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Exine ultrastructure of in situ *Protohaploxypinus* from a Permian peltasperm pollen organ, Russian Platform

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ABSTRACT

The fine morphology and exine ultrastructure are studied in pollen grains of *Protohaploxypinus*-type, which were extracted from a pollen organ of *Permotheca striatifera* from the upper Permian (Lopingian) Isady locality (Vologda Region, Russia). The pollen grains are bisaccate and striate, with up to ten proximal ribs. The ectexine and endexine differ in ultrastructure and electron density. The ectexine is alveolate; the endexine is more electron-dense and appears homogeneous, though some indices of layering were observed under higher magnifications. The sacci appear protosaccate. Areas that flank the body are a diminished and more regular version of the sacci. In ribs, the ectexine includes an outer continuous layer, a thinner underlying alveolate layer, and an inner layer. Grooves between the ribs either retain the inner homogeneous ectexinal layer resting on the endexine or are lined by the endexine alone. The distal face of the body is covered by the endexine alone. The obtained data are compared with available ultrastructural information on pollen grains of the *Protohaploxypinus*-type of different origins and with that on other peltasperm pollen types such as *Vittatina*, *Vesicaspora* and *Cycadopites*. The diversity of species of *Permotheca* is outlined.

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1. Introduction

Peltasperms are a fascinating gymnosperm group with regard to their pollen diversity. Pollen types which have been found in situ in peltasperm pollen organs from deposits of different geological ages and geography are *Vesicaspora* Schemel, 1951, *Falcisporites* Leschik emend. Klaus 1963, *Protohaploxypinus* (Samoilovich) Hart 1964, *Striatopodocarpidites* Sedova, 1956, *Vittatina* Luber ex Jansonius, 1962, and *Cycadopites* Wodehouse, 1933 (Townrow, 1960; Gomankov, 1986; Gomankov and Meyen, 1986; Bomfleur et al., 2011; Zavialova and Van Konijnenburg-van Cittert, 2011). These bisaccate non-striate, bisaccate striate, non-saccate striate and nonsaccate, monosulcate pollen are morphologically very different from each other. We have recently reviewed the diversity of pollen types ascribed to peltasperms (Zavialova and Van Konijnenburg-van Cittert, 2011). Most of this diversity is observed in older members of the group; *Falcisporites* and *Cycadopites* are found in pollen organs of Triassic peltasperms. We hope that ultrastructural data will help in understanding the relationships between peltasperm taxa and in discovering morphological transformations between their dissimilar pollen types.

The pollen types found in peltasperm pollen organs are not confined to peltasperms alone; they were also found in pollen organs of gymnosperms unrelated to peltasperms (Balme, 1995). A detailed comparison at the ultrastructural level between peltasperm pollen types and pollen of the same morphological types that belong to other plant groups is important for determination of botanical affinities of such pollen types in palynological assemblages. Chaloner (2013) discussed the occurrence of very similar striate bisaccate pollen among disparate taxonomic groups of gymnosperms in the Permian–Triassic and considered this phenomenon as a palynological puzzle.

To elucidate the problem, detailed information on well-preserved pollen grains of unequivocal peltaspermous affinity is needed. In this paper, we document the fine morphology and exine ultrastructure of pollen grains of *Protohaploxypinus*-type, which were extracted from a pollen organ of *Permotheca striatifera* Meyen et Gomankov, 1986, found in the late Permian Lagerstädt Isady, Russian Platform (Aristov et al., 2013). As far as we are aware, the present study is the first that shows the ultrastructure of such pollen in situ from a peltasperm pollen organ.

2. Material and methods

2.1. Isady locality

Specimen PIN, no. 5339/3 of *Permotheca striatifera* used for this study was collected on the left bank of the Sukhona River opposite the village of Purtovino (Russia, Vologda Region, Velikoustyugskii District (60°36′56″ N, 45°36′55″ E)). The locality is the uppermost part of the Upper Severodvinian Substage (of the Putyatinian Horizon), near its boundary with the Vyatkian Stage (Bykovian Horizon). The boundary between the Severodvinian and Vyatkian regional stages corresponds

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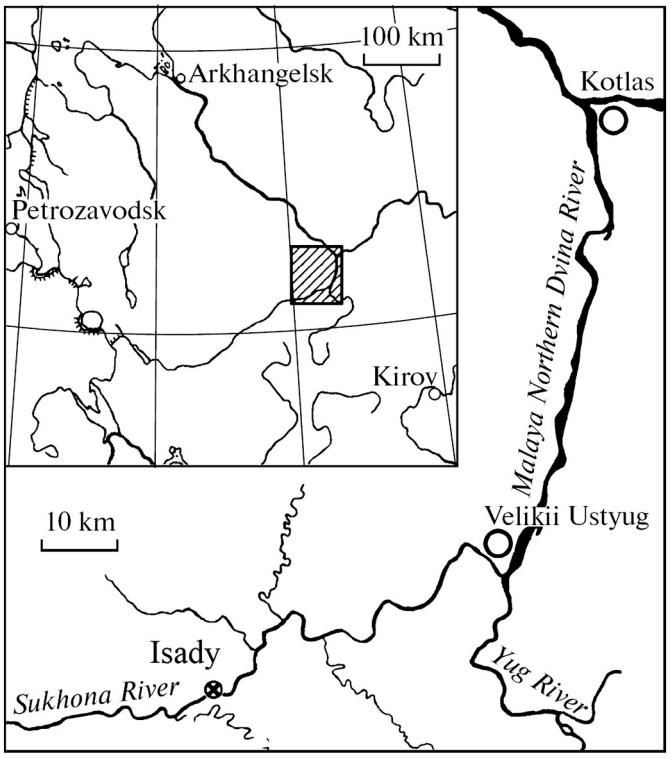


Fig. 1. Schematic map of the Isady locality.

to the middle part of the Wuchiapingian Stage of the International Stratigraphic Chart 2014 (Cohen et al., 2013).

The specimen was found in the middle part of the riverbank slope in Isady (= Mutovino) lens (for details of the locality, see Aristov et al., 2013) and is housed at the Laboratory of Paleobotany, A.A.Borissiak Paleontological Institute, Moscow (no. 5339).

Isady (= Mutovino) is one of the richest localities of late Permian nonmarine organisms in European Russia. Fossils found here include abundant plant remains, bivalves, insects, ostracodes, conchostracans, fishes, and tetrapods. Abundant fish bones belong to taxa specific to zone *Toyemia tverdochlebovi*, subzone *T. tverdochlebovi–Mutovinia stella*. The tetrapods are dominated by the chroniosuchid anthracosaur *Chroniosaurus levis* Golubev, 1998; temnospondyls of *Dvinosaurus primus* Amalitzky, 1921 are less abundant. The tetrapod assemblage corresponds to the *C. levis* tetrapod subzone of the *Proelginia permiana* Zone (Golubev, 1998; Aristov et al., 2013). The bivalves are diverse and typical of the so-called "Doskino association" (Gusev, 1990). Fossil ostracodes and conchostracans belong to the genera typical of the Severodvinian and Vyatkian regional stages (Molostovskii and Minikh, 2001). The insect assemblage is particularly diverse and includes members of 69 families, 81 genera, and 105 species, representing 25 orders (Aristov et al., 2013).

Fossil plants from the Isady locality belong to the Tatarina flora (Gomankov and Meyen, 1986; Meyen, 1997). They are dominated by shoots of the conifers *Quadrocladus schweitzeri* Meyen, 1986 (Plate I, 1) in association with strobili of *Dvinostrobus sagittalis* Gomankov et Meyen, 1986 (Plate I, 2–3). The subdominant fossils are leaves of the peltasperm *Tatarina conspicua* Gomankov and Meyen, 1979 (Plate I, 4–5) in association with peltate ovuliphores of *Peltaspermopsis cf. buevichae* Gomankov and Meyen, 1979 (Plate I, 6–7), seeds of *Salpingocarpus bicornutus* Meyen, 1986, *Salpingocarpus variabilis* Meyen, 1986 and sporangia of *Permotheca striatifera* and *Permotheca vesicasporoides* Meyen, Esaulova et Gomankov, 1986 (Gomankov and Meyen, 1986). There are also abundant leaves of the cardiolepids *Phylladoderma* (subgenus *Aequistomia*) *annulata* Meyen, 1986, *Phylladoderma* (*A.*) *rastorguevii* Meyen, 1986 and *Phylladoderma* (*A.*) *trichophora* Meyen, 1986. In addition, Gomankov and Meyen (1986) reported on leaves of the *Rhaphidopteris* type and fragmentary leaves of an uncertain systematic position *Arisada densa* Meyen, 1986. Spore-bearing plants are represented by leaves and the lycopod *Lepidophylloides delicata* (Gomankov) Gomankov, 2008 and associating megaspores. Other fossil plants include leaves with venation of the *Taeniopteris* type, which Gomankov (Gomankov and Meyen, 1986) assigned to a new fern genus, *Fefilopteris* Gomankov, 1986.

Gomankov (2002) assigned the flora of the Isady locality to the Aleksandrovka Paleofloristic Assemblage, indicating the almost total disappearance of Cordaitales and the absence of sphenophytes of the genus *Sphenophyllum* Brongniart, 1822 as its differences from the preceding Kotel'nich Assemblage and the lower diversity of peltasperms as its difference from the succeeding Vokhma Assemblage. According to palynological data (Gomankov, 2002), the stratigraphic range of the Aleksandrovka Assemblage is limited to the Kovrovo beds of the Severodvinian Stage.

