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On the exine ultrastructure of fossil ginkgoaleans: *In situ* pollen of *Sorosaccus* Harris

Natalia Zavialova [a,*], Natalya Nosova [b], Eugenia Bugdaeva [c]

[a] *A.A. Borissiak Paleontological Institute, Russian Academy of Sciences, Profsoyusnaya 123, Moscow 117647, Russia*
[b] *Komarov Botanical Institute, Russian Academy of Sciences, ul. Professora Popova 2, St. Petersburg 197376, Russia*
[c] *Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far Eastern Branch, Russian Academy of Sciences, Vladivostok, 690022, Russia*

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ABSTRACT

The morphology and exine ultrastructure have been studied of pollen grains from pollen cones of *Sorosaccus sibiricus* Prynada from the Ust'-Baley (Aalenian, Siberia), *Sorosaccus* sp. from the Vladimirovka (Aalenian-Bajocian, Siberia), and *S.* ex gr. *sibiricus* Prynada from the Tyrma (Tithonian–Berriasian, Russian Far East) localities. The pollen grains are boat-shaped and monosulcate. A finely granulate pattern is discernible under high magnification of light microscope in pollen grains from Vladimirovka and Tyrma; SEM shows that this pattern is formed by flat verrucae. TEM shows that sculptural elements are present on the surface of pollen grains from Ust'-Baley, although it is not evident in LM and SEM. By previous data on modern and fossil members, we believed that ginkgoalean pollen grains can be differentiated from similar boat-shaped monosulcate pollen of other affinities by a ratio of ectexinal sublayers (a thick homogeneous tectum, a thin infratectum of one row of structural elements, and a thin foot layer) in combination with an ectexine that is greatly reduced in the aperture region. Freshly obtained data have revealed another set of characters, with a less prominent tectum by comparison to underlying sublayers, an infratectum with small granules within the alveoli, and a prominent verrucate surface pattern that is distinguishable even in transmitted light. Ginkgoaleans are characterized by more than one set of ultrastructural characters of the exine.

1. Introduction

Ginkgoaleans are characterized by boat-shaped monosulcate pollen grains ascribed to *Cycadopites* Wodehouse, *Monosulcites* Cookson ex Couper or *Ginkgocycadophytus* Samoilovich genera of dispersed pollen (van Konijnenburg-van Cittert, 1971; Kvaček et al., 2005; Liu et al., 2006; Wu et al., 2006; Zavialova et al., 2011; Zavialova and Nosova, 2019). Cycadaleans, bennettitaleans, and some other groups of seed plants are also known to have produced such pollen (Balme, 1995; Zavialova et al., 2009; Zavialova and van Konijnenburg-van Cittert, 2011; Nosova and Tekleva, 2022). Although this pollen type is relatively simple in general morphology, it shows various exine ultrastructures, and groups of parent plants can be differentiated on the basis of such differences (e.g., Meyer-Melikian and Zavialova, 1996; Tekleva et al., 2007; Zavialova and van Konijnenburg-van Cittert, 2011). This is important, for instance, for paleoecological reconstructions based on palynological data. So far, producers of such pollen are, of necessity, treated within one group in such reconstructions (e.g., Visscher and Van der Zwan, 1981; Abbink et al., 2004; Zhang et al., 2021), although their ecological preferences were not necessarily identical (Krassilov, 2003; Kvaček et al., 2005; Bugdaeva et al., 2006; Bugdaeva and Markevich, 2007).

The information on the producers of such pollen is still scarce. For example, until recently, our knowledge on the exine ultrastructure of ginkgoaleans has been mostly based on the information derived from the modern *Ginkgo biloba* L., which has been repeatedly studied (Ueno, 1960; Rohr, 1974; Meyer, 1977; Audran and Masure, 1978; Sahashi and Ueno, 1986; Audran, 1987; Zhang et al., 2000). Additional information came from studies of pollen grains extracted from seeds of a presumed ginkgoalean affinity from the Jurassic of Uzbekistan (Zavialova et al., 2014, 2016) and dispersed pollen grains of a hypothesized ginkgoalean affinity from the Early Cretaceous of the Russian Far East (Zavialova et al., 2011). Pollen organs of fossil ginkgoaleans are often found as empty structures that contain no or few pollen grains, and it is impossible to apply such a destructive method as TEM (van Konijnenburg-Van Cittert, 2010). Our study of Jurassic fossil plants from the Irkutsk Coal Basin in Siberia revealed relatively numerous pollen organs of gymnosperms (Nosova et al., 2017; Nosova et al., 2018; Zavialova and Nosova, 2019, 2021; Nosova and Tekleva, 2022). In the

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[*] Corresponding author.
E-mail address: zavial@mail.ru (N. Zavialova).

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Idan locality (Irkutsk Basin), we found a pollen organ with numerous in situ pollen grains; the macrofossil was too fragmentary for an unequivocal taxonomic determination, but the boat-shaped monosulcate pollen grains showed an assemblage of ultrastructural features that we expected to find in a ginkgoalean by the previously available ultrastructural information (Zavialova and Nosova, 2019). Recently, we have studied pollen grains associated with *Schidolepium* cones from the Middle Jurassic of the Irkutsk Basin; among numerous monosaccate pollen grains, which did belong to this conifer, we found a clump of boat-shaped monosulcate pollen grains, which we interpreted as a contamination (possibly brought by a non-specialized pollinator): their ultrastructural characters testified to the ginkgoalean affinity (Zavialova and Nosova, 2021).

In the present paper, we report the morphology and exine ultrastructure of in situ pollen grains extracted from pollen cones of *Sorosaccus* Harris from Siberia (Middle Jurassic) and Russian Far East (Upper Jurassic–Lower Cretaceous). Our aim was to learn more about pollen grains that most probably were produced by ginkgoaleans, to differentiate ginkgoalean pollen from Mesozoic monosulcate boat-shaped pollen grains of other affinities.

2. Previous studies of *Sorosaccus*

Cones of *Sorosaccus* were found in the Middle Jurassic deposits of the Irkutsk Coal Basin among other pollen organs. Initially, Heer (1876) described these pollen cones from the Ust'-Baley locality (Irkutsk Coal Basin) as *Baiera longifolia* Heer and *B. czekanowskiana* Heer and hypothesized that they belonged to ginkgoaleans. The genus *Sorosaccus* was established by Harris (1935) for pollen cones from the Upper Triassic-Lower Jurassic of the Scoresby Sound, East Greenland, with the species *Sorosaccus gracilis* Harris (type species) and *S. minor* Harris. He noted that these cones were found in the association with ginkgoalean (*Baiera* Braun, *Ginkgoites* Seward and *Sphenobaiera* Florin) and conifer (*Podozamites* (Brongniart) Braun) foliage. Harris believed that the pollen cones described by Heer (1876) were identical to *Sorosaccus gracilis*. Prynada (1962) erected the new species *S. sibiricus* from Ust'-Baley and incorporated some Heer's pollen cones of *Baiera longifolia* and *B. czekanowskiana* in this species. This species of *Sorosaccus* was also reported from the Lower Cretaceous of the Bulunsky District (Yakutia, Siberia) but without any illustrations (Vassilevskaya, 1959; Vassilevskaya and Pavlov, 1963).

Two more species of *Sorosaccus* were described later: *S. naitoi* Kon'no, 1962 from the Upper Triassic of Yamaguchi Prefecture, island of Honshu, Japan, and *S. umaltensis* Krassilov, 1972 from the Middle-Upper Jurassic (Callovian-Oxfordian) of the Bureya River Basin, Russian Far East. The only pollen cone found in the Upper Jurassic–Lower Cretaceous deposits of the Tyrma River (left tributary of the Bureya River, Russian Far East) was described as *Sorosaccus* ex gr. *sibiricus* (Krassilov, 1972). Liu et al. (2005) described new findings of gymnospermous pollen cones from the Upper Triassic of China as *Sorosaccus gracilis.* These authors revised the diagnostic features of this species and emended the diagnosis of *Sorosaccus*. They considered the genus as monotypic; *S. sibiricus, S. umaltensis, S. minor,* as well as Greenlandic and Chinese pollen cones of *S. gracilis* were treated within the synonymy of *S. gracilis,* but they did not mention the Japanese species *S. naitoi.*

Nosova et al. (2018) reexamined specimens of *Sorosaccus* previously described from the Ust'-Baley locality (Heer, 1876; Prynada, 1962) and studied newly found pollen cones from the Ust'-Baley and Vladimirovka localities in the Irkutsk Coal Basin. They assigned these pollen cones to *S. sibiricus* since it was revealed that the Irkutsk pollen cones differ from other species of *Sorosaccus* in the shape of the apical part (widely oval distal lamina) of microsporophylls. They also designated the lectotype and gave the emended diagnosis for *S. sibiricus.*

Sorosaccus cones are always preserved as detached organs closely associated with ginkgoalean leaves. Nosova et al. (2018) considered *Sorosaccus* as a member of the Ginkgoales on the basis of the morphology of the cones and on the pollen structure. Liu et al. (2005) related the genus *Sorosaccus* with ginkgoaleans based on the oval microsporangia dehiscing longitudinally, the pollen of the ginkgoalean morphology, and the co-occurrence with ginkgoalean foliage. They believed that *Sorosaccus* represents one of the early steps of the evolutionary line directed to *Ginkgo biloba*, in course of which the number of microsporangia was reduced and the distal portion of the lamina at the distal portion of the microsporophyll became shorter; *G. liaoningensis* Liu et al. was considered as an intermediate between *Sorosaccus* and *G. biloba*. In the Irkutsk Basin, the pollen cones of *Sorosaccus* occur in association not only with ginkgoalean, but also with leptostrobalean leaves (see Chapter 4. Materials and methods). However, *Ixostrobus* Raciborski is regarded as male cones of the leptostrobaleans *Czekanowskia* Heer and *Phoenicopsis* Heer (Zhou, 1963; Krassilov, 1973b), and we suggest that *Sorosaccus* is a reproductive organ of ginkgoaleans.

We have studied the morphology and exine ultrastructure of in situ pollen grains extracted from *Sorosaccus sibiricus* from the Ust'-Baley locality, *Sorosaccus* sp. from the Vladimirovka locality, and *S.* ex gr. *sibiricus* from the Tyrma locality.

3. Occurrences and geological age

We have studied materials from two localities of the Irkutsk Coal Basin of Siberia (Ust'-Baley and Vladimirovka, Fig. 1) and one locality (Tyrma) from the Russian Far East (Fig. 2).

The Irkutsk Coal Basin occupies the south of the Siberian Platform. The basin is stretched along the northeastern slope of the Eastern Sayan, from Lake Baikal in the southeast to the Uda River in the northwest, in the area of Nizhneudinsk town (Fig. 1). Heer (1876, 1878, and 1880) was the first who studied continental deposits of the Irkutsk Basin. The Jurassic deposits of the Irkutsk Basin is subdivided into the Baikal and Dabat formations in the piedmont depression and in the Zalari Formation in the platform limb; upsection, Cheremkhovo, Prisayan, and Kuda formations are developed (Akulov et al., 2015; Kiritchkova et al., 2017).

The specimens studied come from the Prisayan Formation, dated to the Aalenian-Bajocian. The formation is constituted by sandstones with grains of unequal dimensions with sublayers of gritstones and pebbly conglomerates and coaly argillites and coals. The total thickness of the formation is up to 250 m. Sections of this formation are exposed at the right bank of the Angara River from Irkutsk to Usolye-Sibirskoe and at the left bank of the Iya River (Kiritchkova et al., 2017). The formation is subdivided into the lower part dated to the Aalenian and the upper part dated to the Aalenian-Bajocian. Numerous pollen cones of *Sorosaccus* were found in deposits of the lower part of the formation, in Ust'-Baley, and of the upper part of the formation, near the Vladimirovka village.

