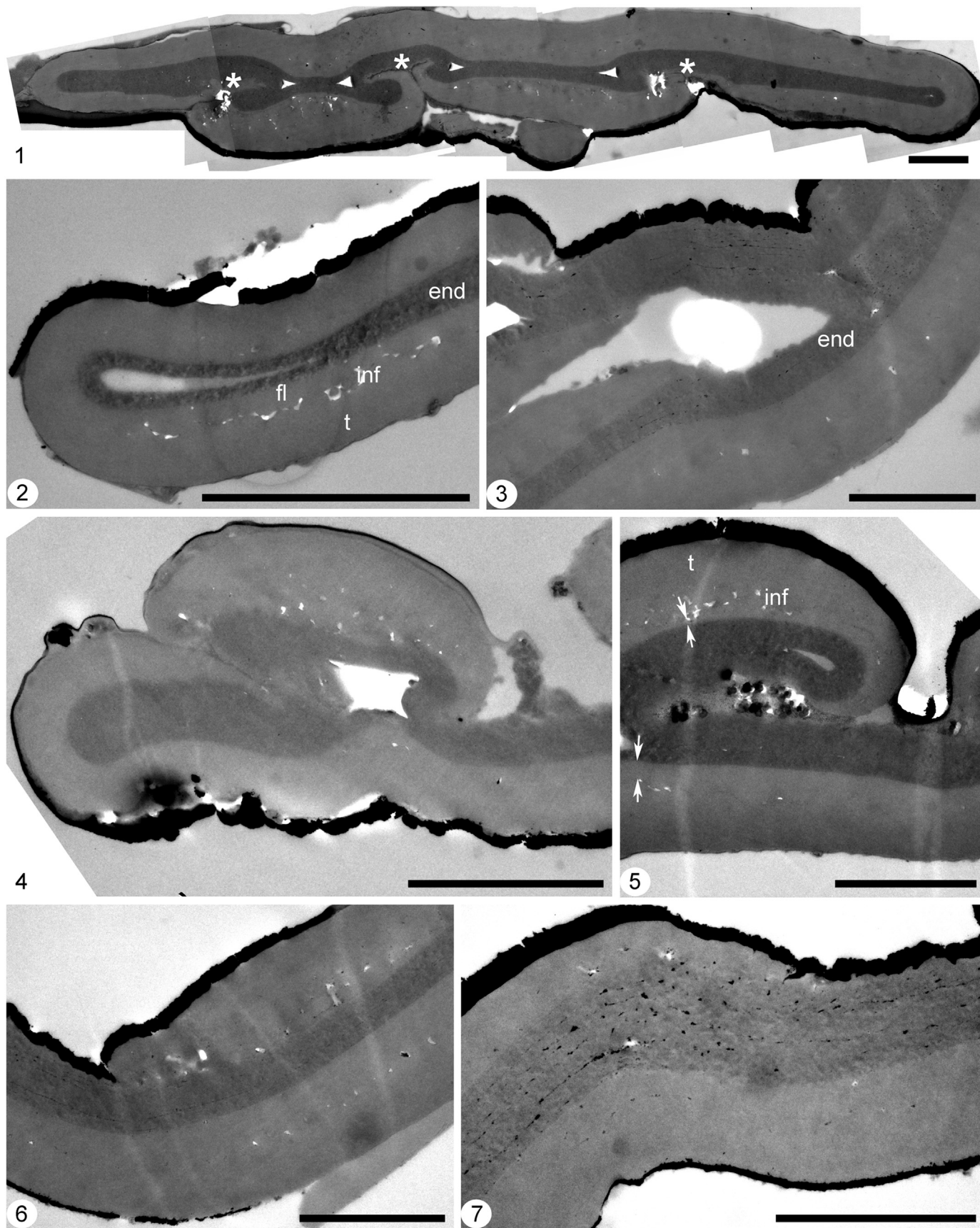


Plate V. Transmission electron microscopy, pollen grain with preserved endexine. 1. Section through the whole pollen grain. 2. Lateral region. 3–6. Aperture region. 7. Aperture region, note the lamellate endexine. Asterisks indicate aperture regions, foot layer on the distal and proximal sides is marked between two arrows, t – tectum, inf – infratectum, fl – foot layer, end – endexine. Scale bar: (1, 3, 5–7) 1 μm; (2, 4) 2 μm.

Bharadwaj et Srivastava, 1969 from the Permian of Australia, *Mulinipollenites bonus* Gomankov, 1998, from the Permian of Russia, and *Cycadopites* from the Permian of Russia and the Triassic of Germany (Foster and Price, 1981; Zavialova et al., 2001; Zavialova and Van Konijnenburg-van Cittert, 2011).

In contrast to the pollen under present study, pollen grains of *Mulinipollenites* are characterized by four furrows and different ectexine structure (Zavialova et al., 2001). Pollen grains of *Praecolpatites* have five longitudinal furrows and “incipient-alveolate” (columella-like?) ectexine, which differs considerably from that of the studied *Pretricolipollenites* pollen (Foster and Price, 1981). Pollen grains of *Marsupipollenites triradiatus* are monosulcate and characterized by a small proximal trilete laesura. Its ectexine structure is described as “incipient-alveolate” by the authors (Foster and Price, 1981) and is interpreted as “granulate” by Balme (1995). Judging from Foster and Price (1981, pl. 4, 12a and pl. 5, 18b) the infratectum appears granulate, although in pl. 5, 18c some “columella-like” elements (“incipient-alveolae” sensu Foster and Price) are seen. Therefore, the ultrastructure of pollen grains of this species needs more research.