2.2. Light and electron microscopy of the material

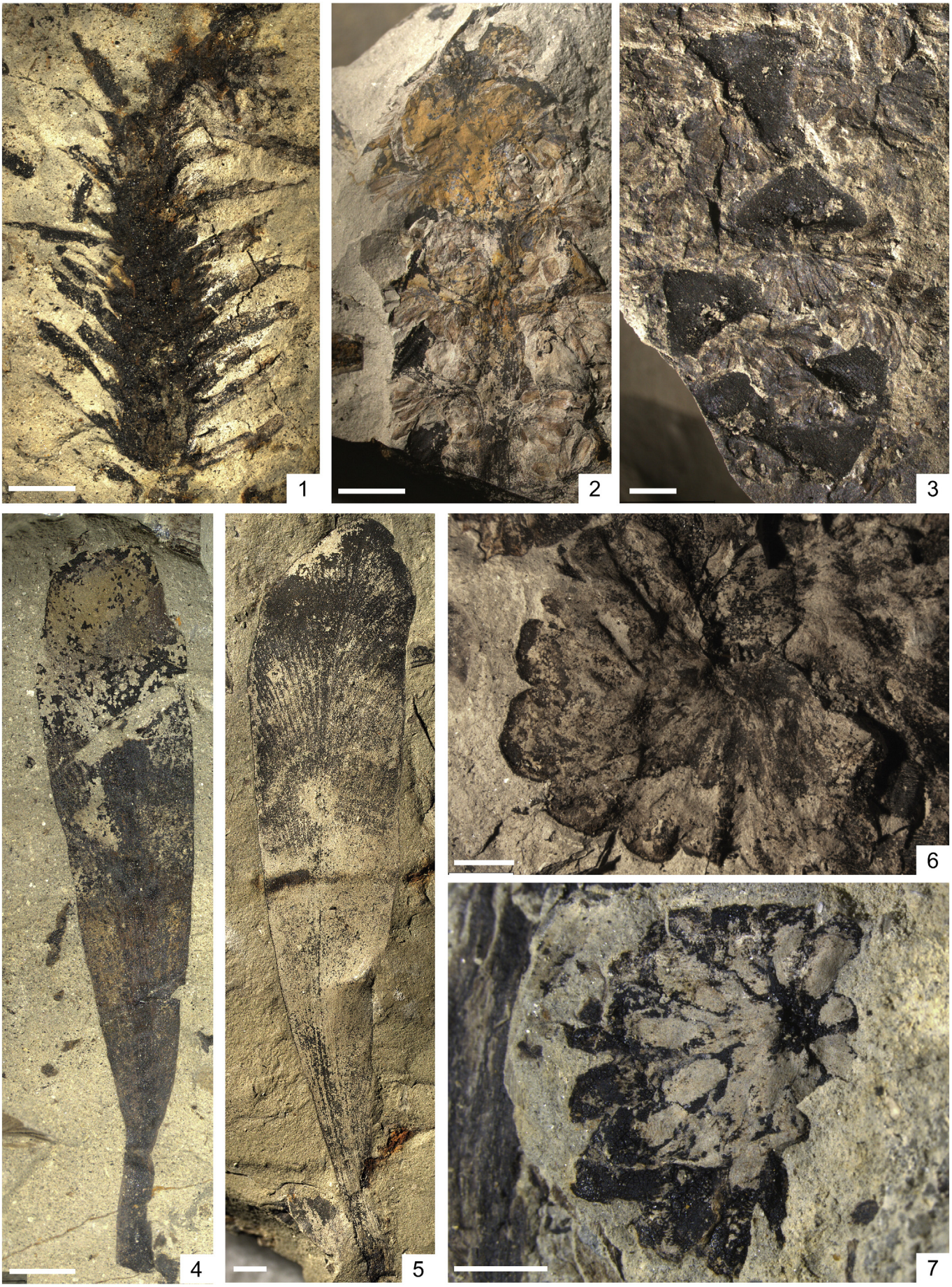
We have observed with light microscopy 16 samples with numerous specimens of *Permotheca* (Zalessky) emend. Naugolnykh, 2007 on their surface. A Leica MZ16 stereomicroscope equipped with a DFC320 camera was used.

Pollen grains were extracted from pollen sacs, which were treated with 65% HNO_3 about 15–20 min and then in distilled water. A tablet of KOH of about 0.03 g was dissolved in 4 ml of distilled water. This solution was added to the glass containing the pollen sacs in distilled water until bleached. The pollen grains studied were extracted from one of the sporangia. Individual pollen grains were difficult to detach from the pollen mass undamaged. We only managed to have separated small groups of pollen grains, which were proceeded for LM and EMs. The general pollen morphology was observed with a Carl Zeiss Axioplan-2 light microscope equipped with a 100× oil immersion objective and a Leica DFC-420 digital camera; and the fine morphology was studied with help of a TESCAN VEGA-II XMU SEM (accelerating voltage 30 kV) at the A.A.Borissiak Paleontological Institute (Moscow) and a Jeol 100B TEM (accelerating voltage 80 kV) at the Electron Microscope Laboratory of the Lomonosov Moscow State University. In total, we have observed numerous pollen grains in seven pollen groups under LM and about 20 pollen grains of one of the groups under SEM. For SEM, one pollen group was placed on the emulsion face of a piece of photographic film, which was then attached to a SEM stub with a drop of enamel. The stub was coated with gold and viewed under SEM. For TEM, pollen groups were extracted from LM slides and embedded in a mixture of epoxy resins [Epon-812, dodecenyl succinic anhydride (DDSA), methyl nadic anhydride (MNA), and an accelerator as 17:15:8:1 volume ratios] for 48 h at 60 °C. We have embedded five pollen groups; twelve individual pollen grains of these groups were cut. Sectioning was accomplished with a Leica EM UC6 ultramicrotome

Plate I. Fossil plants from the Isady locality, late Permian of Vologda Region, Russia, LM.

1. Fragments of branch of *Quadrocladus schweitzeri* Meyen, 1986, 5339/10.
2. General view of *Dvinostrobus sagittalis* Gomankov et Meyen, 1986, 5339/185.
3. Part of specimen 5339/185, showing morphology of distal shield with attached synangia, 5339/186.
4. Leaf of *Tatarina conspicua* Gomankov and Meyen, 1979, 5339/171.
5. Leaf of *T. conspicua*, 5339/170.

6, 7. Peltate ovuliphores of *Peltaspermopsis buevichae* Gomankov and Meyen, 1979, 5339/4. Scale bar (1–2) 5 mm, (3–7) 2 mm.


1
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at the A.A.Borissiak Paleontological Institute. The sections were observed unstained.

We tried to orientate the pollen grains transversely and longitudinally. Since we dealt with groups of pollen grains, variously stuck to each other, we got oblique sections as well. We made a series of ultrathin sections of 60 nm thick, which we collected on a grid, then several thick sections, which were discarded, with a total thickness of about 4 μm, then the next series of ultrathin sections, etc. This way, we cut out the specimen throughout and hoped to observe all morphological features that are present in the pollen under study. Otherwise, the pollen grains were too big for us to make and observe one huge continuous series of ultrathin sections. This approach provided us with a better understanding of the pollen morphology and ultrastructure, in comparison, for example, with our earlier study of the same morphotype, when we cut each pollen grain at one or two levels (Zavialova, 1998; Zavialova et al., 2001). In particular, this concerns the mutual arrangement of the exine layers and the degree of their development in different areas of the pollen grain.