The Tyrma locality represents the Tyrma Unit outcropping in the Alanap section of the Tyrma River, which is a left tributary of the Bureya River, Khabarovsk Region, Russian Far East (Fig. 2). The Upper Mesozoic non-marine sedimentary sequence of the Tyrma Basin consists of the coal-bearing Dublikan and Soloni formations. The Upper Jurassic to Lower Cretaceous strata unconformably overlie the Middle Jurassic marine Elga and Epikan formations (Kirillova, 2012). The Tyrma Unit is correlated to the Dublikan Formation (Krassilov, 1973b). The strata of the Dublikan Formation comprise an upward-fining kilometer-thick sequence from coarse matrix-supported fanglomerate and conglomerate to fine sandstone, siltstones, mudstones, and coal suggestive of a mudload-dominated, meandering fluvial environment. The base of the formation is composed of conglomerate with poorly rounded fragments of metamorphic rocks, granites, and felsic volcanic rocks. The lenses and interbeds of unsorted coarse-grained sandstones occur. The upper part of this formation is dominated by fine-grained arkosic, less often polymictic sandstones with lenses and interlayers of felsic tuffs,

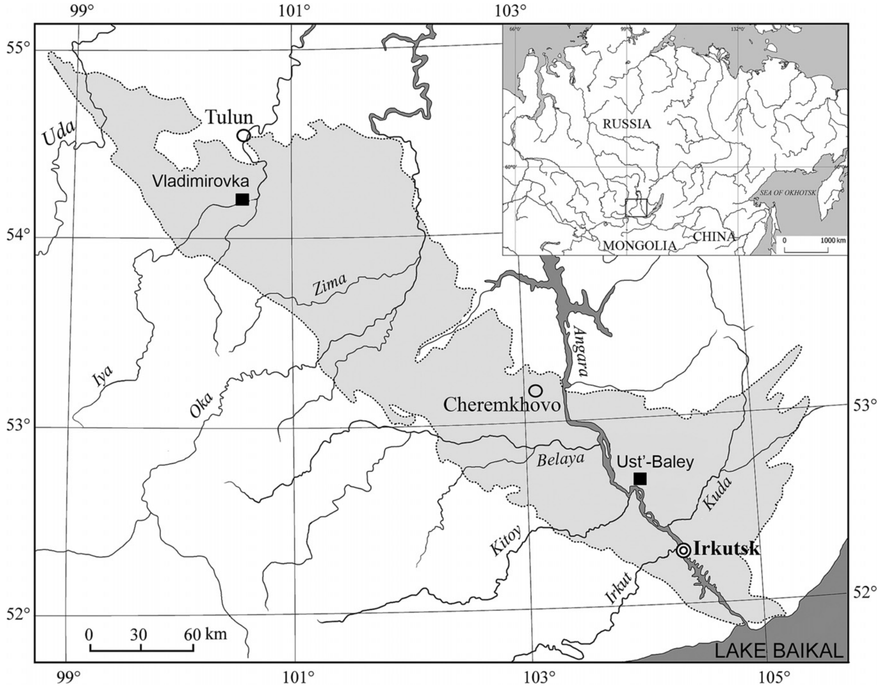

Fig. 1. Map of the Irkutsk Coal Basin (East Siberia, Russia) showing outcrops where the remains of *Sorosaccus* were found.

siltstones and mudstones, often containing coal seams of productive thickness. The tuffs and siltstones contain abundant fossil plants. Krassilov (1973a) dated the Dublikan Formation to the Tithonian–Berriasian (also see discussion in Nosova et al., 2021).

4. Materials and methods

The studied specimens of *Sorosaccus* from the Irkutsk Coal Basin are housed in the Laboratory of Palaeobotany of BIN RAS in St. Petersburg, Russia (collections BIN 6a, 139 and 1434); and from the Tyrma River, in the Laboratory of Palaeobotany of the Federal Scientific Center of the East Asia Terrestrial Biodiversity of the Far Eastern Branch of the Russian Academy of Sciences, Vladivostok (FSC EATB FEB RAS), Russia (collection 550). Remains of polymerized resins with embedded pollen grains, grids with ultrathin sections, digital files from LM, SEM, and TEM are retained in the Laboratory of Palaeobotany of PIN RAS, Moscow, Russia.

In the Irkutsk Basin, the remains of *Sorosaccus* were found associating with leaves of *Ginkgoites sibirica* (Heer) Seward, *Sphenobaiera czekanowskiana* (Heer) Florin and *Czekanowskia rigida* Heer in Ust'-Baley and with *G. heeri* Doludenko et Rasskazova, *S. longifolia* (Pomel) Florin, *Phoenicopsis irkutensis* Doludenko et Rasskazova, *C. obiensis* Kiritchkova et Samylina, and *C. vera* Kiritchkova et Samylina in Vladimirovka (Kiritchkova et al., 2018). Pollen grains were extracted from specimens BIN 6a/84 and BIN 1434/410 (Ust'-Baley), and BIN 1434/1496-3 and BIN 1434/1493-3 (Vladimirovka). Of these specimens, we studied BIN 6a/84 and BIN 1434/1493-3 with SEM and TEM.

In Tyrma, the only found *Sorosaccus* cone is associated with *Baiera kidoi* Yabe et Oishi, *Phoenicopsis* sp., and *Ixostrobus* ex gr. *heeri* Prynada (Krassilov, 1972). Krassilov defined it as *Sorosaccus* ex gr. *sibiricus*. For the present study, we extracted pollen grains from this cone (spec. 550/105).

The samples were first treated with HF for about one day, followed by Schulze's reagent (HNO_3 catalyzed with $KClO_3$) for about 1 h. Then the material was rinsed with water, followed by solution of NaOH for a few minutes. Hand specimens were photographed with a Canon EF-S60 digital camera. Details were taken with a Stemi 2000-CS stereomicroscope and Carl Zeiss Axio Scope.A1 light microscope (LM; equipped with the Lomo Microsystems MC-6.3 camera) at the Komarov Botanical Institute of the Russian Academy of Sciences (BIN RAS) in St. Petersburg. The general morphology of the pollen grains was observed in transmitted light, with help of a Carl Zeiss Axioplan 2 transmitted light microscope equipped with an AxioCam 105 digital camera at A.A. Borissiak Paleontological Institute of the Russian Academy of Sciences (PIN RAS). Some images were processed with Helicon Focus 6.6.1 software. For SEM, pollen grains were cleaned with alcohol, mounted on a SEM stub, sputtered with gold and palladium, and observed under a Tescan Vega, 20 kV, at PIN RAS. For TEM, pollen grains were embedded unstained after Zavialova et al. (2018). Sections of 70 nm thick were prepared using a Leica EMUC6 ultramicrotome equipped with a diamond knife at PIN RAS. They were viewed and photographed on a Jeol JEM-1011 (accelerating voltage 80 kV) TEM, 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.

Pollen terminology follows Punt et al. (2007) and Halbritter et al. (2018).

5. Systematic descriptions

Order: GINKGOALES? Gorozhankin, 1904
Genus: **Sorosaccus** Harris, 1935 emend. Liu et al., 2005
Species: Sorosaccus sibiricus Prynada, 1962 emend. Nosova et al., 2018

Plates I, 1–5; II, III

Synonymy and selected references:

1962 *Sorosaccus sibiricus* – Prynada, p. 289, pl. XIII, figs. 7, 8; pl. XVIII, figs. 4a, 5–7; pl. XXI, fig. 5.

2018 *Sorosaccus sibiricus* – Nosova et al., p. 6, pl. I, figs. 1–11, 13–15, 19; pl. II, figs. 1, 8; text-fig. 2.

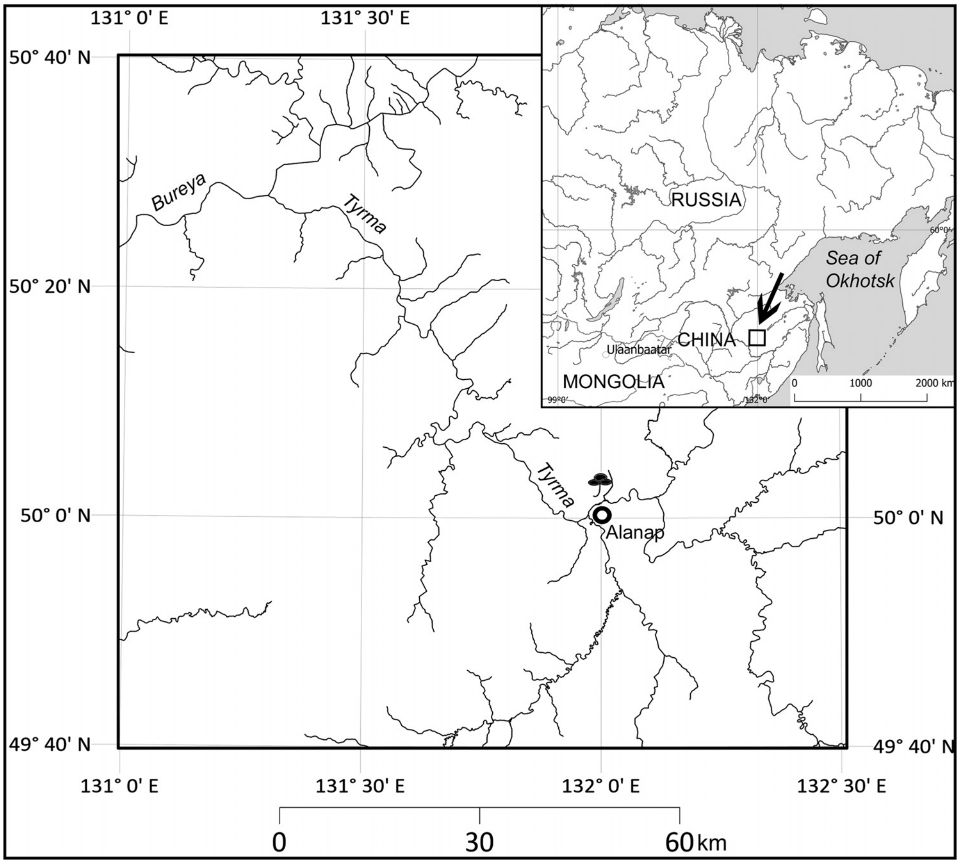

Fig. 2. Map of the Tyrma River Basin (Khabarovsk Region, Russian Far East) showing outcrop where the cone of *Sorosaccus* ex gr. *sibiricus* Prynada was found.

2020 *Sorosaccus sibiricus* – Kiritchkova et al., p. 107, pl. CXXIII, figs. 1–11, 13–15, 19; pl. CXXIV, figs. 1, 8.

1876 *Baiera czekanowskiana* – Heer, p. 56, pl. X, fig. 5.

1878 *Baiera czekanowskiana* – Heer, p. 63, pl. X, fig. 5.

1876 *Baiera longifolia* auct. non Pomel – Heer, p. 52, pl. IX, fig. 8, 9.

1878 *Baiera longifolia* auct. non Pomel – Heer, p. 59, pl. IX, fig. 8, 9.

1880 *Baiera longifolia* auct. non Pomel – Heer, p. 11, pl. II, fig. 4b, pl. IV, fig. 1b.

Lectotype: Coll. CNIGRM 5392, spec. 130, Ust'-Baley, Irkutsk Coal Basin, Eastern Siberia, Russia, lower part of the Prisayan Formation, Aalenian, Middle Jurassic; Prynada, 1962, pl. XIII, fig. 7; designated in Nosova et al., 2018.

Locality and age: Ust'-Baley, Irkutsk Coal Basin, East Siberia, Russia; lower part of the Prisayan Formation, Aalenian, Middle Jurassic.

Material studied: Coll. BIN 6a, spec. 84; coll. BIN 139, spec. 6; coll. BIN 1434, specs. 410, 414, 415.

Description: Pollen cones are elongated cylindrical (Plate I, 1–5). The main axis is 1–1.5 mm in diameter, with a faintly striated surface. The basal part (free from microsporophylls) of the main axis is more than 12 mm long. The microsporophylls are arranged helically, at 40–100° to the main axis. Pollen cones are without the basal sterile part, they reach 16–35 mm long and 5–13 mm wide. The microsporophyll consists of a petiole (2–4 mm long) with six to eight helically attached microsporangia (pollen sacs) and a widely oval distal lamina (1.2–2 × 2–3.6 mm) with an acute apex commonly bending upward. The lamina is thin, often folded and became lanceolate, linear, or fan-shaped with an uneven to toothed margin. The microsporangium is oval, 0.6–1.6 × 0.3–0.9 mm. Many microsporangia show a longitudinal slit opening the pollen sac.

In situ pollen. In transmitted light we observed numerous pollen grains embedded in cuticles and richly covered by orbicules (Plate II, 1–3). The pollen grains differ from the non-pollen material by a more uniform coloring (= a less variable thickness of the wall, Plate II, 3). Most pollen grains are elongated-rounded (Plate II, 1), and some are boat-shaped (Plate II, 2). Relatively long folds of the exine commonly occur (Plate II, 3). Some of these folds (particularly those in boat-shaped specimens) probably are situated on the place of the sulcus, but as all pollen grains are superimposed on each other and on the cuticle, we cannot point on an unequivocal sulcus. We measured 33 pollen grains, which are 35.9–64.2 × 57.2–77.7 μm, 57.9× 61.2 μm (average) and 48.8 × 65.0 μm (median). Nearly all pollen grains appear psilate even under magnification of ×100.