Sverdrupollenites and *Kingiacolpites* are monosulcate pollen and have been studied only in LM. In contrast to *Pretricolipollenites*, *Sverdrupollenites* also has a monolet to geniculate mark on the proximal surface (Utting, 1994). Among five known *Kingiacolpites* species only *K. vetus* (Balme et Hennelly, 1956) Tiwari et Moiz, 1972 (formerly *Entylissa vetus* Balme et Hennelly, 1956) has pollen of the same size as *Pretricolipollenites*; other species are much larger (Tiwari and Moiz, 1972). Interestingly, according to Tiwari and Moiz (1972) *Cycadopites* differs from *Kingiacolpites* Tiwari et Moiz in its spindle-shaped outline (versus elongate oval to subcircular in *Kingiacolpites*), “leathery, smooth exine” (versus distinctly intrapunctate exine in *Kingiacolpites*) and the absence of exine folds along the aperture. So, *Cycadopites* and *Kingiacolpites* differ from each other by almost the same characters as *Pretricolipollenites* from *Eucommiidites*.

The ultrastructure of *Cycadopites* was studied for dispersed Permian pollen from Russia (Zavialova et al., 2001) and in situ pollen from the Triassic peltasperm pollen organ *Antevsia zeilleri* (Nathorst, 1908) Harris, 1937 from Germany (Zavialova and Van Konijnenburg-van Cittert, 2011). Both *Cycadopites*-type pollen grains notably differ from *Pretricolipollenites bharadwajii* in the infratectum structure. Permian dispersed *Cycadopites* has smaller granules in one row and a thicker foot layer (being quite similar to *Eucommiidites* pollen from pollen organs of *Bayerithecya hughesii*). In contrast to *Pretricolipollenites*, pollen grains from pollen organs of *Antevsia zeilleri* have larger infratectal elements (Zavialova and Van Konijnenburg-van Cittert, 2011) which can be interpreted as alveolae, large granules or columella-like elements. Furthermore, these two studies of *Cycadopites*-type pollen show a different exine structure (apart from their difference in the aperture type) from our material.

Species of *Pocockipites* Bharadwaj, 1974 and some of *Ovalipollis* Krutzsch, 1955 have been interpreted differently in terms of their “aperture” location and show two additional poroid or sulcoid tennitates on one pollen side, which are less prominent than a distal leptoma (e.g., Pocock and Jansonius, 1969; Bharadwaj, 1974) or, in an alternative interpretation by Scheuring (1970, 1974), a proximal leasure. This in general resembles the aperture type observed in *Eucommiidites* and *Pretricolipollenites* pollen. However, *Pocockipites* and *Ovalipollis* have weakly developed sacchi and an alveolate infratectum (Scheuring, 1970, 1974).

Another group of somewhat similar pollen taxa are taeniate pollen including *Striasulcites* Venkatachala et Kar, 1968, *Vittatina* Luber, 1940 ex Jansonius, 1962 (*Vittatina*-like pollen), *Weylandites* Bharadwaj et Srivastava, 1969, and *Lagenella* Malyavkina, 1949 ex Klaus, 1960. Though differing in general morphology (a single sulcus and a striate surface) some of these taxa show somewhat similar exine structure, such as *Lagenella martini* Klaus, 1960 (Tekleva and Roghi, 2018) and several *Vittatina* species (Koloda and Molin, 1986) with an infratectum

of small granules, often situated in one or several rows, and a thin foot layer. The tectum is rather thick in *Lagenella martini*, similar to that of *Pretricolipollenites bharadwajii* and thin in *Vittatina* sectioned by Koloda and Molin (1986). *Weylandites* is characterized by much larger granules in the infratectum (Zavialova, 1998; Afonin, 1999; Gomankov and Tarasevich, 2008) in comparison with our material; some studied species of *Vittatina* were described as having an alveolate infratectum (Meyer, 1977; Afonin, 1999; Lupia et al., 2015). *Striasulcites* has not been studied in TEM.

6. Concluding remarks

In paleobotanical and palynological studies, exine ultrastructure has proved to be a key character for systematic and evolutionary-level description of taxa, especially in the case of dispersed pollen taxa, pollen grains with poorly expressed sculpture or in situ pollen with poorly preserved macroremains (Zavialova et al., 2011; Zavialova and Nosova, 2019). Characters of the inner exine structure have been shown to be a good distinguishing tool for a number of plant groups – bennettitaleans, cycadaleans, gnetaleans, araucarians (e.g., Osborn, 2000; Tekleva et al., 2007).

The present state of knowledge of *Pretricolipollenites* pollen does not allow any definite conclusion on its relationship with other similar taxa. Most probably, *Pretricolipollenites* species are related to some *Eucommiidites* species, so these two genera might require taxonomic reconsideration. The main impediment is the lack of studies by SEM and TEM on *Pretricolipollenites* species.

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