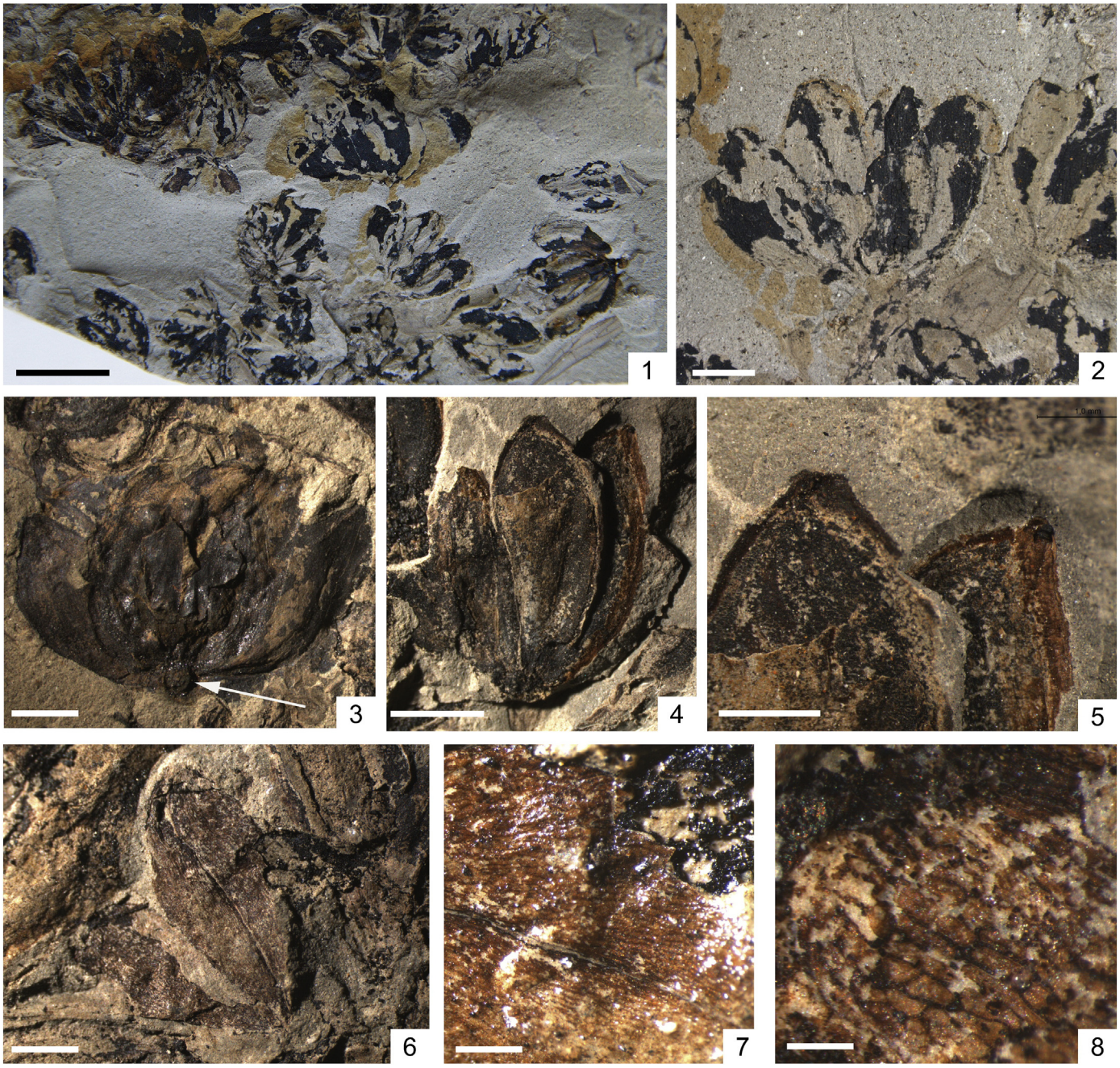


Plate II. General morphology of pollen sacs of *Permotheca striatifera* Gomankov et Meyen, 1986, the Isady locality, late Permian of Vologda Region, Russia, LM.

1. General view of 5339/3.
2. Part of specimen 5339/3, showing general view of synangia.
3. 5339/191A, note a discoid scar of synangia (arrow).
4. 5339/189B, general view of synangia.
5. Enlargement of 5339/189B, showing acuminate apices of sporangia.
6. 5339/189D, synangia with well preserved wall.
7. Enlargement of Fig. 6, showing longitudinal rows of cell walls of the sporangium.
8. Enlargement of Fig. 6, showing trapezoid or rectangular outline of cell walls of the sporangium. Scale bar (1) 10 mm, (2–4, 6) 2 mm, (5) 1,2 mm, (7) 500 μm, (8) 190 μm.

3. Results

3.1. Pollen organs

Genus *Permotheca* Zalessky, 1929 emend. Naugolnykh, 2007
Permotheca striatifera S. Meyen et Gomankov, 1986

1986 *Permotheca striatifera* S. Meyen et Gomankov, pp. 120–122, pl. XIII, figs. 11–13, pl. XIV, figs. 1–3; text-fig. 63 (a–c, k)

Isolated synangia are racemose, with 5 to 9 sporangia (Plate II, 1–2). The adaxial surface of the synangium shows an abscission scar (Plate II, 3). The sporangia are elliptic or with rounded or acuminate apices, about 10 mm long and 5 mm wide. The sporangia are fused at their bases, whereas their apices remain unfused (Plate II, 4–5). The maximal width of the sporangium is near its middle part. The sporangium surface is weakly longitudinally striated. The sporangium wall consists of long trapezoid or rectangular cells, which are longitudinally arranged (Plate II, 6–8).

3.2. Pollen grains

Pollen grains superimpose over each other in pollen masses, so that the margins of individual pollen grains were not always visible: only one of the sacci was clearly seen in some specimens, or only ribs of the body in others (Plate III, 5; Plate IV, 1). Though we have numerous pollen grains at hand, we managed to measure only 18 pollen grains (in some only the length or only the width), which range from 81.0 to 101.0 μm in length and from 50.0 μm to 68.4 μm in width. Pollen grains are bisaccate and striate (Plate III, 1–6). Most pollen grains bear 6 to 10 ribs at the proximal face of the body (Plate III, 4), but there were a few specimens, in which we observed only three indistinct ribs (Plate III, 6). The ribs vary in width and are situated at different angles to each other, in a way that some of them stretch from one saccus to the other, whereas other ribs do not reach the other saccus (Plate III, 3). The maximal width of a rib is about 5.3–6.8 μm. Pollen grains more commonly are flattened in the polar position (Plate III, 5). Pollen grains in the equatorial position show that the distal face of the body do not bear ribs and is lighter in transmitted light (= thinner) than the proximal face. The length of the striate proximal face of the body (= cappa) is about two thirds of the total length of the pollen and the length of the psilate distal face of the body is about one quarter of the total length of the pollen (Plate III, 2). The sacci are slightly inclined toward the distal side (Plate III, 2).

The surface of the pollen grains is almost psilate (Plate IV, 1–3). Proximally, the ribs are clearly visible (Plate IV, 3). The sacci are somewhat pitted (Plate IV, 2, 3). It appears from the SEM images that the outermost layer of the exine is continuous, covering the underlying layers (if any) completely. Two sacci are connected (Plate IV, 2).

TEM shows that the exine consists of an ectexine and endexine, which differ in ultrastructure and electron density (Plate V, 2). The ectexine is alveolate; the endexine is more electron dense and appears homogeneous.

The sacci are covered by a continuous outer ectexinal layer (Plate V, 1). The pits which were observed under SEM are due to the undulations of this layer; we do not see any perforations in sections in the outer layer of the exine (Plate V, 1, 2). Under this layer, the sacci are completely filled with ectexinal partitions (Plate VI, 4). However, since the pollen grains are strongly flattened and bear quite thin sacci (varying from 1.4 to 2.0 μm in thickness), they may merely appear protosaccate (Scheuring, 1976) at this stage of preservation. The partitions are variously directed that in sections they appear as rods of changing width, if cut longitudinally or obliquely, or from irregular to regular granules, if transversely (Plate VI, 7).

Some extremely thin threads of the endexine enter the saccus already in peripheral sections (Plate V, 1, 8). The endexine demarcating the body of the pollen is thick, constant in thickness over the perimeter of the body, and appears homogeneous in the overwhelming majority of sections (Plate V, 2–4) even under high magnifications (Plate VI, 6). We observed indices of layered organization in few sections under magnifications of 40000× and higher in the inner (Plate V, 5, 6) and in the outer (Plate VII, 4, 5) areas of the endexine. The thin threads of the endexine, which were detected in saccate areas, belong to outer areas of the endexine and peel off them (Plate VI, 5, 8). This phenomenon additionally counts for the layered nature of the endexine, in spite of its homogeneous appearance in most sections. Though being considerably thick, the endexine is easily foldable (Plate V, 4, 7).

Ultrastructurally, the areas that flank the body are a diminished and more regular version of the sacci: a continuous outer ectexinal layer is underlined by partitions (Plate V, 3, lower part of this figure).

The proximal and distal faces of the body are very different. The ribs are present only proximally (Plate V, 4, 6, 7; Plate VI, 1). Their ectexine includes an outer continuous layer, a thinner underlying alveolate layer, and an inner layer. Grooves between the ribs either retain the inner homogeneous ectexinal layer resting on the endexine or are lined by the endexine alone. The grooves vary in width. Those that are relatively wide are constituted by the endexine alone (Plate VI, 2). Distally, the body is covered by the endexine alone (Plate VI, 3, 6): it is the outer surface of the endexine that we observed in distal views of the pollen grains under SEM (Plate IV, 2).

4. Discussion

4.1. Permotheca and other pollen organs of peltasperms

Zalessky (1929) introduced the genus *Permotheca* with the type species *Permotheca sardykensis* Zallesky, 1929 for isolated synangia on the material from the Upper Kazanian deposits of the Kullarovo locality, Sardyk river, Tatarstan. However, the holotype was not designated and the diagnosis was not given. Fefilova and Pukhonto (1983) provided a very brief diagnosis of the genus. Gomankov and Meyen (1986) published a more detailed diagnosis and were the first who demonstrated relationships between *Permotheca* and other Peltaspermales. Naugolnykh (2007) revised the genus and emended the diagnosis; he added to the diagnosis the information about the structure of microstrobiles and treated *Anthicocladus* Zalessky, 1937 and *Asterodiscus* Zalessky, 1937 as younger synonyms of *Permotheca* based on the similar general morphology. Some Late Paleozoic and Mesozoic pteridosperms show similarities to *Permotheca*. Thus, Euromerian peltasperms *Callipterianthus* Roselt, 1962 and *Pterispermostrobus* Stopes, 1914 from the Late Carboniferous–Early Permian deposits have similar synangiate (fused) agglomerations of sporangia, but differ by flattened microsporophylls and pinnate fertile branches (Taylor et al., 2006). The glossopterid *Arberiella* Pant et Nautiyal, 1960 has similar elliptic to falcate pollen sacs and fine longitudinal striation of sporangia (Gomankov and Meyen, 1986). In addition, in situ *Protohaploxypinus* is known from sporangia of *Arberiella* (Zavada, 1991). Unlike *Permotheca*, pollen sacs of *Arberiella* are unfused and attached to modified scale-like leaves of *Eretmonia* Du Toit 1932 emend. Lacey et al. 1975 or *Glossotheca* Surange et Maheshwari, 1970. Pollen sacs of *Arberiella* are 0.5–1 mm long in comparison to those of *Permotheca*, which are 1.5–10 mm long. Microsporophylls of Triassic peltasperms *Antevsia* Harris, 1937 and *Townrovia* Retallack, 1981 resemble *Permotheca*, but differ in having flattened and pinnate fertile axes and free sporangia (Taylor et al., 2006; Taylor and Taylor, 2009; Bomfleur et al., 2011).