It was difficult to evaluate the surface pattern via SEM (Plate II, 4–7), and TEM images helped us to understand why: the surface of nearly all pollen grains is covered by the non-exinal material (Plate III, 1, 11, 12) and numerous orbicules that hide and smooth out the surface pattern (Plate II, 4–7; Plate III, 1, 5, 8, 12). However, the weakly undulated outer contour of sectioned pollen grains, observed in TEM (Plate III, 1, 11), proves that some indistinct verrucate pattern is present.

The preservation of Ust'-Baley pollen grains appears the worst among these three studied pools of the materials and the most difficult to interpret. We often fail to trace closed (= intact, uninterrupted) contours of individual pollen grains, although we did it for some pollen grains (e.g., Plate III, 1, red line). There is a significant variation in the exine thickness. There are thick areas that, in their turn, vary from 0.3 to 0.6 μm, because of undulations of what we interpret as the outer surface of the pollen. In addition, there are continuous areas of about 0.06–0.11 μm thick, which often roll into strange balls (Plate III, 1, 11).

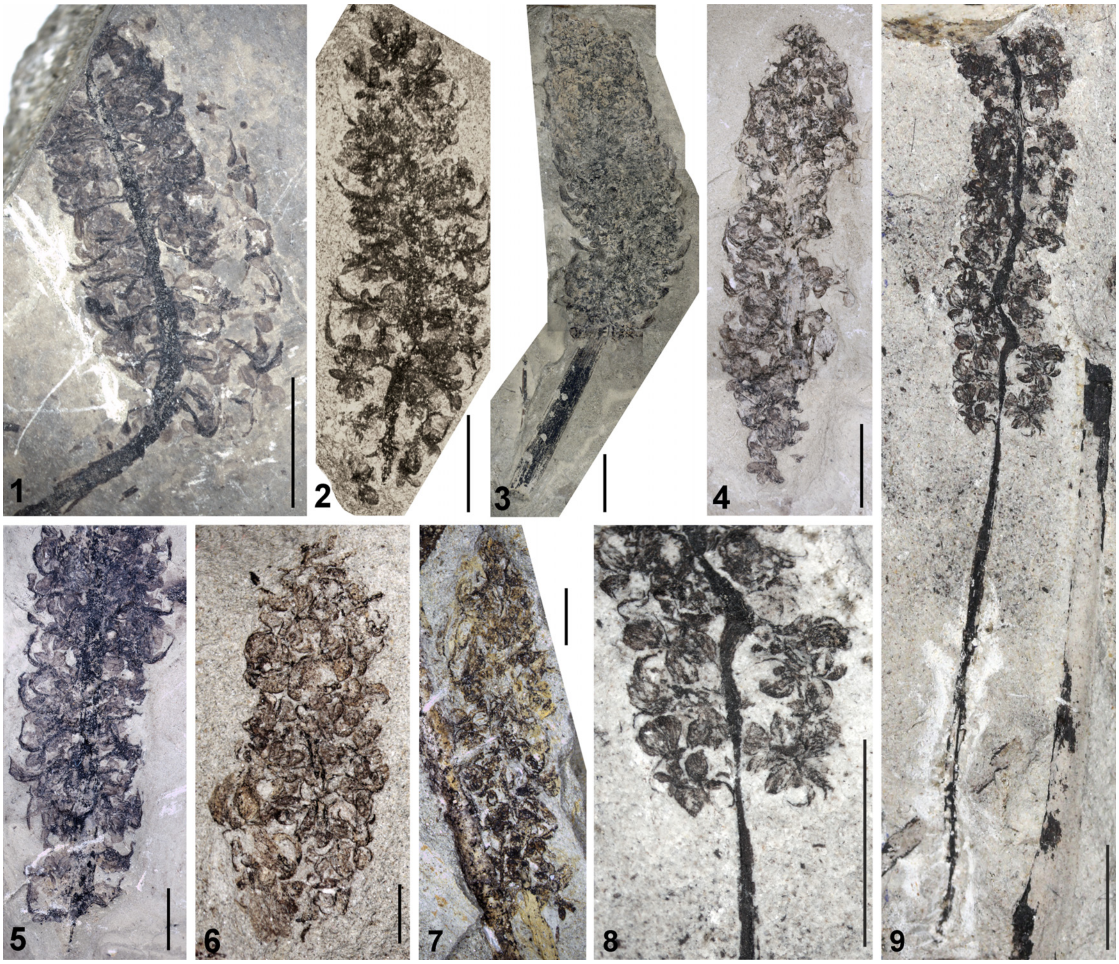

Plate I. Pollen cones of *Sorosaccus:*
1–7 – pollen cones, Irkutsk Coal Basin, East Siberia: 1–5 – *Sorosaccus sibiricus* Prynada, Ust'-Baley, lower part of the Prisayan Formation (Aalenian); 6, 7 – *Sorosaccus* sp., Vladimirovka, upper part of the Prisayan Formation (Aalenian-Bajocian); 8, 9 – pollen cone of *Sorosaccus* ex gr. *sibiricus* Prynada, Tyrma River Basin, Russian Far East, Dublikan Formation (Tithonian–Berriasian), 8 – details of microsporophylls from fig. 9. Specimen numbers: 1 – spec. BIN 139/6; 2 – spec. BIN 1434/414; 3 – spec. BIN 6a/84; 4 – spec. BIN 1434/410; 5 – spec. BIN 1434/415; 6 – spec. BIN 1434/1496–3; 7 – spec. BIN 1434/1493–3; 8, 9 – spec. 550/105.
Scale bars: 1–4, 9 – 5 mm; 5–8 – 2 mm.

In several places, we traced an uninterrupted transition from the thick areas to such thin areas through areas of an intermediate thickness of about 0.26 μm (Plate III, 12). Our interpretation is that the thick areas are a non-apertural exine, and the thin areas are an apertural exine. Our explanation is that the apertural exine is very thin, became easily torn and rolled after being torn. In other places, such rolls of thin exine appear unrelated to thick areas of the exine or we cannot decide to which of several adjacent thick exines they belong (Plate III, 11). These fragile regions can be detached from the rest of the pollen grain and preserved as patches. They easily folded and these folds can be cut several times by the same plane of section, and this is why we observe branching within such balls (Plate III, 1).

No subdivision into a tectum/infratectum/foot layer was detected in the overwhelming majority of the sections. The exine is nearly totally homogeneous in most pollen grains (Plate III, 1). Rounded holes are occasionally present (Plate III, 6, 7, 10). Of them, many are situated in the inner part of the exine, but in general their distribution is rather irregular (Plate III, 6), they are detected even between two tightly adpressed to each other faces of the exine (Plate III, 7). This is why we think that they are preservational rather than original features of this exine. Just in several places we have also observed different lacunae, which are short, narrow and orientated perpendicularly to the pollen surface (Plate III, 9) or a bit wider and orientated obliquely (Plate III, 12). There were few regions where we observed what we suppose to be unaltered alveoli (Plate III, 2–4), but innumerable homogeneous exines totally prevail. In addition, there are areas where the exines show an abrupt unnatural change in thickness (e.g., Plate III, 11). No endexine was detected.

Numerous orbicules were observed, a more electron dense central area was remarked in some of them (Plate III, 5). The orbicules are often associated with a thin lamella (Plate III, 8), but are also present on the pollen surface directly (Plate III, 1). It is not always easy to differentiate between these lamellae and detached thin areas of the exine (Plate III, 12). These lamellae differ in being even thinner, bearing numerous orbicules, not forming balls, and occurring on the external surfaces of pollen clumps. They occur also without orbicules, adpressed to pollen grains. This time, they mimic an endexine. However, they cannot be an endexine, since they are adpressed to the undulating (=external) surface of the exine (Plate III, 11). We think that they are the reason why the exine pattern is poorly visible under SEM: they reproduce the surface pattern allowing us to understand it, but they make it

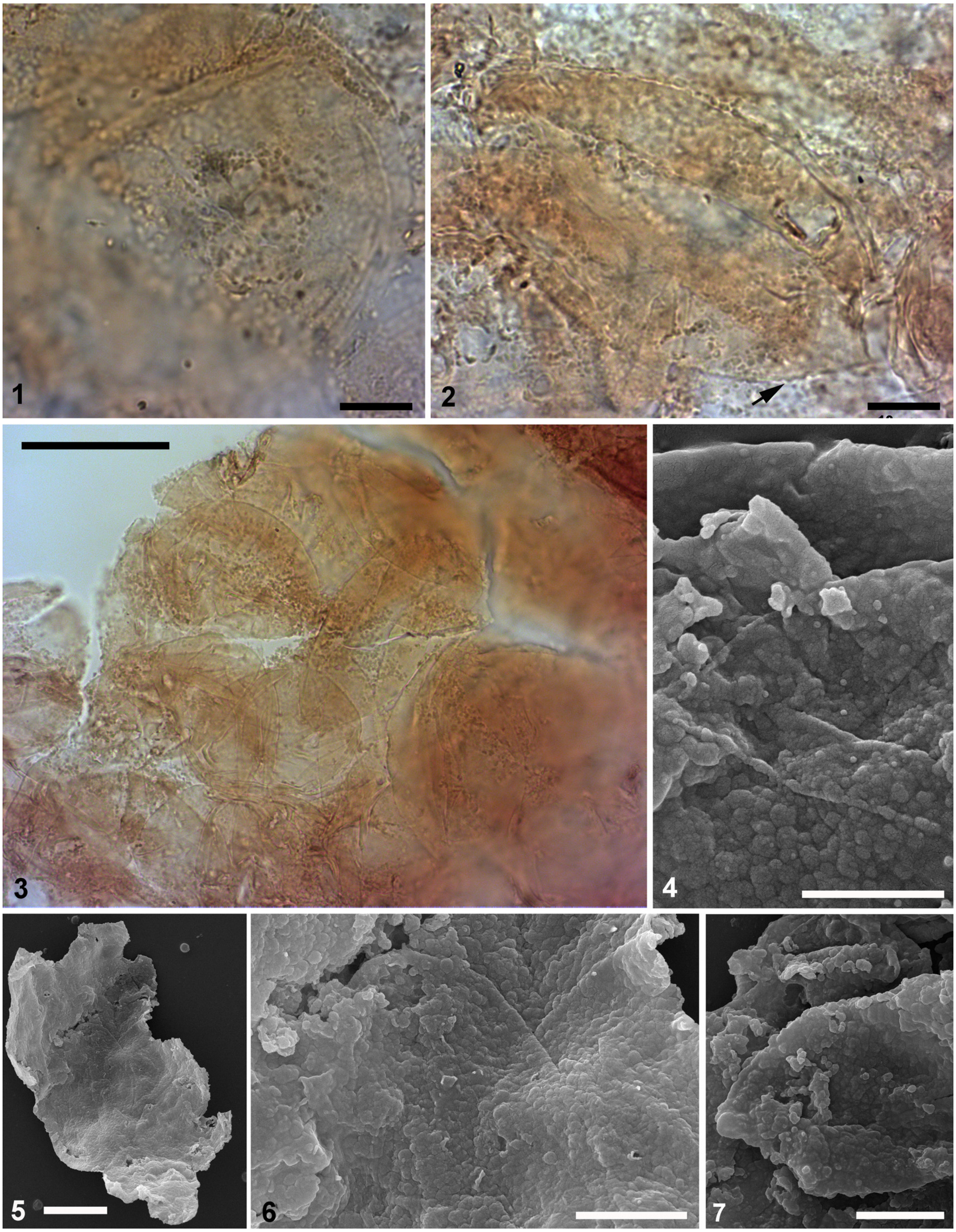

Plate II. *Sorosaccus sibiricus* Prynada, spec. BIN 6a/84, Ust'-Baley, lower part of the Prisayan Formation (Aalenian), *in situ* pollen grains, LM (1–3) and SEM (4–7). 1 – rounded pollen grain with an even contour in a clump of pollen grains, two more pollen are partly visible in the upper left and lower right corners of the figure, as well as numerous orbicules; 2 – boat-shaped pollen grain, which is probably folded by the sulcus, the only specimen where we noted a slightly undulated contour (arrow); 3 – pollen grains on the cuticle; 4 – pollen surface, a supposedly clean area is visible at the bottom of the figure; 5 – portion of the cuticle with embedded pollen grains, the central one is relatively undamaged; 6 – enlargement of Plate II, 5, the pollen surface seems to be masked by a supposed non-exinal material and orbicules; 7 – pollen grain, the surface is hidden under orbicules and non-exinal material.
Scale bars: 1, 2, 6, 7 – 10 μm; 3 – 50 μm; 5 – 25 μm; 4 – 5 μm.

