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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.

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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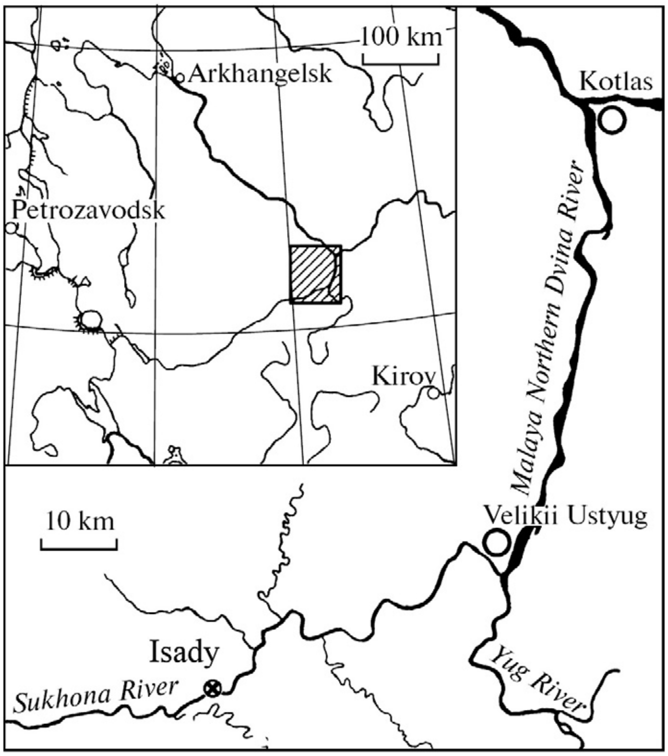

Fig. 1. Schematic map of the Isady locality.

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.