Currently, the genus *Permotheca* includes nine species from the Permian (Russian Platform) and one from Triassic (Australia). We have grouped the Permian species in three pools by their age, geography of the locality, and in part, the general morphology of the sporangia (Table 1). Some of the species occur in more than one group. The Cisuralian group includes *Permotheca fimbriata* (Zalessky) Naugolnykh, 2007, *Permotheca bifurcata* Naugolnykh, 2007, *Permotheca deodara* Naugolnykh, 2007, *Permotheca disparis* (Zalessky) Naugolnykh, 1999, and *Permotheca colovratica* Naugolnykh, 2013; the Biarmian group

includes *P. disparis*, *P. colovratica* and *Permotheca sardykensis*; and the Tatarian group includes *Permotheca vesicasporoides*, *Permotheca striatifera* Meyen et Gomankov, 1986, and *Permotheca*? *vittatifera* Meyen et Gomankov, 1986.

Five species of *Permotheca* are known from Cisuralian deposits of Late Artinskian, Kungurian and Ufimian ages from the Chekarda-1, Krasnaya Glinka, Kuedinsky Klyuchiki and other localities (Naugolnykh, 1998, 2007, 2013). The discovered remains of these species are preserved in different degrees; and the completeness of information about each species is unequal. Three of them are so far represented by imprints of pollen organs with partially or completely preserved bearing shoots. Pollen organs of Cisuralian *Permotheca* are not flattened; they are represented by a main straight axis with spirally attached synangia. The thickness of the main axis varies among the species: it is thick in *Permotheca disparis* and *Permotheca deodara*, thinner in *Permotheca fimbricata*, or bifurcated in *Permotheca bifurcata* (Naugolnykh, 2007). Other species are represented by isolated synangia with partially or completely preserved sporangia (Table 1). Pollen grains of *Vesicaspora* type were found in sporangia of *P. disparis* and *Permotheca colovratica* (Krassilov et al., 1999a; Naugolnykh, 2013).

The Biarmian group of species includes three species. Esaulova (1989) restudied Zalessky's material and suggested an association between synangia of *Permotheca sardykensis* and leaves of *Phylladoderma* Zalessky emend. Neuburg, 1960. She found isolated synangia of *Permotheca* in Sentyak locality (Soksky Horizon, Tatarstan) with in situ pollen of *Vesicaspora*-type and with associating leaves of *Phylladoderma* and ovuliferous organs of *Angaropeltis* Doweld, 2001 (= *Cardiolepis* Neuburg emend. Meyen, 1977 nom. illeg.) (Esaulova, 1998). Fefilova and Pukhonto (1983) and Meyen (1997) reported isolated synangia of *Permotheca* sp. from the Kazanian deposits of the Adzva River (Pechora basin, Talbey formation) and Kityak locality (Kirov Region, Belebey Formation).

The Tatarian species of *Permotheca* are known mainly from the sediments of Upper Severodvinian and Vyatkian stages of the Vologda Region. Gomankov and Meyen (1986) identified three species of *Permotheca*. The material is represented by isolated synangia and sporangia. The Isady is the type locality for *Permotheca striatifera* and *Permotheca vesicasporoides*; *Permotheca*? *vittatinifera* was described from deposits of the Aristovo locality of a younger age (Salarevo Formation, Vyatkian Stage). *P. striatifera*, *P. vesicasporoides*, and *P.*? *vittatinifera* differ by the type of pollen in the sporangia: *Protohaploxypinus*, *Vesicaspora*, and *Vittatina*, correspondingly; they are difficult to differentiate by the morphology of their sporangia. In our study of *P. striatifera* we observed scars in the area where synangia are attached to the axes. These scars resemble rounded disks of attachment which were observed by Naugolnykh (2013) in the central part of the adaxial face of synangia of *Permotheca colovratica*. Numerous aggregations of synangia on the bedding plane and the presence of the scars support the idea by Naugolnykh (2007) that synangia of *Permotheca* had a separation layer and were naturally shed from bearing axes. We have some doubts whether *P.*? *vittatifera* should be included in the genus *Permotheca*. Sporangia of *P.*? *vittatifera* were found detached, unlike other remains of *Permotheca*, which all were found as isolated synangia, and there is a possibility that sporangia of *P.*? *vittatifera* were originally free, which contradicts the current diagnosis of the genus. It should be pointed out that this is the only find of *Vittatina* in peltasperm pollen organs. The relation of *Vittatina* to peltasperms was additionally substantiated by finds of such pollen in pollen chambers of seeds of *Salpingocarpus* Meyen, 1986, which were found in the attachment to an ovuliferous disc of *Peltaspermopsis* Gomankov, 1986. However, *Vittatina* was not the only pollen type that they found associated with such seeds (Gomankov and Meyen, 1986). We cannot exclude the possibility that pollen of *Vittatina* was produced by another gymnosperm group and contaminated female reproductive structures of peltasperms.

The three groups of Permian species of *Permotheca* differ from each other by the general morphology of synangia and type of in situ pollen. Thus, the Cisuralian group is characterized by flattened, radially symmetrical and rosette-like synangia, whereas the Tatarian group of species has racemose synangia with a sporangium onto the abaxial side (Naugolnykh, 2013). Most species of the Biarmian group have racemose synangia (*Permotheca colovratica* that has radial synangia occurs both in the Cisuralian and Biarmian groups). Only bisaccate non-striate pollen of *Vesicaspora*-type is known from sporangia of Cisuralian and Biarmian species. *Vesicaspora*, *Protohaploxypinus*, and *Vittatina* are known from sporangia of the Tatarian group.

The Triassic *Permotheca helbyi* Retallack, 2002 from Gondwana of Australia is clearly separated from the Permian species from the Angaraland both stratigraphically and geographically. It has the most numerous sporangia, which are basally fused in racemose or radial synangia. *P. helbyi* differs from most of the Permian species by having branching fertile axes. The only Permian species which also has branching fertile axes is *Permotheca bifurcata*. However, they are quite thin in *P. helbyi*, deviated at an acute angle, and are reconstructed as pinnate (Retallack, 2002), unlike the bifurcate axes of *P. bifurcata*. The general morphology of synangia of *P. helbyi* Retallack, 2002 has not been fully understood. Although Retallack (2002) reconstructed the racemose synangia, the photo and drawing show that they are racemose or capitate with a radial arrangement of sporangia. *P. helbyi* is associated with bisaccate non-striate pollen of *Falcisporites*-type.

Other characters used to distinguish species of *Permotheca* are the outline, size and degree of the proximal fusion of sporangia into synangia. The species under the present study, *Permotheca striatifera*, is the only species of the genus that has pollen of *Protohaploxypinus*-type. Unlike the radial synangia of species of the Cisuralian group, synangia of *P. striatifera* are racemose. It differs from the Triassic *Permotheca helbyi* by a lesser number of sporangia in synangia.

4.2. The exine ultrastructure of Protohaploxypinus

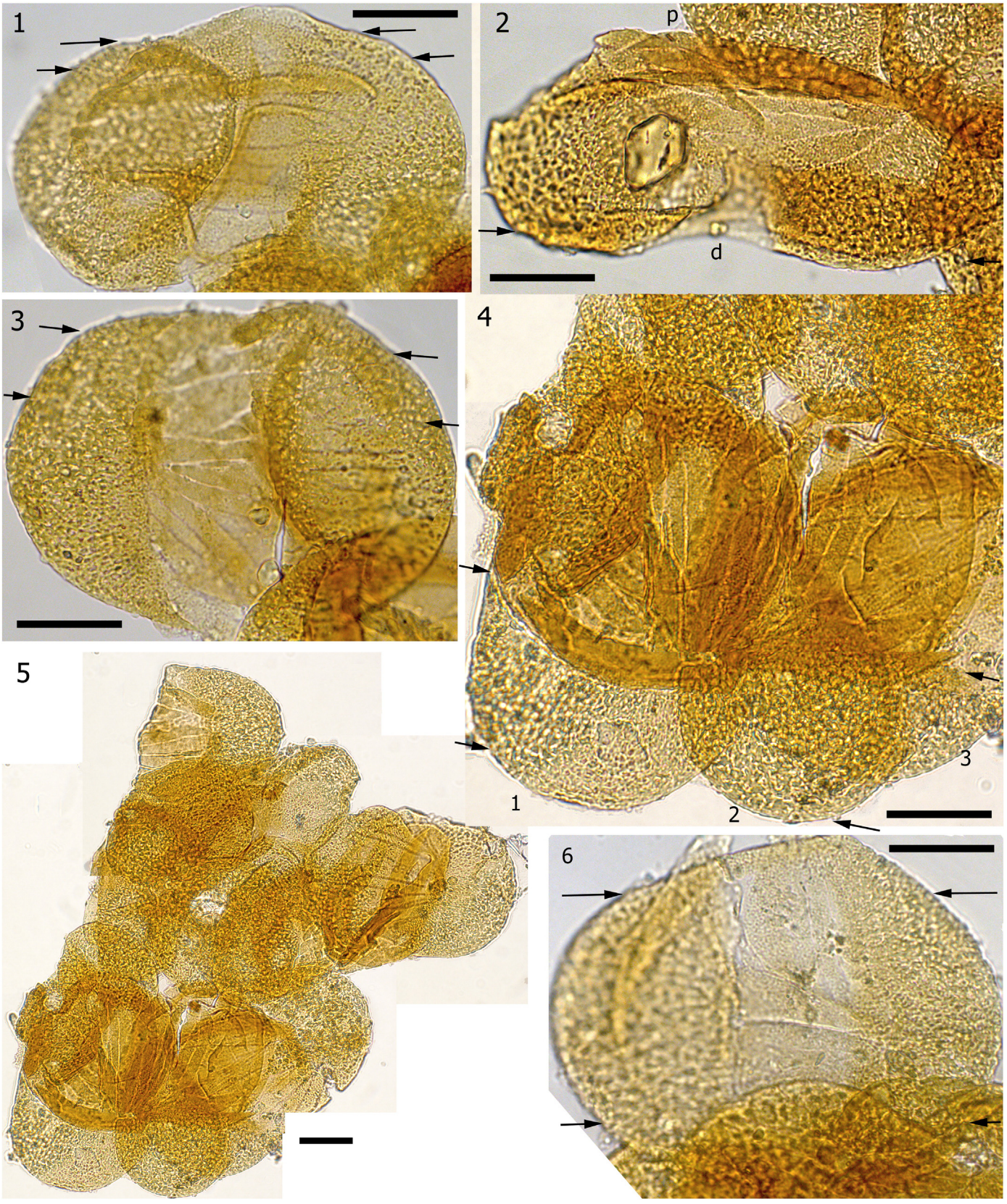
Permian pollen grains of *Protohaploxypinus*-type have been repeatedly studied with the help of TEM; pollen grains of this type from Triassic deposits still remain unstudied. The exine ultrastructure of a presumably glossopterid *Protohaploxypinus* was reported by Foster (1979) from the Baralaba Coal Measures (Australia) of the Chhidruan age on the basis of dispersed pollen material. Zavada (1991) studied *Protohaploxypinus* from the glossopterid pollen organ *Arberiella* found in the upper Permian deposits of South Africa. Zavialova (1998) and Zavialova et al. (2001) studied dispersed pollen grains of *Protohaploxypinus* that supposedly derived from peltasperms from the Upper Tatarian of the Vyatka River. Krassilov et al. (1999b) studied pollen grains of this type found in guts of a fossil insect from the Kungurian of the Chekarda locality, Urals of Russia. The present study elucidates the ultrastructure of such pollen from peltasperm pollen organs.