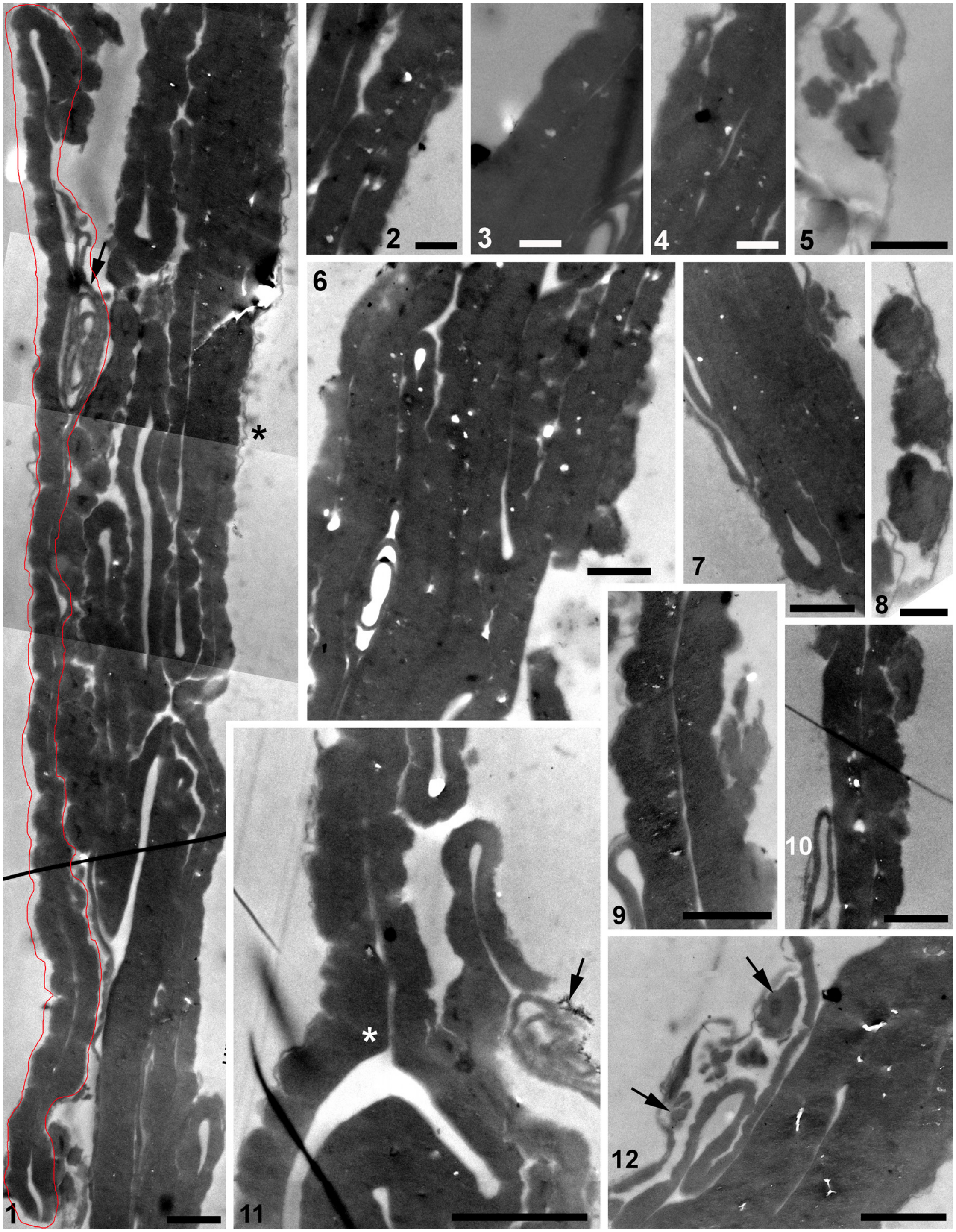

Plate III. *Sorosaccus sibiricus* Prynada, spec. BIN 6a/84, Ust'-Baley, lower part of the Prisayan Formation (Aalenian), *in situ* pollen grains, TEM. 1 – clump of compressed pollen grains is sectioned, their exine is predominantly homogeneous, the outer contour is weakly undulated, the surface is at places covered by non-exinal material (asterisk). Note the pollen grain to the left (marked with a red line), the exine becomes thinner and rolls into a ball (arrow) in the apertural region. Note numerous orbicules to the right from the pollen grain outlined by the red line; 2–4 – areas of sections with supposedly unaltered alveoli; 5 – orbicules associated with a non-exinal lamella, the centers of the orbicules are more electron dense; 6 – rounded holes, which, as we suppose, are preservational; 7 – rounded holes, some of them are situated at the boundary between tightly adpressed exines; 8 – orbicules associated with a non-exinal lamella; 9 – short narrow perforations, which we also consider preservational; 10 – rounded supposedly preservational perforations; 11 – abrupt change in the thickness of the exine (asterisk); non-exinal material covering the pollen surface is visible to the left, and a detached apertural exine rolled in a ball is present to the right (arrow); 12 – from the left to the right are visible non-exinal material, orbicules (arrows), a thinned apertural exine transforming into thicker exine, and a thick non-apertural exine of another pollen.
Scale bars: 1, 5–7, 9, 10, 12 – 1 μm; 2–4, 8 – 0.5 μm; 11 – 2 μm.

smoother. They probably represent tapetal remnants. LM photos show that both the exine and some other plant materials are present (Plate II, 3).

We incline to the view that the exines were compressed too strongly to reveal their true ultrastructure. We suspect that originally the exine was not homogeneous, but some alveoli were situated in the deep region of the ectexine, since many of rounded small holes occur deeper in the exine and those few alveoli that we considered as unaltered, but we cannot be sure about it. The Ust'-Baley pollen grains were extracted from the type material of the species, this is why it was very important to understand their exine ultrastructure, and we did our best for it, but we fear that the exines did not reveal their original ultrastructure. Nonetheless, we think that it is worthwhile to document the observed inner structure. We hope that as the information is accumulated, we will be able to interpret the Ust'-Baley pollen ultrastructure more successfully. This could become possible if more variants of exine preservation become known. When we are able to reconstruct a succession of such variants, starting from perfectly preserved and finishing by poorly preserved, showing a continuous deterioration of the exine ultrastructure, we will be able to interpret with confidence the final, worst-preserved members of this row.

Species: Sorosaccus sp.

Plates I, 6, 7; IV–VI

Synonymy and selected references:

2018 *Sorosaccus sibiricus* – Nosova et al., p. 6, pl. I, figs. 12, 16–18; pl. II, figs. 2–7, 9–14.

2020 *Sorosaccus sibiricus* – Kiritchkova et al., p. 107, pl. CXXIII, figs. 12, 16–18; pl. CXXIV, figs. 2–7, 9–14.

Locality and age: Vladimirovka, Irkutsk Coal Basin, East Siberia, Russia; upper part of the Prisayan Formation, Aalenian-Bajocian, Middle Jurassic.

Material studied: Coll. BIN 1434, specs. 1490-3, 1493-3, 1496-3.

Description: Pollen cones are elongated cylindrical (Plate I, 6, 7). The main axis is 0.5–1 mm in diameter, with a faintly striated surface. The basal part (free from microsporophylls) of the main axis is more than 5 mm long. Microsporophylls are arranged helically, at 30–50° to the main axis. The pollen cones without the basal sterile part are 13–16 mm long and 4–5.5 mm wide. The microsporophyll consists of a petiole with helically attached microsporangia (pollen sacs) and a distal lamina. It is difficult to calculate the number of microsporangia per microsporophyll since petioles of the microsporophylls are not visible, except the basal microsporophylls where the petioles are relatively thick (0.3–0.4 mm wide) and have six and more microsporangia (Plate I, 7). The distal lamina is thin, lanceolate with an acute apex. The microsporangium is oval, 0.6–1.1 × 0.3–0.7 mm.

Remarks. We have only tree moderately preserved pollen cones from Vladimirovka. They are slightly smaller than *S. sibiricus*. Additionally, the shape of the distal lamina of their microsporophylls is not clearly visible so it is difficult to compare them with those of *S. sibiricus*. In addition, we have found some differences in the structure of the in situ pollen grains (see below) extracted from these cones. Based on these we designate pollen cones from Vladimirovka as *Sorosaccus* sp.

In situ pollen. In transmitted light, we observed groups and individual pollen grains and measured 17 pollen grains (Plate IV, 1–7). We observed about 20 pollen grains with SEM and 6, with TEM. The pollen grains are ellipsoidal (Plate IV, 1, 7; Plate V, 1, 5), monosulcate (Plate IV, 5), and 37.7 × 59.5 μm (average) and 36.6× 60.2 μm (median) in size. The pattern of the exine as evident in transmitted light is finely granulate (Plate IV, 1, 2, 4–6). SEM shows that the surface pattern is formed by densely situated flat verrucae and is developed over proximal and lateral surfaces (Plate V, 2, 5, 6). The verrucae are roundly polygonal, varying from 0.5 to 1.6 μm in size; they are separated by narrow grooves about 0.1–0.2 μm wide (Plate V, 6). The sulcus is stretched from one extremity of the pollen grain to the other (Plate IV, 5, 6; Plate V, 2). Orbicules are occasionally present, ranging from 0.6 to 1.1 μm in diameter (Plate V, 4). Occasional orbicules about 0.4 μm in diameter were observed with TEM (Plate VI, 2, 3, arrows). An eroded surface of one of the pollen grains showed that granules of about 0.16–0.33 μm in diameter are present within the exine (Plate V, 3). Ultrathin sections revealed an ectexine and an endexine, which are sufficiently well-preserved and show an understandable ultrastructure (Plate VI, 3, 4). The ectexine is about 0.4–0.8 μm thick in non-apertural regions and is subdivided into a tectum, an infratectum, and a foot layer (Plate VI, 4). The ectexine has a wavy outer contour because of the sculptural elements; it reaches the maximal thickness over their summits and becoming thinner between them (Plate VI, 1, 3). The length of the sculptural elements varies from 0.3 to 0.8 μm. The tectum is continuous, varying in thickness from 0.17 to 0.38 μm. Its internal contour is also wavy; occasionally the tectum even touches the foot layer. The compartments of various sizes and outlines that are bounded by the tectum from the above and foot layer from below can be called alveoli of the infratectum (Plate VI, 4). Most often, they are 0.2–0.4 μm long, occasionally up to 0.9 μm. Fine granules are discernable within them (Plate V, 8; Plate VI, 4). The diameter of the granules usually varies from 0.05 to 0.09 μm, occasionally reaching 0.16 μm. The foot layer is about 0.13 μm. The endexine is more electron-dense than the ectexine. It is about 0.09 μm thick. We did not detect any traces of lamellations (Plate VI, 4). In the apertural region the exine is represented by an extended homogeneous thinning (Plate V, 7; Plate VI, 1).

Species: Sorosaccus ex gr. *sibiricus* Prynada

Plates I, 8, 9; VII, VIII

Synonymy and selected references:

1972 *Sorosaccus* ex gr. *sibiricus* – Krassilov, p. 97, pl. XIX, figs. 3, 8.

Locality and age: Tyrma River Basin, Russian Far East, Dublikan Formation, Tithonian–Berriasian, Upper Jurassic–Lower Cretaceous.

Material studied: Coll. 550, spec. 105.

Description: See Krassilov, 1972.

Remarks. The only pollen cone from Tyrma (Plate I, 8, 9) is very similar to *Sorosaccus sibiricus*, but we did not find a wide-oval distal lamina in the microsporophyll characteristic of this species. Taking this into account, as well as the different age of the Tyrma and Ust'-Baley remains, we cannot determine this cone with certainty as *S. sibiricus* and use the name *Sorosaccus* ex gr. *sibiricus* as was proposed by Krassilov (1972).

In situ pollen: Pollen grains are preserved in clumps together with a supposedly non-exinal material, which appears in transmitted light as threads bearing granules (orbicules?) or consisting of them. In their turn, the threads are occasionally fused in folded laminae. Threads covered with verrucae or consisting of them were also detected under SEM (Plate VII, 5). Since the pollen grains and this material are compressed in tight clumps, superimposed on each other, and similar in color, it was not easy to differentiate between them under LM. In transmitted light, we managed to discern with confidence boundaries of 14 monads, which are 22.4–43.3 × 40.2–76.7 μm, 32.37 × 58.31 μm (average) and 36.45 × 55.25 μm (median). Most pollen grains are boat-shaped, with relatively acute extremities (Plate VII, 3), but some are rounded-oval (Plate VII, 4). We discerned an unequivocal sulcus in eight of the measured pollen grains (Plate VII, 1). The finely granulate pattern of the exine is visible in transmitted light under ×100 (Plate VII, 1–4), and flat polygonal verrucae with narrow grooves between them are visible under SEM (Plate VII, 6). In places, the grooves are slightly wider (Plate VII, 6), and the verrucae can be occasionally bound with each other via narrow short connectives (Plate VII, 8). The tightly packed verrucae gradually transform into smaller and more distantly situated verrucae in the apertural region (Plate VII, 7).

The fact that the pollen grains in clumps are repeatedly folded and invaginated one into the others impedes our LM and SEM observations, but makes most difficult the understanding TEM sections, since we succeeded to trace only few closed (=intact, uninterrupted) contours (corresponding to the exine of particular pollen grains, like that marked with a red line in Plate VIII, 1, 14) among innumerable contours of

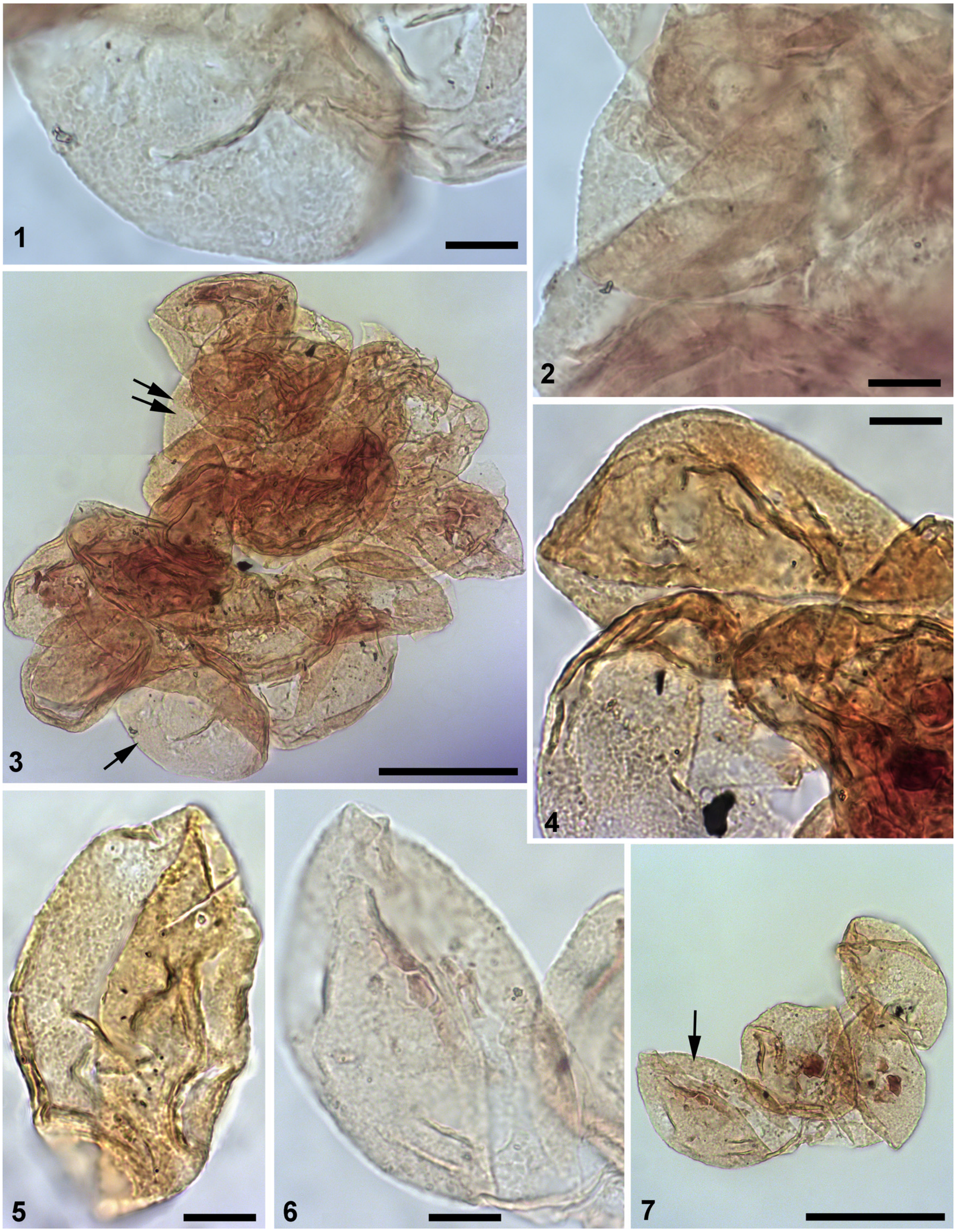

Plate IV. *Sorosaccus* sp., spec. BIN 1434/1493–3, Vladimirovka, Irkutsk Basin, East Siberia, upper part of the Prisayan Formation (Aalenian–Bajocian), *in situ* pollen grains, LM. 1 – enlargement of Plate IV, 3 (arrow), finely granulate pattern is visible; 2 – enlargement of Plate IV, 3 (two arrows), it is evident that the finely granulate pattern is related to the surface; 3 – a clump of pollen grains; 4 – several pollen grains, the upper one shows a distinct sulcus, the lower left pollen shows a distinct finely granulate pattern; 5 – individual pollen grain, the sulcus and finely granulate pattern are discernible; 6 – enlargement of Plate IV, 7 (arrow); 7 – group of four pollen grains.
Scale bars: 1, 2, 4–6 – 10 μm; 3, 7 – 50 μm.

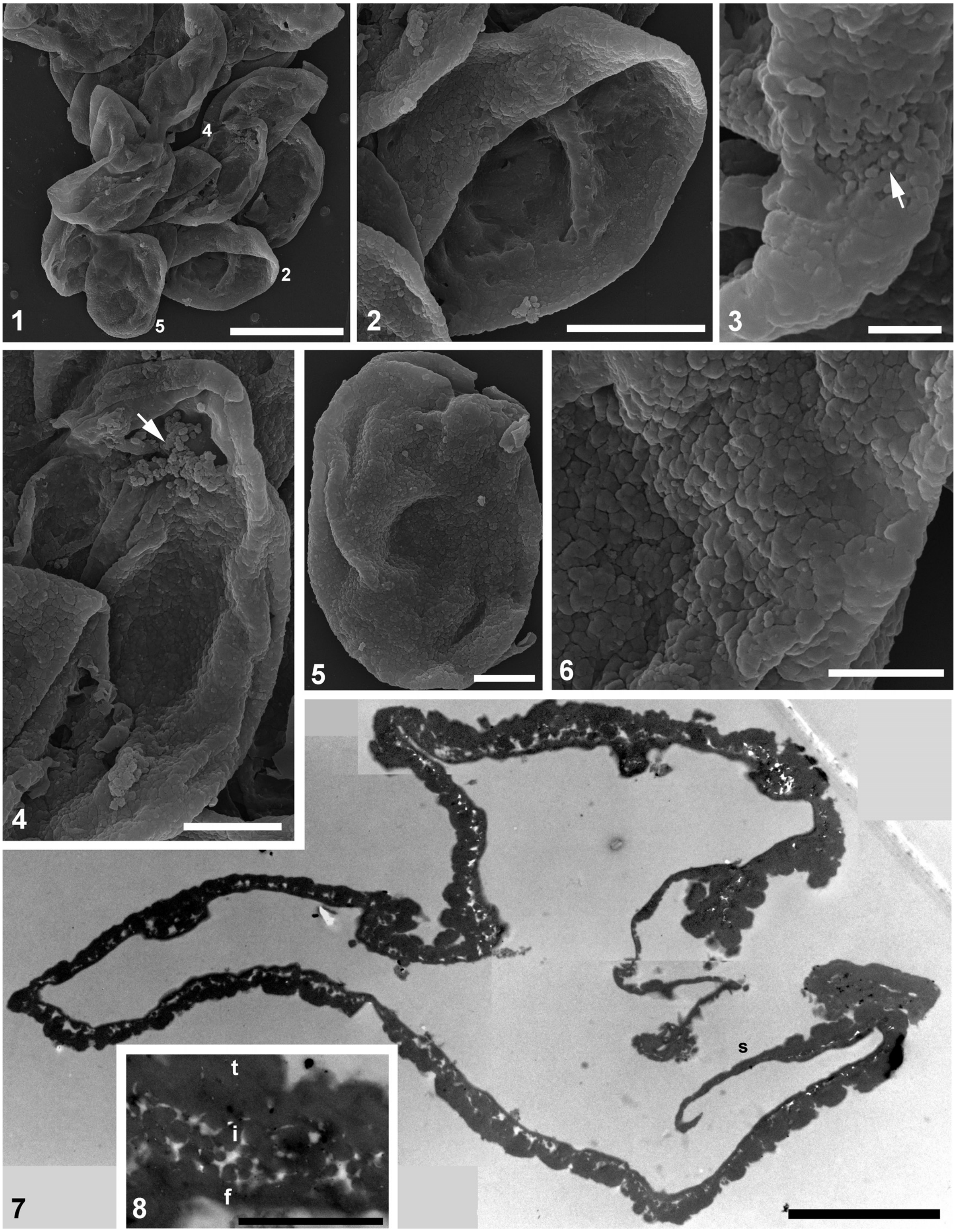

Plate V. *Sorosaccus* sp., spec. BIN 1434/1493–3, Vladimirovka, Irkutsk Basin, East Siberia, upper part of the Prisayan Formation (Aalenian–Bajocian), *in situ* pollen grains, SEM (1–6), TEM (7, 8). 1 – clump of pollen grains, see Plate IV, 3, digitals mark enlargements; 2 – enlargement of Plate V, 1, pollen grain shows the distal sulcus, compare Plate IV, 1; 3 – eroded surface of a pollen grain showing inner granules (arrow); 4 – enlargement of Plate V, 1, note orbicules (arrow); 5 – pollen grain in proximal view; 6 – enlargement of Plate V, 5, verrucae of the proximal surface; 7 – partially oblique section of a pollen grain, note the apertural region (s); the pollen belongs to the group shown in Plate IV, 7; 8 – area of a section of a different pollen grain from the group shown in Plate IV, 7, note a tectum varying in thickness (t), granules in the infratectum (i), and a thin and poorly distinguishable foot layer (f).
Scale bars: 1 – 50 μm; 2 – 20 μm; 3, 8 – 2 μm; 4, 5 – 10 μm; 6, 7 – 5 μm.