Plate III. General morphology of pollen grains of *Protohaploxypinus* (Samoilovich) Hart, 1964, extracted from sporangia of *Permotheca striatifera* Gomankov et Meyen, 1986 from the Isady locality, Late Permian, Volodga Region, Russia, LM.

1. Pollen in obliquely lateral position (group P4).
2. Pollen in lateral position (group P5); (p) proximal face, (d) distal face.
3. Pollen in polar position, proximal ribs are distinct (group P2).
4. Enlargement of Plate III, fig. 5, showing three pollen grains of this group (P7) which were cut for TEM. These three pollen grains are numbered as 1, 2, and 3, the same digits are used to mark their sections in Plate V.
5. Group of pollen grains (P7).
6. A pollen grain with weakly developed ribs (group P3). Arrows indicate the position of series of sections. Scale bar (1–6) 20 μm.

We observe a high degree of similarity in specimens from all pools. We also observe differences, but there is a problem how to estimate them properly, which relates in part to probable various degrees of the preservation of pollen grains from different sources and in part to variations in the techniques applied to the materials in the previous studies.

All pollen grains under consideration, in which sacci were cut, appear protosaccate in sections. However, all specimens are flattened in



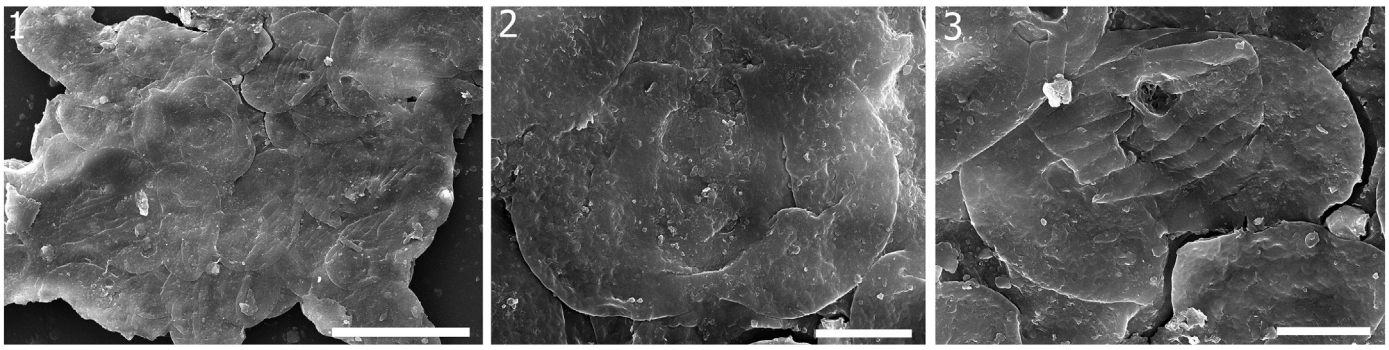


Plate IV. Surface of pollen grains of *Protohaploxypinus* (Samoilovich) Hart, 1964, extracted from sporangia of *Permotheca striatifera* Gomankov et Meyen, 1986 from the Isady locality, Late Permian, Volodga Region, Russia, SEM.

1. Pollen mass extracted from the sporangium.
2. Blowing up of Fig. 1 shows the distal face of one of the pollen grain.
3. Blowing up of Fig. 1 shows a pollen grain compressed in an obliquely-proximal position. Sacci and striate proximal face of the body are visible. Scale bar (1) 100 μm, (2, 3) 20 μm.

various degrees, and the sacci are very thin in sections. Thus, a section of a dispersed pollen of *Protohaploxypinus* show a cavity in one part of the saccus (Zavialova et al., 2001, pl. 1, fig. 10), but no cavity in the other (Zavialova et al., 2001, pl. 1, fig. 9). Therefore, the protosaccate appearance could be a preservational feature. Three-dimensionally preserved specimens, similar to those studied by Osborn and Taylor (1993), are needed to resolve this question and there is a possibility that the interpretation will be changed.

A transverse section published by Foster (1979) shows a saccus and proximal ribs. The sacci occupy a greater area distally than proximally, and the distal portion of the body remained unstudied. The exine includes an ectexine and endexine. The former is densely alveolate with rare and small alveolae both in the saccus and ribs. The endexine is prominent, much more electron dense than the ectexine, and appears homogeneous under a magnification of 8000×. Proximally, the ectexine varies in thickness considerably: it becomes very thin and homogeneous between the ribs. The endexine is uniform in thickness.

Oblique sections made by Zavada (1991) show a saccus and both proximal and distal areas of the body. The exine is two-layered. The ectexine is alveolate and seems less dense (= alveolae are more voluminous and partitions are thinner) than that in the Australian material, though it can be related to the different position of the sections.

Plate V. Exine ultrastructure of pollen grains of *Protohaploxypinus* (Samoilovich) Hart, 1964, extracted from sporangia of *Permotheca striatifera* Gomankov et Meyen, 1986 from the Isady locality, Late Permian, Volodga Region, Russia, TEM. Three pollen grains of Group P7 were cut more or less transversely (Plate III, 4).

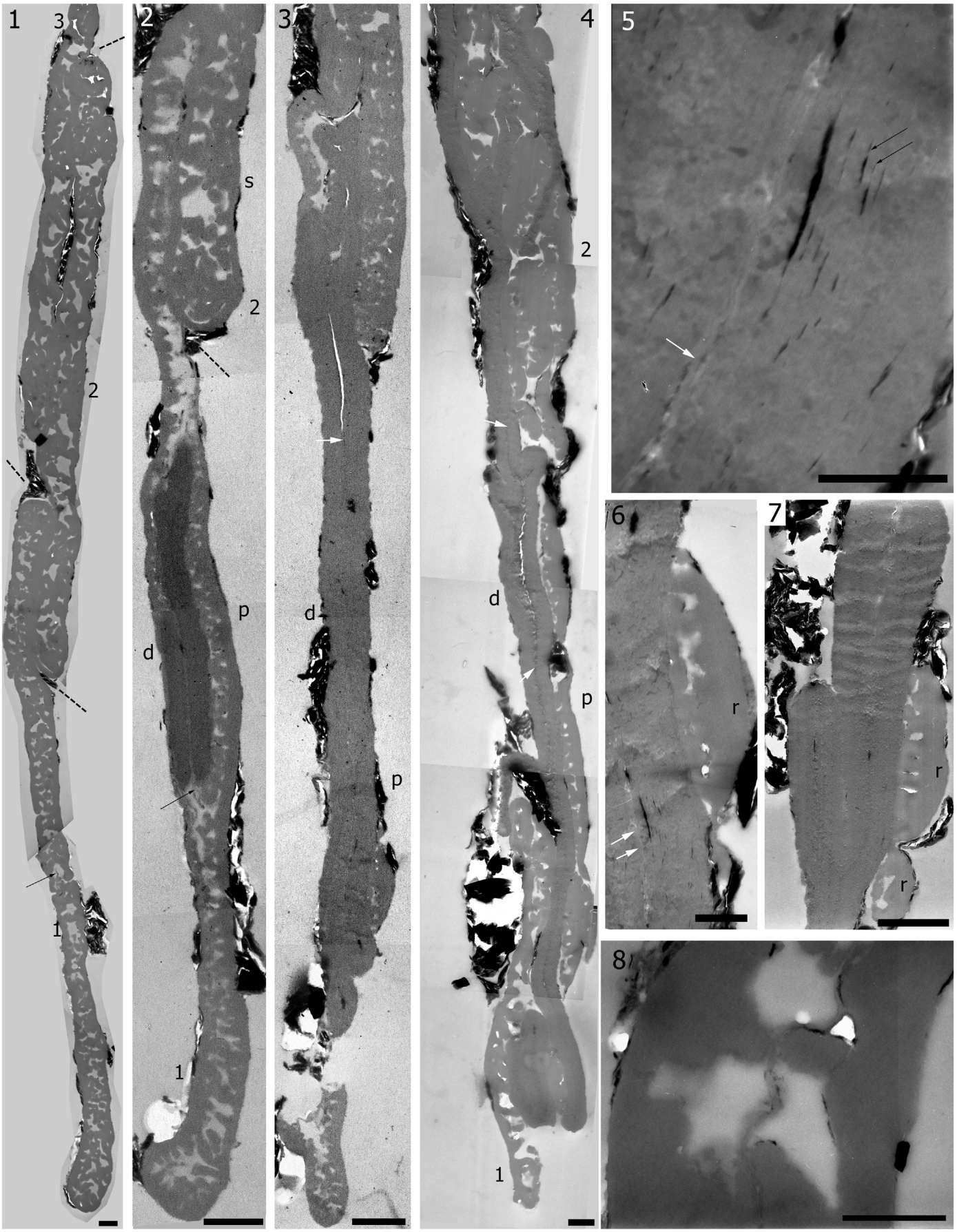
1. Section through sacci of the pollen grains, the deepest section is through pollen grain 1 (some thin threads of the endexine are already present in the saccus, arrow); section through a saccus of pollen grain 2 is more superficial; and section through pollen grain 3 is through the most peripheral region of one of its saccus. Interrupted lines mark boundaries between the pollen grains.
2. Deeper section: a thick, homogeneous and electron-dense endexine is present in pollen 1. The endexine is easily folded and cut twice. The arrow points on endexinal threads that shed out of the main portion of the endexine. Distally, merely a very thin ectexinal layer retains. A portion of the saccus of pollen 2 is visible; transversely cut partitions of the sacci appear as granules.
3. Deeper section: distally, the endexine is exposed; proximaly, first ribs appear, the endexine also is exposed over a considerable distance.
4. Deeper section: the endexine is still the only layer of the exine that is present in the distal area of the body; proximal ribs are distinct. The endexine shows folds in several areas. The pollen grains are tightly posed over each other, one can trace individual pollen via endexinal contour, but it is difficult to decide which rib belongs to which pollen grain.
5. Endexine, layered nature can be observed (black arrows). Enlargement of Plate V, fig. 6.
6. Proximal rib, enlargement from a section close to that shown in Plate V, fig. 3.
7. Two proximal ribs, enlargement from a section close to that shown in Plate V, fig. 3.
8. A thread of endexine in the saccus region, enlargement from Fig. 1 (arrow). (s) saccus; (p) proximal face of the body; (d) distal face of the body; white arrow points on the position of the gametophyte cavity; (r) rib. Scale bar (1, 4) 1 μm, (2, 3) 2 μm, (5, 8) 0.5 μm, (6) 0.67 μm, (7) 1.25 μm.