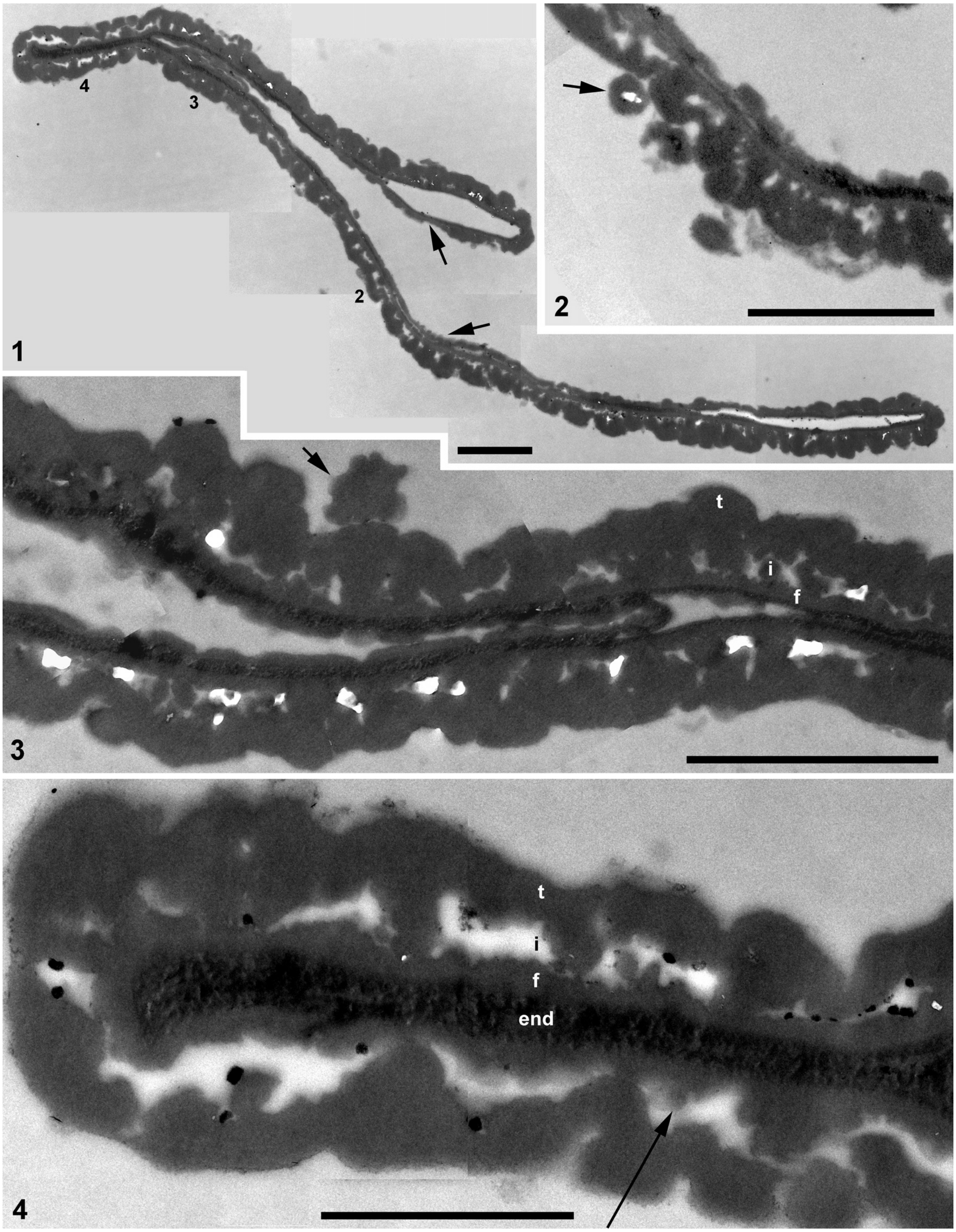

Plate VI. *Sorosaccus* sp., spec. BIN 1434/1493–3, Vladimirovka, Irkutsk Basin, East Siberia, upper part of the Prisayan Formation (Aalenian–Bajocian), *in situ* pollen grains, TEM. 1 – pollen grain shown in Plate IV, 5, the invaginated apertural area is indicated with arrows; digitals show the approximate position of enlargements; 2 – enlargement of a section of the pollen grain shown in Plate VI, 1, but made at a different level, arrow indicates one of the orbicules; 3 – area of a section of the pollen grain shown in Plate VI, 1, but made at a different level, note an orbicule (arrow), granules in the infratectum (i), the tectum (t) and foot layer (f); 4 – enlargement of Plate VI, 1, note a variable in thickness tectum (t), rare small granules (arrow) within the voluminous alveoli of the infratectum (i), and an electron dense endexine (end) without lamellations.
Scale bars: 1–3 – 2 μm; 4 – 1 μm.

supposed exines. There are many areas in composite sections of clumps where an exine first seems to correspond to one pollen grain, but then seems to continue into another exine, and this one to one more (Plate VIII, 1). Certainly, many pollen grains are torn, repeatedly folded, and/or cut several times by the same plane of the section. The external and internal contours of the exine differ from each other and this helps to understand the ultrastructure. The external one is undulating because it reproduces the surface pattern and the internal contour is more or less straight (Plate VIII, 14). Keeping in mind this difference, we were able to differentiate between them, even where we failed to trace an uninterrupted exine of a given pollen grain. Extended thinned areas within exine obviously represent apertural regions. Keeping in mind these facts, we realized that the exines of several pollen grains that were torn via apertural thinning were occasionally turned inside out (not shown).

Rare solid orbicules are detected in sections (Plate VIII, 13, 14). Where present, they additionally help to differentiate between the external and internal surfaces of the exines, since they occur on the external surface. However, some of them also are associated with a thin short and supposedly non-exinal lamella (Plate VIII, 13). These structures correspond to threads bearing orbicules that we observed in LM and SEM (Plate VI, 5).

The ectexine in non-apertural regions varies in thickness from 0.16 to 0.63 μm because of the undulating external contour. The ectexine appears nearly homogeneous, with occasional lacunae (Plate VIII, 1, 13). We observed several variants of hollows, some of which were interpreted as preservational. In particular, there were cleavages situated more or less perpendicular to the exine surface and passed through two or more exines (Plate VIII, 2, 3). It was easy to conclude that they were formed when the exines were already devoid of the living content and compressed to each other. Similar, but shorter, cleavages are situated within one exine and pass it perpendicularly from the outer to the inner surface or nearly to the inner surface (Plate VIII, 4, 5, 7). Keeping in mind their similarity to the longer cleavages, we conclude that both are preservational. Obliquely passed cleavages occur very rarely, they also pass from the external to the internal surface and, since they differ from the prevailing variant of hollows that are present in the exine, we treat them as preservational as well (Plate VIII, 14, lower left corner).

Although the exines are predominantly homogeneous, at places sublayers are discerned in the non-apertural ectexine: a tectum, an infratectum, and a foot layer (Plate VIII, 6, 8–12). The tectum is quite prominent; it varies in thickness due to the sculpturing. Since we disregard the artificial hollows discussed above, we think that only quite rare unaltered alveoli arranged in one row are present in the central and inner portion of the ectexine, bounded by a thin and constant in thickness foot layer (Plate VIII, 8–12). The alveoli are quite irregular in outlines, many of them are narrow (more or less perpendicular to the pollen surface), but become wider towards the foot layer assuming a shape of a triangle (more often) or a polygon (rare) with a wider base, as if big fused granules or other robust structural elements like stalactites hang from the tectum and the alveoli are spaces between them. We observe small rounded elements within the alveoli in few regions of composite sections (Plate VIII, 8, 9), but alveoli without any content prevail. We think that these rounded elements are more probably extremities of the bigger structural elements cut perpendicularly rather than independent small granules.

The endexine is lacking in most pollen grains and preserved only in places in few, usually in the apertural and equatorial areas (Plate VIII, 8, 14). Its poorer preservation is probably the reason why the exines are so often torn and turned inside out. If the endexine is the only layer that lines the apertural floor, when it disappears the exine loses its integrity. We observed a solitary thin (0.04 μm) lamella that is slightly less electron-dense than the overlying ectexine (Plate VIII, 8).

Proximally, the ectexine is thicker than in other areas. Towards the aperture, the ectexine changes as follows. First, its thicker areas (under verrucae) become two times thinner than proximally and its thinner areas (under grooves) become longer (Plate VIII, 1). A thinner ectexine often forms folds (Plate VIII, 14). Closer to the aperture, the ectexine transforms into a patchy structure, without alveoli and differentiation into sublayers. In some pollen grains, the endexine was repeatedly cut in one and the same plane of section because it forms folds (Plate VIII, 14). Since it is cut at different angles, it varies in thickness from 0.04 to 0.27 μm, with the smaller value corresponding to the transverse section. Where it is cut obliquely and reaches 0.27 μm in thickness, its less intense electron density (by comparison to the ectexine) is more obvious.

6. Discussion

6.1. Variations among the materials under study

The pollen cones that yielded the pollen grains under study come from three localities, one of which is distant from the two others in terms of geography and geological age, but they are similar enough to be assigned to the same genus, if not species. However, we have revealed significant variations between the pollen grains from the three sources. The worse thing is that we have faced severe difficulties in understanding the exine ultrastructure of the Ust'-Baley and Tyrma materials (*Sorosaccus sibiricus* and *S.* ex gr. *sibiricus*, correspondingly), which, as we suppose, are more probably related to their preservation. Therefore, it was needed to imagine how their ultrastructures looked in the original state and to compare these reconstructed ultrastructures to understand the taxonomic value of the differences among them. We have not fully succeeded in these reconstructions. Nonetheless, we think that the right choice is to document the observations rather than to discard them. We stress again that even if obtained data are difficult to interpret at the moment, it is important to make them available for consideration of subsequent scientists (Zavialova et al., 2022).

The pollen grains from Vladimirovka (*Sorosaccus* sp., Plate IV, 3, 5–7; Plate V, 1, 5) and Tyrma (*S.* ex gr. *sibiricus*, Plate VII, 1) are similar in general morphology, size and outlines; pollen grains from Ust'-Baley (*S. sibiricus*, Plate II, 1–3) are somewhat larger and in general more rounded in outline, boat-shaped specimens occur more rarely among them. By light-microscopical observations, the sulcus is obvious in Vladimirovka pollen, visible in some of Tyrma pollen grains, and its presence can also be assumed in Ust'-Baley pollen; TEM clearly shows that an extended aperture is present in all pollen grains (Plates III, 1, V, 7; Plate VI, 1; Plate VIII, 14). In sum, all pollen grains are monosulcate, even though it is not always detectable in LM or SEM.

The pollen grains have a developed surface pattern. In case of Vladimirovka (Plate IV, 1, 2) and Tyrma pollen (Plate V, 3, 4), this can be discerned even in LM, under ×100 oil immersion, as a finely granulate pattern, but the Ust'-Baley pollen grains appear psilate in transmitted light (Plate II, 3). SEM clearly reveals flat polygonal verrucae on the Vladimirovka (Plate V, 6) and Tyrma pollen (Plate VII, 6), which are slightly larger in the latter. The surface of Ust'-Baley pollen is difficult to evaluate with confidence since it is mostly hidden under the non-exinal material (Plate II, 6), but TEM reveals the undulated outer contours in the pollen grains from the three localities (Plate VI, 2; Plate VIII, 14; Plate III, 6). Orbicules are occasionally present on the Vladimirovka (Plate V, 4; Plate VI, 2, 3) and Tyrma (Plate VII, 2; Plate VIII, 14) pollen and numerous on the Ust'-Baley pollen (Plate III, 1). The orbicules are often associated with non-exinal lamellae in the Tyrma (Plate VIII, 13) and Ust'-Baley (Plate III, 5, 8) pollen.

The ectexine is clearly subdivided into a tectum, an infratectum and a foot layer in the Vladimirovka pollen (Plate VI, 4). The exines of the Tyrma pollen appear nearly homogeneous, merely in a few areas of a few pollen grains we distinguished the tectum/infratectum/foot layer subdivision (Plate VIII, 1, 6). This is even more true for the Ust'-Baley pollen grains, which exines mostly appear homogeneous (Plate III, 1), and we found merely several small areas where the subdivision into

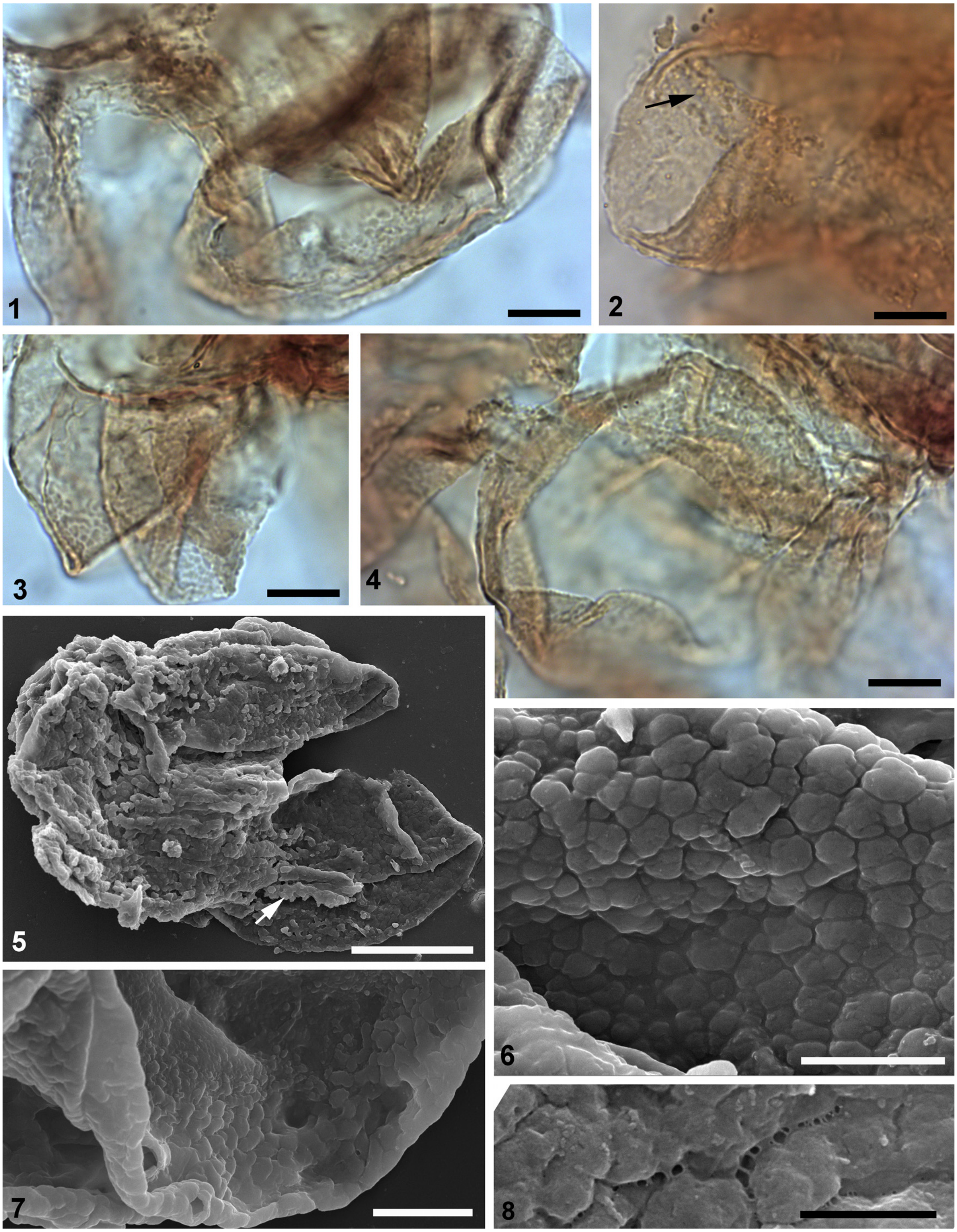

Plate VII. *Sorosaccus* ex gr. *sibiricus* Prynada, spec. 550/105, Tyrma River Basin, Russian Far East, Dublikan Formation (Tithonian–Berriasian), *in situ* pollen grains, LM (1–4), SEM (5–8). 1 – two pollen grains, monosulcate state is evident in the right pollen; 2 – pollen grain with an open sulcus, note supposed orbicules (arrow); 3 – two boat-shaped pollen grains, the exine pattern is evident; 4 – rounded-oval pollen grain in the center, other pollen grains of the clump are partly visible around it; 5 – several pollen grains detached from a clump, threads with verrucae (arrow) partly cover the pollen surface; 6 – pollen surface with flat polygonal verrucae; 7 – verrucae become smaller towards the aperture; 8 – pollen surface, note connectives that bound verrucae. Scale bars: 1–4 – 10 μm; 5 – 20 μm; 6, 7 – 5 μm; 8 – 2 μm.

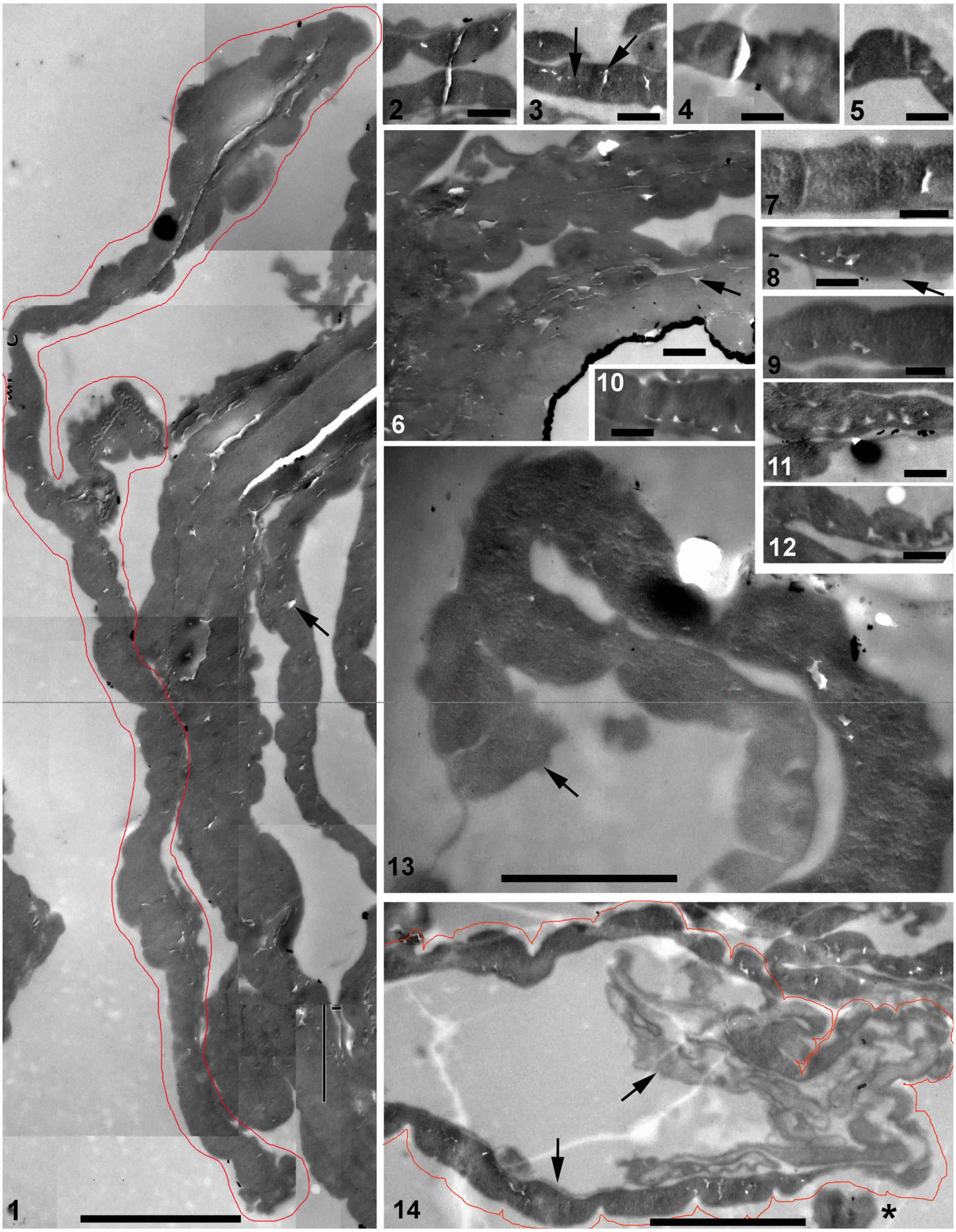

Plate VIII. *Sorosaccus* ex gr. *sibiricus* Prynada, spec. 550/105, Tyrma River Basin, Russian Far East, Dublikan Formation (Tithonian–Berriasian), *in situ* pollen grains, TEM. 1 – clump of compressed pollen grains, aperture region (to the right) is visible in a pollen grain indicated by a red line, the undulated outer surface of the pollen is obvious, only ectexine is preserved, rare alveoli (arrow) are present; 2–5, 7 – areas of the ectexine with various gaps interpreted as artificial; 2 – areas of exines of two pollen grains are visible. Note from the top to the bottom: a thin apertural exine, a compressed gametophyte cavity, and a thick non-apertural exine with the outer undulated surface of the first pollen and a thick non-apertural exine of the second pollen; a cleavage continues through both pollen grains; 3 – two exines are so strongly compressed that the gametophyte cavity was obliterated, vertical arrow points to its approximate position. Two cleavages continue through both exines, one of them is indicated by an obliquely directed arrow; 4 – a cleavage that passes one exine completely; 5, 7 – similar cleavage that passes one exine, but not completely; 6 – exines of two compressed pollen grains; outer pollen surfaces are undulated. One can distinguish a prominent tectum varying in thickness because of the undulations, rare alveoli (e.g., arrow) of the infratectum, and a thin foot layer of a constant thickness; 8–12 – areas of the exine with supposedly unaltered alveoli, the external surface is to the top of the figures: 8 – a granule rests on the foot layer. A thin less electron-dense layer to the bottom of the figure represents remnants of the endexine (arrow); 9–12 – endexine is not preserved; 11 – a thin homogeneous layer below the exine layer with alveoli is the opposite (apertural) face of the pollen grain; 13 – non-apertural area of a pollen, the gametophyte cavity is compressed, but still present. The outer surface is distinctly undulated. Several unaltered alveoli can be seen. A few orbicules, associated with a non-exinal lamella, are present (arrow) near the external surface of the pollen; 14 – a section of a pollen grain (its external surface is reproduced with a red contour), note the apertural area, where the endexine (arrows) is preserved, being less electron dense than the ectexine, varying in thickness and showing folds because of the oblique orientation of the plane of section, an orbicule is present (asterisk).
Scale bars: 1, 14 – 2 µm; 2–6, 8, 10 – 12 – 0.5 µm; 7, 9 – 0.25 µm; 13 – 1 µm.

three sublayers can be assumed (Plate III, 2–4), with much less certainty than for the Tyrma pollen. If to consider that these several areas with a non-homogeneous ectexine in the Tyrma and Ust'-Baley pollen grains are remnants of the original ultrastructure, then they differ from the Vladimirovka pollen by the tectum/ectexine ratio: their tectum occupies a greater part of the ectexine than that in the Vladimirovka pollen grains. In the Vladimirovka pollen grains, we observed small granules in the infratectum (Plate V, 8). We found only two areas in numerous sections of the Tyrma pollen with small rounded elements within the infratectum (Plate VIII, 8), and nothing of this kind was observed in the Ust'-Baley pollen. We think that small granules in the infratectum characterize only the Vladimirovka pollen, but the poor preservation of the Tyrma and Ust'-Baley pollen grains should not be forgotten.

The aperture is formed similarly in all pollen: it is a thinned homogeneous ectexine. The three pools differ as far as concerns the endexine: the Vladimirovka pollen shows a homogeneous, more electron-dense endexine that develops over the entire perimeter of the pollen grain and shows a constant thickness (Plate VI, 4). The endexine is preserved in some pollen grains, only in places, usually distally and, occasionally, equatorially, in the Tyrma pollen grains (Plate VIII, 8, 14); it is homogeneous and less electron-dense than the ectexine. No endexine was found in the pollen grains from the Ust'-Baley locality.

There are some hints allowing one to suggest that the Tyrma and Ust'-Baley pollen grains are less mature than the Vladimirovka pollen, such as numerous orbicules, the presence of non-exinal lamellae associated with orbicules, the occurrence of the pollen grains in clumps and impossibility to disintegrate them into monads, the absence of the endexine in the Ust'-Baley pollen and an only occasionally preserved and less electron-dense endexine in the Tyrma pollen. On the other hand, explanations can be generated that are not related to the alleged immature state of the pollen grains. Orbicules are known to occur on mature pollen grains as well, even on dispersed ones. Pollen grains can be compressed during fossilization and preserved in clumps because of this. The endexine is often preserved less perfectly than the ectexine, because of the difference in their chemical compositions. A less electron-dense endexine was described in slightly immature conifer pollen (Kurmann, 1990), but such a difference in the electron density was also reported for mature pollen grains of angiosperms (e.g., Denk and Tekleva, 2006). In addition, although the pollen grains are preserved in clumps, they are not in tetrads, that means that the endexine already should have been initiated. The exines of the pollen grains from Tyrma and Ust'-Baley are predominantly or nearly totally homogeneous, by contrast to the Vladimirovka pollen. If to consider Tyrma and Ust'-Baley as less mature and the Vladimirovka as more mature pollen grains of ginkgoaleans that belonged to the same taxon or closely related taxa, the exines of the less mature pollen grains should have appeared less homogeneous. Thus, the exine of immature pollen grains of the modern *Ginkgo* contains much more cavities that the mature exine (Meyer, 1977). Therefore, although immature state of the Tyrma and Ust'-Baley pollen grains cannot be excluded, the appearance of their ultrastructure is strongly affected by preservation.

The pollen grains from the three localities are light in color, that means that the level of the organic matter maturation is low, allowing to expect a sufficiently well-preserved ultrastructure of the exine. However, our experience with Upper Triassic Circumpolles from several European sites (Zavialova and Roghi, unpublished data) shows that the exine ultrastructure can be poorly preserved (as we suppose secondarily homogenized) even if the organic matter is immature. In the Tyrma and Ust'-Baley pollen, we observed with LM and SEM numerous marks of corrosion. With TEM, we observed occasional cleavages in the Tyrma (Plate VIII, 2–5) and Ust'-Baley (Plate III, 1) exines and irregularly scattered rounded perforations (Plate III, 6) and unnatural variations in thickness (Plate III, 11) in the Ust'-Baley exines as well as exines that were torn via the aperture thinning and turned inside out. The exines are so strongly compressed that the gametophyte cavities of the pollen grains often appear as narrow slits or cannot be detected as well as boundaries between individual pollen grains. These hints point to the poor preservation of the Tyrma and Ust'-Baley pollen grains.