Plate VI. Exine ultrastructure of pollen grains of *Protohaploxypinus* (Samoilovich) Hart, 1964, extracted from sporangia of *Permotheca striatifera* Gomankov et Meyen, 1986 from the Isady locality, Late Permian, Volodga Region, Russia, TEM, group P7 (1, 2, 7) and group P2 (3–6, 8). (see on page 10)

1. Pollen 3 of group P7, a portion of a section showing proximal ribs (r); the endexine is much thinner than in previous sections and very variable in thickness.
2. Pollen 3 of group P7, a deeper section in the same area as in Fig. 1, note a considerable groove (g) between two of the ribs (r).
3. Longitudinal section of a pollen grain from group P2. Distal face is covered by the endexine alone.
4. Group P2. Saccus area. A thin thread is shed out from a thick endexine toward the saccus area.
5. Group P2. Shedding threads of the endexine.
6. Group P2. Longitudinally cut rib. An enlarged area of a section adjacent to that shown in Fig. 3.
7. Group P7 (pollen 3), saccus area. Most partitions are cut transversely and appear as granules; the outer layer is continuous (without perforations).
8. Group P2. Endexinal thread enters the saccus area. Enlargement of Plate VI, fig. 4. Scale bar (1–4, 7) 1 μm, (6, 8) 0.67 μm.

Plate VII. Exine ultrastructure of pollen grains of *Protohaploxypinus* (Samoilovich) Hart, 1964, extracted from sporangia of *Permotheca striatifera* Gomankov et Meyen, 1986 from the Isady locality, Late Permian, Volodga Region, Russia, TEM, groups P5 and P3. (see on page 11)

1. A portion of a longitudinal section through a pollen grain of group P5. The pollen was pressed in equatorial position and the section passed through the distal area and sacci.
2. Enlargement of a section adjacent to that shown in Plate VII, 1. Many partitions of the sacci are cut transversely.
3, 6. Portion of a section of group P4. Ectexine and endexine remarkably differ in electron density.
4, 5. Areas of longitudinal section of a pollen grain of group P3 (Plate III, 6). Arrows point white lines in outer portions of the endexine.
7. Area of a longitudinal section of a dispersed *Protohaploxypinus* studied by Zavialova (1998). Arrows point white lines in outer portions of the endexine. (p) proximal face, (d) distal face. Scale bar (1, 3) 0.67 μm, (2, 5) 1 μm, (4, 6) 0.5 μm, (7) 0.25 μm. *Gomankov and Tarasevich (2011) argued that the specimen shown by Afonin (1999) should be more suitably incorporated in *Vittatina costabilis* Wilson, 1962.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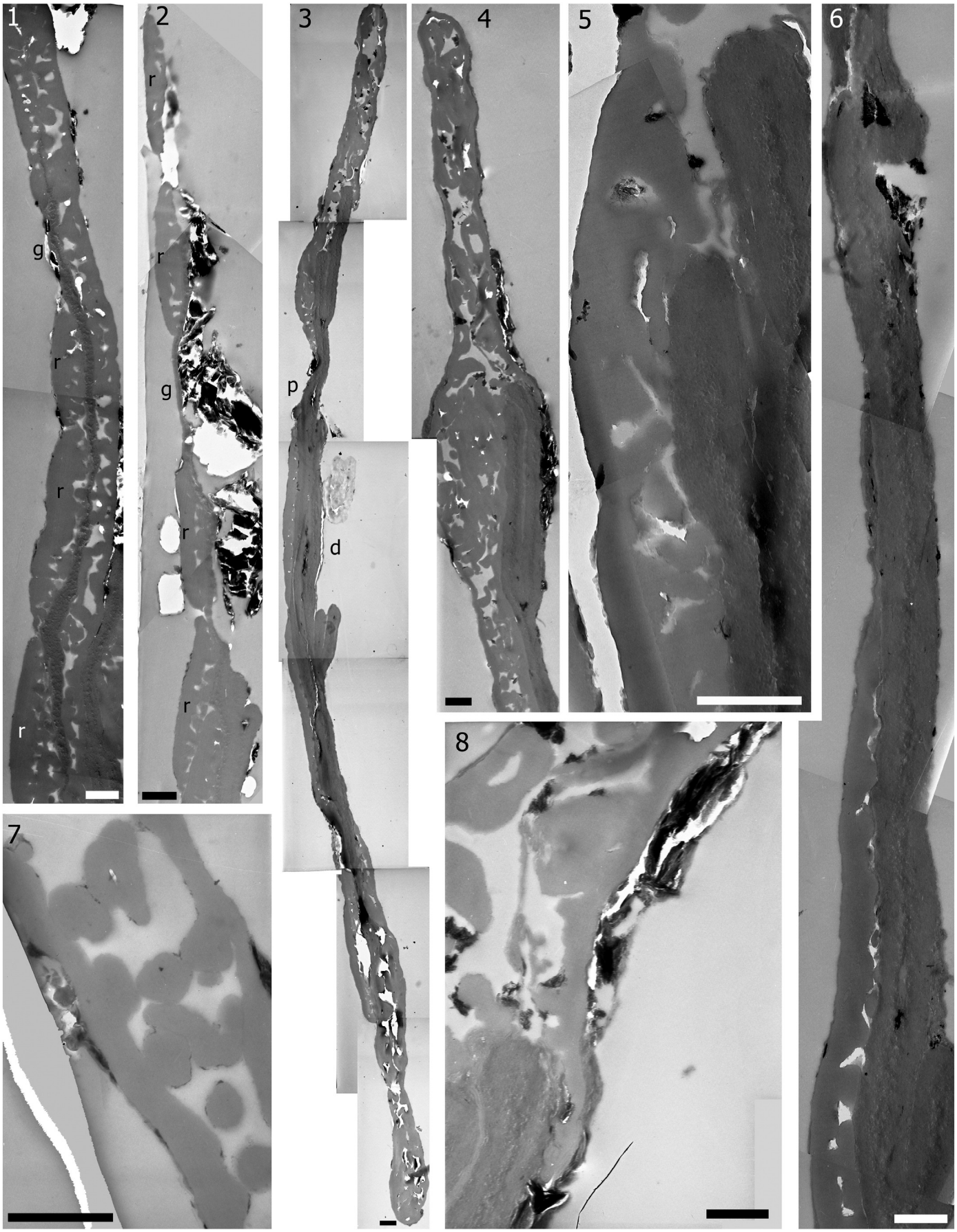

Plate VI. (*caption on page 8*)

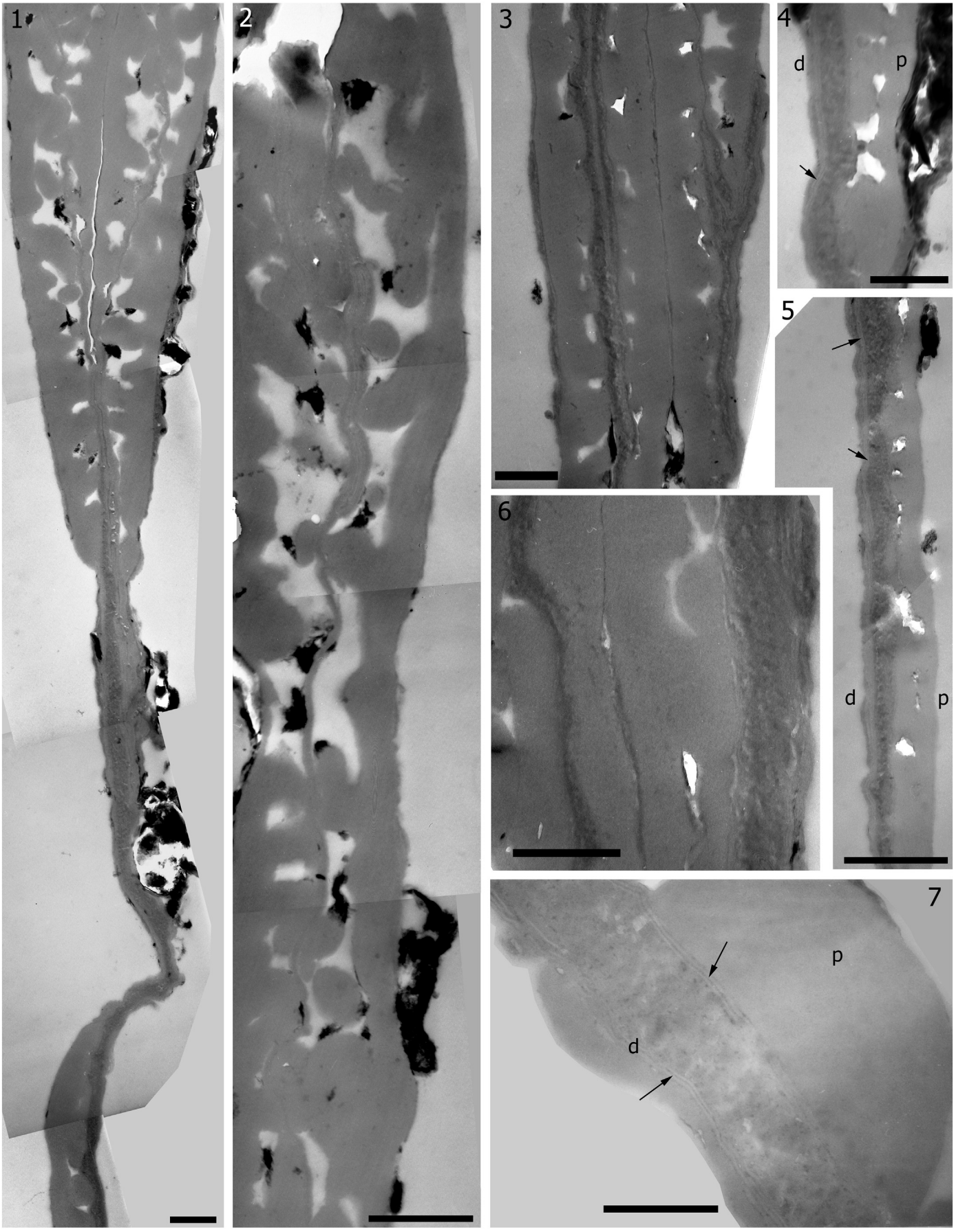

Plate VII. (*caption on page 8*)

Table 1
Comparison between species of *Permotheca* (Zalessky, 1929) emend. Naugolnykh, 2007.

	Cisuralian group of species				Mixed Biarmian group of species			Tatarian group of species		Triassic sp.
	P. fimbriata (Zal.) Naug., 2007	*P. bifurcata* Naug, 2007	*P. deodara* Naug., 2007	*P. disparis* (Zalessky) Naug., 1999	*P. colovratica* Naug., 2013	*P. sardykensis* Zalessky, 1929	*P. vesicasporoides* Meyen, Esaulova et Gomankov, 1986	*P. striatifera* Meyen et Gomankov, 1986	*P.? vittatinifera* Meyen et Gomankov, 1986	*P. helbyi* Retallack, 2002
Condition	Loose strobiles	Fragmentary strobiles	Loose strobiles	Loose strobiles	Isolated synangia	Isolated synangia	Isolated synangia	Isolated synangia	Isolated sporangia	Fragmentary strobiles
Main axis	Slender	Slender, bifurcate	Thick, woody	Thick, woody	?	?	?	?	?	Slender
Type of synangia	Flattened, radial	Rosette-like	Flattened, radial	Flattened, radial	Flattened, like propeller	Radial, racemose	Racemose	Racemose	?	Rosette-like, racemose
No. pollen sacs	14–16	8–9	8–9	6–10	4	4–8	4?–15	5–8	?	15–20
Resin bodies	Unknown	Unknown	Unknown	Secretory (resin) channels	Secretory (resin) channels	?	Resin body	Resin body	Not found	Not found
Pollen in situ	Unknown	Unknown	Unknown	*Vesicaspora–Falcisporites*	*Vesicaspora–Falcisporites*	?	*Vesicaspora–Falcisporites*	*Protohaploxypinus Tatarina*, *Peltaspermopsis*	*Vittatina Tatarina*, *Peltaspermopsis*?	*Vesicaspora–Falcisporites*
Associating organs	*Psygmophyllum*, *Muerites*			*Rhachiphyllum*	*Psygmophyllum*	*Phylladoderma* (Phylladoderma)?	*Phylladoderma* (Aequistomia)			*Lepidopteris*
Type locality	Krasnaya Glinka	Chekarda-1	Chekarda-1	Kazarinovsky	Chekarda-1	Kullarovo	Isady	Isady	Aristovo	Oakdale Colliery
Region	Cisurals	Cisurals	Cisurals	Cisurals	Cisurals, Samara	Tatarstan	Vologda, Tatarstan, Pechora basin	Vologda	Vologda	Australia
Stratigraphy	Kungurian Stage, Filippovian Horizon, Lekskian Formation	Kungurian Stage, Irenian Horizon, Koshelevskian Formation	Kungurian Stage, Irenian Horizon, Koshelevskian Formation							
Age	Kungurian	Kungurian	Kungurian	Kungurian, Ufimian[a]	Kungurian, Kazanian[b]	Kazanian, Severodvinian	Kazanian, Severodvinian, Vyatkian[c]	Severodvinian, Vyatkian[d]	Vyatkian	Early Triassic
References	Naugolnykh (2007)	Naugolnykh (2007)	Naugolnykh (2007)	Krassilov et al. (1999a) and Naugolnykh (1998, 2007)	Naugolnykh (2013)	Zalessky (1929), Naugolnykh (2007), and Gomankov (1997)	Gomankov and Meyen (1986)	Gomankov and Meyen (1986)	Gomankov and Meyen (1986)	Retallack (2002)

[a] Kungurian (Krasnaya Glinka, Krutaya Katushka, Matveevo, and Chekarda-1) and Ufimian (Kazarinovsky).
[b] Kungurian (Chekarda-1), Kazanian (Kuedinskie Klyuchiki, Novyi Kuvak).
[c] Kazanian (Sentjak); Severodvinian (Isady); and Vyatkian (Aristovo, Titiovo borehole, and Krasnyi Kamen).
[d] Severodvinian (Alexandrovka and Isady); Vyatkian (Aristovo and borehole Titiovo).

Similar to the Australian material, the endexine is much more electron dense than the ectexine, of a constant thickness, and appears homogeneous under low magnifications, but white lines were detected in the outer areas under greater magnifications (Zavada, 1991, fig. 17). Perhaps, they would have been found in the Australian material as well, if greater magnifications were applied. The ultrastructure of the ribs is the same as in the Australian pollen. Distally, the ectexine is thinned but present and retains the alveolate organization. The saccus is thin and filled with partitions (= protosaccate or at least appears protosaccate).

Krassilov et al. (1999b) wrote that their section through a pollen grain of *Protohaploxypinus*-type extracted from the guts of a Kungurian book louse was longitudinal. Indeed, only one unequivocal thinning between two ribs is visible on the proximal face. Their LM and SEM images show a pollen grain with approximately ten ribs, which would have been reflected in repeated thickened and thinned areas of the exine if the section were situated transversely. Probably, this thinning was a groove between ribs, one of which was shorter than the other; or the direction of the section was not completely parallel to the ribs. Only the ultrastructure of the body was shown and described. The exine is two-layered. The endexine is prominent, uniform in thickness, does not differ by electron density from the ectexine (it is not said were the pollen grains stained or not) and appears homogeneous under magnification of 4000×. The authors remarked that the *Protohaploxypinus* that they studied differed from that found in *Arberiella* by a homogeneous endexine, so we imply that sections under greater magnifications were checked, though not illustrated. The ribs are constructed in the same way as in glossopterid *Protohaploxypinus*. The distal ectexine is reduced to a single thin thread.

Pollen grains studied by Zavialova (1998) and Zavialova et al. (2001) have a variously thinned distal ectexine. Sections of different specimens and, supposedly, in slightly different areas show either an ectexinal layer with rare alveolae that is thinner than the proximal ectexine, or a thin repeatedly varying in thickness homogeneous layer which does not possess alveolae, or no distal ectexine at all (the distal portion is lined with an endexine alone). We suspect that the ectexine is wedged out distally up to the complete disappearance over the apertural area. In addition, most pollen grains of this pool differ by a very thin endexine, which is slightly more electron dense than the ectexine and appears as a fine-grained thread. Such interrupted threads may occur quite deep in saccate areas. However, there was a specimen which possessed a much thicker endexine than the others. The endexine of this specimen is a thin fine-grained thread in saccate areas, but thick and loosely homogeneous in the area of the body, where, as greater magnifications (80000×) show, it is delimited from the ectexine by two white-centered lamellae (Plate VII, 7). By this character, this specimen is similar to *Protohaploxypinus* from *Arberiella*.