For the comparison with earlier published data, we have decided to use only the information obtained from the Vladimirovka locality, since we are sure only in the interpretation of its exine ultrastructure among the three studied materials. As to the Tyrma and Ust'-Baley pollen grains, we think that their original ultrastructure was not homogeneous, but we are not sure how it looked like. Currently, we do not see the way of the post-mortal transformation from the ectexine we observed in the Vladimirovka pollen to the ectexine we observed in the Tyrma and Ust'-Baley pollen, and this leads us to an option that the parent plants might have been not as closely related as the morphology of the cones suggest. Our hope is to find more materials which would show transitional stages of deterioration of the exine ultrastructure, and to reveal by their study how the transformation took place, if it did. The pollen grains from three localities are probably similar by their exine surface (this is certain for Vladimirovka and Tyrma and is supposed for Ust'-Baley), which is a hint for the closeness of their parent plants. However, ultrastructural characters are commonly considered as more taxonomically valuable than sculptural ones.

6.2. Comparison with published data

In situ pollen grains of *Sorosaccus* were previously studied in LM. Thus, Harris (1935) described pollen grains of *S. gracilis* as oval, 90 × 60 μm, with a very thin and very finely granular (almost smooth) exine and a longitudinal fold. Pollen grains of *S. naitoi* are subspheroidal, about 35 × 30 μm in diameter (Kon'no, 1962). Krassilov (1972) noted that in situ pollen grains of *S. umaltensis* were broadly oval to elongated, the extremities varied from rounded to narrowed. The exine was psilate and relatively thin. The sulcus was occasionally opened, with thickened margins. The dimensions were 49–50 × 27–36 μm. The first data on the surface pattern of *S. sibiricus* pollen grains, on the basis of SEM observations, were provided by Nosova et al. (2018).

The present study is the first to observe *Sorosaccus* pollen in TEM, which is important for the differentiation of ginkgoalean pollen from the Mesozoic monosulcate boat-shaped pollen grains of other affinities on the basis of the ultrastructural characters of the exine. By previous data on the modern and fossil members, we believed that ginkgoalean pollen can be differentiated by a ratio of ectexinal sublayers (a thick homogeneous tectum, a thin infratectum of one row of structural elements, and a thin foot layer) in combination with an ectexine that is greatly reduced in the aperture region (Zavialova and Nosova, 2019). Although a thinned apertural ectexine is a very common feature in gymnosperms, it allows one to differentiate ginkgoalean pollen grains from some cycadalean pollen grains; for example, pollen grains of *Cycandra profusa* Krassilov et Delle and *Androstrobus prisma* Thomas et Harris, although boat-shaped, do not possess an apertural thinning of the exine (Tekleva et al., 2007; Zavialova and van Konijnenburg-van Cittert, 2012). A thin infratectum of *Ginkgo biloba* is constituted of pillars, most of which hang from the inner surface of a thick tectum into the infratectal cavity and reach a thin foot layer; some pillars arise from the foot layer (Zavialova et al., 2011). An ectexine that is more or less similar to that of *G. biloba* was revealed in pollen grains discovered in ginkgoalean seeds from the Jurassic of Uzbekistan (Zavialova et al., 2014) and in an unnamed supposedly ginkgoalean pollen organ from the Jurassic of Siberia (Zavialova and Nosova, 2019). Zavialova et al. (2011) studied the exine ultrastructure of presumably ginkgoalean pollen grains from a coal seam formed by ginkgoalean foliage, the Early Cretaceous deposits of the Russian Far East. In course of their study of in situ pollen grains of *Schidolepium* cones from the Jurassic of Siberia, Zavialova and Nosova (2021) found a small clump of boat-shaped monosulcate pollen along with innumerable in situ saccate pollen grains of this conifer; the boat-shaped pollen grains were interpreted as contamination supposedly brought by a non-specific pollinator from a ginkgoalean plant. The Far-Eastern and Siberian pollen grains also demonstrated a thick tectum, a thin infratectum, and a thin foot layer, but their infratectum is represented by one row of large granules between the overlying and underlying layers (Zavialova et al., 2011; Zavialova and Nosova, 2021).

The pollen grains under present study, although boat-shaped and monosulcate, differ significantly by their exine ultrastructure from other ginkgoaleans. Before the present study, the available data on the supposedly ginkgoalean exine ultrastructure have formed quite a uniform picture, with the nature of the infratectal elements as the only important variable. The *Sorosaccus* pollen grains differ from other ginkgoalean pollen grains not only by the exine ultrastructure, but also by their surface pattern, which is visible even in transmitted light. Finely granulate pollen grains were reported from the Early Jurassic ginkgoalean *Stachyopitys preslii* Schenk (van Konijnenburg-van Cittert, 2010). It is quite possible that these pollen grains are more similar by ultrastructural features to the pollen grains of *Sorosaccus* than *G. biloba* and other ginkgoalean pollen grains with the known exine ultrastructure (Zavialova et al., 2014; Zavialova and Nosova, 2019). Only few pollen grains were extracted by van Konijnenburg-van Cittert (2010); and our attempt to extract pollen from microsporophylls kindly provided by Prof. van Konijnenburg-van Cittert did not yield pollen. So far, the comparison between *Sorosaccus* and *Stachyopitys* Schenk pollen is restricted to light-microscopical information. The pollen cones of *Sorosaccus* are comparable to those of *Stachyopitys* (Kirchner and van Konijnenburg-van Cittert, 1994; Schweitzer and Kirchner, 1995; Anderson and Anderson, 2003). In contrast to *Sorosaccus*, the microsporophylls of *Stachyopitys* are located quite rarely on the main axis, and microsporangia are arranged radially at the end of the microsporophyll axis, there is no free distal lamina.

Pollen grains associated with the Late Cretaceous ginkgoalean ovuliferous reproductive structure *Nehvizdyella bipartita* J. Kvaček, Falcon-Lang et Dašková from the Czech Republic are also not psilate (Kvaček et al., 2005). This find may represent another indirect indication that pollen grains of ginkgoaleans were more diverse than we previously thought. Regretfully, only few pollen grains were found by Kvaček et al. (2005), and it is impossible to accomplish a TEM study. It also should be pointed out that these pollen grains were found adhered to the seed surface, and, thus, their belonging to the plant is less secure. For example, monosulcate pollen grains found by Crane and Herendeen (2009) on the surface of interseminal scale of *Williamsoniella coronata* Thomas differ at least by their surface characteristics from pollen grains extracted from microsporangia of this species (Zavialova et al., 2009) and most probably did not belong to this plant.

Nosova and Tekleva (2022) have studied species of *Aegianthus* from several Jurassic localities of Siberia, including Ust'-Baley, from which *Sorosaccus sibiricus* is studied in the present paper. The attribution of this genus to a high-rank group of gymnosperms is still under debate, with ginkgoaleans among possible variants (Nosova and Tekleva, 2022). Similarly to *Sorosaccus*, its male cones also yield monosulcate boat-shaped pollen grains, but they are smaller than the pollen grains under study and possess a surface pattern that can be described as psilate or scabrate in LM and scabrate to granulate with rare perforations in SEM. The surface sculpture of *Sorosaccus* pollen is more pronounced: verrucae are visible in SEM, and this pattern is also distinguishable in transmitted light, under × 100 oil immersion. This is clearly visible in pollen grains of *Sorosaccus* sp. from Vladimirovka and *S.* ex gr. *sibiricus* from Tyrma, but not in *S. sibiricus* from Ust'-Baley. In sum, there is a hope that one can differentiate between dispersed pollen grains of the two genera by size in case of poor preservation or by size and exine pattern in case of sufficient preservation. The ectexine of the *Aegianthus* pollen has a tectum of a moderate thickness continuously grading into a prominent infratectum with large granules or columella-like elements and a thin foot layer and appears quite different from the exine ultrastructure under present study. The tectum/ectexine ratio in *Aegianthus* pollen is lower than we originally hypothesized for the ginkgoalean type of the exine ultrastructure (Zavialova et al., 2011; Zavialova and Nosova, 2019), but this criterion does not work for *Sorosaccus* pollen as well. Now we think that the ultrastructural data do not exclude the ginkgoalean affinity of *Aegianthus*, since ginkgoaleans were probably more diverse in terms of the exine ultrastructure and were characterized by more than one set of ultrastructural characters of the exine.

An exine ultrastructure that is very similar to that observed in the pollen grains of *Sorosaccus* sp. from Vladimirovka was reported by Zavada and Dilcher (1988) for one of several dispersed pollen types they studied from the Late Cretaceous of North Dakota (USA). Pollen grains of this dispersed species, *Granamonocolpites asymmetricus* Pierce, show a wavy tectum that is very similar to what we observed in our material, an alveolate infratectum with occasional small granules within alveoli, a thin homogeneous foot layer, and a supposedly homogeneous endexine of constant thickness. We think that these similarities testify that the parent plant of this dispersed pollen might belong to the same group as *Sorosaccus*.

So far, it seems that the exine ultrastructure often works well enough for differentiation of the ginkgoalean pollen from the Mesozoic boat-shaped pollen grains of other botanical affinities. Ginkgoalean pollen can be confidently differentiated from cycadalean pollen (Hill, 1990; Archangelsky and Villar de Seoane, 2004; Tekleva et al., 2007; Zavialova and van Konijnenburg-van Cittert, 2012, 2016; Zavialova et al., 2016), which have a foveolate-fossulate surface, a narrow tectum, and elongated alveoli, arranged perpendicular to the exine surface, clearly visible in transverse sections and appearing as rounded alveoli in oblique sections. Ginkgoalean pollen can be differentiated from bennettitalean pollen, because its ectexine is not subdivided into a tectum, an infratectum and a foot layer, and is either homogeneous as in *Williamsoniella coronata* (Zavialova et al., 2009) or composed of numerous small densely packed granules as in *Cycadeoidea dacotensis* (MacBride) Ward and *Leguminanthus siliquosis* (Leuthardt) Kräusel (Ward et al., 1989; Osborn and Taylor, 1995). The pollen of the peltaspermalean *Antevsia zeilleri* (Nathorst) Harris (Zavialova and van Konijnenburg-van Cittert, 2011) is more challenging, because its ultrastructure has much in common with that of modern *Ginkgo* and similar fossil ginkgoalean pollen, but not with *Sorosaccus* sp.; other pollen types known in peltasperms are saccate and/or striate and, thus, are very different even by the general morphology from any ginkgoalean pollen. The *Sorosaccus* sp. pollen clearly differs from pollen grains of the pentoxylalean *Sahnia laxiphora* Drinnan et Chambers (Osborn et al., 1991) by the surface pattern and ratio of ectexine sublayers, as well as by the ultrastructure since the thick tectum of the *S. laxiphora* pollen grades into a granular infratectum continuously.

Pollen cones of *Sorosaccus* differ considerably from those of seed ferns (Harris, 1964; Kirchner and Muller, 1992; Taylor and Taylor, 2009, etc.), Mesozoic Cycadales (van Konijnenburg-van Cittert, 1993; Schweitzer et al., 2000; Deng et al., 2014, etc.), Bennettitales (Delevoryas, 1963; Harris, 1969; Taylor et al., 2009, etc.), Leptostrobales (Krassilov, 1972; Taylor et al., 2009) and Mesozoic conifers (Grauvogel-Stamm, 1969; Maheshwari and Meyen, 1975; Taylor et al., 2009, etc.), and are comparable with the Mesozoic ginkgoalean *Stachyopitys* (see the comparison above). *Sorosaccus* resembles the Cretaceous *Ginkgo liaoningensis* (Liu et al., 2006) and the modern *G. biloba* by the morphology of microsporangia; however, microsporangia of *Sorosaccus* are more numerous and arranged on the microsporophyll in a different way than two to four microsporangia of *G. liaoningensis* and two microsporangia of *G. biloba*, which are situated on the abaxial side of the microsporophyll.

7. Conclusions

We believe that gymnosperm groups that are characterized by monosulcate boat-shaped pollen grains (such as cycads, ginkgoaleans, bennettites, and several others) can be differentiated by the fine morphology of their pollen, mostly by their exine ultrastructure. In particular, the previous studies show that ginkgoalean pollen is characterized by a certain ratio of ectexinal sublayers (a thick homogeneous tectum, a thin infratectum of one row of structural elements, either pillars as in *Ginkgo biloba* or granules in one row as in pollen grains from a coal seam in the Russian Far East, and a thin foot layer) plus a thinned apertural ectexine and an indistinct surface pattern. Freshly obtained data on *Sorosaccus* in situ pollen have revealed another assemblage of characters, with a less prominent tectum by comparison to underlying sublayers, an infratectum with small granules within the alveoli, and a prominent verrucate surface pattern that is distinguishable even in transmitted light. This testifies to a greater morphological diversity of the group than we earlier thought. The obtained information on in situ ginkgoalean pollen can be helpful for understanding the affinity of some dispersed monosulcate pollen, not only with available ultrastructural information, but also those observed in routine palynological analysis, since the revealed surface pattern is assessible via light microscopy.

Data availability

Data will be made available on request.

Declaration of Competing Interest

The author declare that there is no conflict of interest.

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