The pollen grains of *Permotheca striatifera* (present study) bear up to ten ribs. The ectexine and endexine differ in the ultrastructure and electron density. The ectexine is alveolate; the endexine is more electron-dense and appears homogeneous, though some indices of layering were observed under higher magnifications. The sacci appear protosaccate. In ribs, the ectexine includes an outer continuous layer, a thinner underlying alveolate layer, and an inner layer. Grooves between the ribs either retain the inner homogeneous ectexinal layer resting on the endexine or are lined by the endexine alone. The distal face of the body is covered by the endexine alone.

The pollen grains under comparison show a considerably high level of similarity, in spite of the fact that they derive from two supposedly unrelated groups of parent plants. In the current absence of 3-D material, the sacci are interpreted as protosacci, which appear quite similar in all pools (the denser ultrastructure of the Australian pollen can be explained by a relatively central position of the section).

The arrangement of the ribs is more or less the same. A thin ectexinal layer is present over the grooves in some, but only the endexine in others. However, as far as this variation occurs as well within pollen grains under the present study, extracted from one sporangium, we do not think that it can be used as a differentiating feature. If the sacci merely simulate protosacci, the interrupted endexinal threads in saccate areas, which we saw in the present and our earlier materials, might point out to the presence of a once existing cavity of the saccus.

The endexine shows more promising variations, such as being thick and homogeneous, homogeneous with white lines in outer areas, homogeneous with indices of layered organization, thin fine-grained, and thick and homogeneous with peeling thin threads. Again, the pollen grains cannot be divided on the basis of this diversity in two groups. The layering observed in outer areas of the endexine of the present material is less distinct, but probably comparable with white lines detected by Zavada (1991) and (in one specimen) by Zavialova (1998). We incline that the differences in the endexine ultrastructure are preservational, with a possible exception of threads entering the saccate areas. Probably, there are no differences between the pools either by the saccus or by endexine ultrastructure.

There is a possibility that Angaran pollen grains do differ from Gondwanan pollen by a greater degree of reduction of the ectexine over the distal area of the body. Even if this is correct, it is quite a minor differentiating feature for pollen grains of supposedly unrelated groups as peltasperms and glossopterids.

4.3. The exine ultrastructure of other peltasperm pollen types

Among the pollen types found in situ in peltasperms, *Vesicaspora*, *Vittatina*, and *Cycadopites* are the types about which some ultrastructural data are available.

Pollen grains of *Vittatina subsaccata* f. *connectivalis* Samoilovich, 1953 were reported by Gomankov and Meyen (1986) from isolated sporangia defined as *Permotheca? vittatinifera*. It should be pointed out that *Vittatina*-like pollen grains were very diverse: several genera and up to about 30 species are sometimes distinguished within the group. The diversity stretches from asaccate pollen to pollen bearing incipient (reduced?) sacci, from psilate pollen to pollen with prominent sculpture over some regions of the surface; the ribs vary in the width, number, orientation, and presence/absence over some areas of the pollen grain (Gomankov and Tarasevich, 2014). This complicated diversity has been still waiting for a thorough morphological study and established system. The existence of the Gondwanan counterpart makes the situation more intricate.

Electron microscopy has been so far applied only to dispersed pollen: SEM (Koloda, 1986, 1989, 1997) and SEM and TEM (Meyer, 1977; Koloda, 1986; Afonin, 1999; Gomankov and Tarasevich, 2008, 2011, 2014). SEM shows that unlike a virtually psilate surface of *Protohaploxypinus*, the pollen grains of the *Vittatina* group often show various verrucae on some areas of the surface.

Meyer (1977) showed that *Vittatina* sp. has a thick tectum formed by fused granules and an infratectum of smaller granules; the endexine is prominent and shows indices of lamellations (two figures were reproduced by Zavialova and Van Konijnenburg-van Cittert, 2011 in their pl. VI, 1, VII, 8). Koloda (1986) characterized the ectexine of *Vittatina subsaccata* Sam. ex Wil. as formed by columella-like elements and did not discuss the endexine structure. It seems to us from the illustrations that these pollen grains have a granulate ultrastructure, similarly to other studied members of this pollen type. Sections of *Vittatina connectivalis** (Sauer) Warjuchina, 1971 ex Utting published by Afonin (1999) show a thick homogeneous tectum underlined by a thinner infratectum formed by granules of various sizes. The tectum reduces in grooves. No footlayer was detected. The endexine, where is present, is formed by several lamellae. SEM shows that the surface of ribs (the surface of the tectum) is pitted. Some areas of the surface of the pollen grains are verrucate. Gomankov and Tarasevich (2008, pl. 1.11) show a section of an incipient sacci of a psilate form of *Vittatina costabilis* Wilson, 1962: the layer underlying the tectum is granulate both in the body and in the incipient saccus, unlike the ultrastructure of

Protohaploxypinus. Later, they studied a verrucate form of the same species (Gomankov and Tarasevich, 2011). Each of numerous ribs is a row of verrucae. The verrucae are composed of a tectum of fused granules of various sizes and an underlying layer of smaller granules, at places aligned into columellate-like structures. The tectum diminishes between the verrucae. This organization is characteristic of the proximal face, which is covered by these verrucate ribs. Distally, merely the underlying granulate layer remains. The endexine is thick and appears homogeneous (under magnification of 8000×), and of constant thickness around the perimeter of the pollen. Gomankov and Tarasevich (2014) studied members of *Vittatina* from deposits ranging in age from the Kungurian to Tatarian and concluded that all of them shared the same ultrastructural organization, which was similar in ribs and in incipient sacci.

In their light-microscopical study of the morphology of dispersed pollen grains of *Protohaploxypinus* and *Striatopodocarpidites* from the upper Tatarian of the Vyatka River, Foster and Gomankov (1994) hypothesized that striate bisaccate pollen grains of these types could have lost sacci in the course of fossilization and, as a result, can be identified in palynological assemblages as separate striate entities. Such specimens of *Protohaploxypinus* and *Striatopodocarpidites*, which are devoid of sacci, resemble pollen grains of *Vittatina*-type. However, available TEM data show that the exine ultrastructure of pollen grains of *Protohaploxypinus* and *Striatopodocarpidites* in areas of the body differs from the exine ultrastructure of pollen grains of *Vittatina*.

All ultrastructurally studied pollen grains of *Vittatina* show variants of a granulate ultrastructure, that is in contrast to the ultrastructure of *Protohaploxypinus*. SEM studies show significant dissimilarities between *Vittatina* and *Protohaploxypinus*. The evolutionary transformation of the granulate wall structure to the alveolate structure (or vise versa) is not apparent in these taxa nor do any intermediate morphologies exist. This supports our doubts about assigning *Permotheca* (?) *vittatinifera* to the genus *Permotheca*. We are looking forward to finding better preserved specimens of this species allowing a more confident morphological comparison with other species of *Permotheca* and an ultrastructural study of in situ *Vittatina* which will elucidate the relation with peltasperms and to understand the nature of the diversity of *Vittatina*.

Krassilov et al. (1999a) published ultrathin sections of in situ *Vesicaspora* from early Permian *Permotheca*. Dispersed pollen grains of *Vesicaspora* which supposedly derived from peltasperm were ultrastructurally studied by Zavialova (1998) and Zavialova et al. (2001) from the upper Permian of the Russian Platform. Early Permian pollen were interpreted as protosaccate, and the Late Permian pollen also appear protosaccate or intermediate proto/eusaccate, although it can be a preservational feature, since the dispersed pollen grains were strongly flattened. Lamellae were found in the endexine of the early Permian pollen grains, but were not detected in the Late Permian dispersed pollen. Both Early and Late Permian pollen have a thicker proximal ectexine, with outer and inner homogeneous layers, and a row of alveolae between them. The distal aperture is formed by a considerable thinning of the ectexine. The morphology of the proximal area of the body in *Protohaploxypinus* has something in common with that of *Vesicaspora*; the outer and inner homogeneous layers and intermediate alveolate layer are present in both pollen types. The main features distinguishing *Protohaploxypinus* from *Vesicaspora* at the level of exine ultrastructure are strong variations in thickness and presence of the outer and intermediate layers due to the striations.

The pollen grains of *Antevsia zeilleri* (Nathorst) Harris, 1937 from the Upper Triassic of Germany are of the *Cycadopites*-type (Zavialova and Van Konijnenburg-van Cittert, 2011). 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, at places resembling a saccus-like ultrastructure. The endexine includes white-line-centred lamellae. Basing on ultrastructural data, Zavialova and Van Konijnenburg-van Cittert (2011) hypothesized a transformation from Permian *Vesicaspora* into Triassic *Cycadopites* extracted from pollen sacs of *Antevsia*. Proximal areas in the exine of pollen of *Antevsia* are usually more homogeneous than in the cappa of Permian *Vesicaspora*; however, some sections of *Antevsia* pollen appear very similar. 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.

5. Conclusions

The exine ultrastructure of *Protohaploxypinus* pollen grains extracted from a peltasperm pollen organ was investigated. Our present and previous (Zavialova and Van Konijnenburg-van Cittert, 2011) results contribute to the understanding of the diversity of pollen types occurring in Permian and Triassic peltasperms. Several similarities are observed between the ultrastructure of *Protohaploxypinus* and *Vesicaspora*. The exine ultrastructure of *Vittatina* differs principally from other peltasperm pollen types (*Protohaploxypinus*, *Cycadopites* and *Vesicaspora*). No ultrastructural information is still available about *Falcisporites*. Once more we stress the necessity of TEM studies of in situ pollen grains. Scanty data so far available for many of the fossil plant groups cannot provide a solid basis for analysis, and the palynological puzzles are doomed to remain puzzles.

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