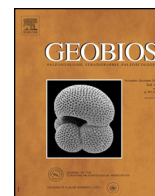




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## Research paper

# The morphology and ultrastructure of Jurassic *in situ* ginkgoalean pollen<sup>☆</sup>



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## ABSTRACT

A fragmentary pollen organ with four to six microsporangia is discovered from the Middle Jurassic of the Irkutsk coal basin, Siberia. The *in situ* pollen grains are boat-shaped, monosulcate, and with a nearly psilate surface. The non-aperture ectexine is composed of a thick solid tectum, a thin infratectum, and a thin foot layer. The infratectum includes one row of small rare alveolae. The supposedly poorly preserved endexine is thin and grainy. The ectexine reduces greatly in the aperture area, where only homogeneous ectexinal patches are present over the endexine. The pollen grains under study resemble in their exine ultrastructure pollen grains of the modern *Ginkgo biloba* and pollen grains from dispersed seeds of a presumably ginkgoalean affinity from the Middle Jurassic of Uzbekistan. This suggests that the ginkgoalean exine ultrastructure of the modern type existed as early as the Middle Jurassic. The exine ultrastructure under study is also similar, though to lesser degree, to that of dispersed pollen grains of a presumed ginkgoalean affinity from the Cretaceous of the Russian Far East. The diversity of such a long-living group as ginkgoaleans is apparently reflected in the diversity of their exine ultrastructure. To the present knowledge, ginkgoalean pollen grains can be differentiated from similar boat-shaped monosulcate pollens by the following co-occurring characters: a thick homogeneous tectum, a thin infratectum with one row of structural elements, a thin foot layer, and an ectexine that is reduced in the aperture region to patches.

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## 1. Introduction

Ginkgoalean pollen grains are described as boat-shaped and monosulcate. The information about pollen grains from pollen organs of fossil ginkgoaleans is scarce and mostly comes from light-microscopical observations (Balme, 1995). We summarized the published information on the morphology of fossil ginkgoalean pollen and pollen morphology and ultrastructure of the modern *Ginkgo biloba* L. in Tekleva et al. (2007), Zavialova et al. (2011), and Zavialova et al. (2014). Since ginkgoalean pollen grains belong to a rather simple and very common morphological type, the information about their exine ultrastructure can be a promising source of data for phylogenetic analysis, as well as for differentiation from pollen grains of the same type, but of other botanical affinities. Nonetheless, until now fossil ginkgoaleans have remained virtually unstudied in terms of their exine ultrastructure. This

is in part explained by the fact that ginkgoalean pollen organs are often preserved as opened structures that contain few (if any) pollen grains.

Up to date, the exine ultrastructure of fossil ginkgoalean pollen has been deduced from the only modern taxon *Ginkgo biloba*. Some information is available from a pollen assemblage from the Cretaceous of the Russian Far East dominated by monosulcate pollen extracted from a coal seam that contains exclusively ginkgoalean leaves (Zavialova et al., 2011). The exine ultrastructure was also studied in pollen extracted from the pollen chambers of dispersed seeds of *Allicospermum budantsevii* Gordenko from the Jurassic of Uzbekistan (Zavialova et al., 2014, 2016). Nosova and Hvalj (2017) stated that these seeds possessed a *Ginkgo* type of stomata and had a megaspore membrane similar to that in *Ginkgo biloba*, both features rather suggesting a ginkgoalean affinity of *A. budantsevii*.

In this work, we studied a pollen organ from the Middle Jurassic of Siberia, and managed to extract a sufficient amount of pollen grains for an electron-microscopical study. Our aims were to describe the morphology of the pollen organ, to obtain the

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information on the morphology and exine ultrastructure of *in situ* ginkgoalean pollen grains, and to compare the pollen grains under study with monosulcate pollen grains of other affinities. The present study contributes to our knowledge of fossil ginkgoaleans.

## 2. Material and methods

The material comes from the Irkutsk coal basin, which occupies the south of the Siberian Platform for ca. 530 km. The basin is stretched along the northeastern slope of the Eastern Sayan, from Baikal Lake in the southeast to the Uda River in the northwest, in the area of Nizhneudinsk town (Fig. 1). Heer (1876, 1878, 1880) was the first to study continental deposits of the Irkutsk basin. The Jurassic deposits of the Irkutsk basin are subdivided into the Baikal and Dabat formations in the piedmont depression, and the Zalari Fm. in the platform limb; upsection, Cheremkhovo, Prisayan, and Kuda formations are developed (Saks et al., 1981; Akulov et al., 2015; Kiritchkova et al., 2017a).

The specimens under study come from the lower subformation of the Prisayan Fm. of the Idan locality (2 km upstream the Ust'-Kuda settlement, near the mouth of the Idan creek valley; N 52.438036, E 104.149345), dated to the Aalenian (Kiritchkova et al., 2017b). The total thickness of the Prisayan Fm. is up to 250 m. It is constituted by inequigranular sandstones with sublayers of gritstones and pebbly conglomerates, and coaly argillites and coals.

Fragments of a pollen cone were found in association with leaves of *Ginkgoites heeri* Doludenko et Rasskazova and *Sphenobaiera vigentis* Kiritchkova et Batjaeva. The samples were treated with HF for about one day, followed by Schulze's reagent ( $\text{HNO}_3$  catalyzed with  $\text{KClO}_3$ ) for about 1 h. Then the material was rinsed with water, followed by solution of NaOH for a few minutes. The specimens were first photographed with a Stemi 2000-CS stereomicroscope and, after maceration, with a 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), in Saint Petersburg. The general morphology of pollen grains was observed with help of a Carl Zeiss Axioplan 2 transmitted light microscope equipped with an AxioCam 105 digital camera at the A.A. Borissiak Paleontological Institute of the Russian Academy of Sciences (PIN), in Moscow. Some images were processed with Helicon Focus 6.6.1 software. For SEM, groups of pollen grains on cuticles, pollen clumps, and monads were cleaned with alcohol, mounted on a SEM stub, sputtered with gold and palladium, and observed under a Tescan, 20 kV, at PIN. For TEM, groups of pollen grains and monads were embedded unstained in a mixture of epoxy resins (Epon-812, dodecyl succinic anhydride (DDSA), methyl nadic anhydride (MNA), and an accelerator as 17:15:8:1 volume ratios) for 48 h at 62 °C. Sections of 70 nm thick were prepared using a Leica EMUC6 ultramicrotome equipped with a diamond knife at PIN. Most grids were observed unstained. Some grids were post-stained after Reynolds, but those sections showed no unequivocal differences from unstained sections. They were viewed and photographed under a Jeol JEM-1011 TEM (accelerating voltage 80 kV) at the Electron Microscope Laboratory, Lomonosov Moscow State University. The TEM was 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 images using Photoshop 7.0. In total, we have measured 15 pollen grains in transmitted light; about ten pollen grains have been observed under SEM. Sections of two clumps of numerous pollen grains and two individual pollen grains have been observed under TEM; sections of the monads turned to be more informative and confidently interpretable.

The studied specimens are housed at the Laboratory of Palaeobotany, BIN (specimens BIN 1434/864-2a and 1434/864-3 – part and counterpart). Remains of polymerized resins with embedded pollen grains, grids with ultrathin sections, files of LM, SEM, and TEM images are retained at the Laboratory of Palaeobotany, PIN. Pollen terminology follows Punt et al. (2007).

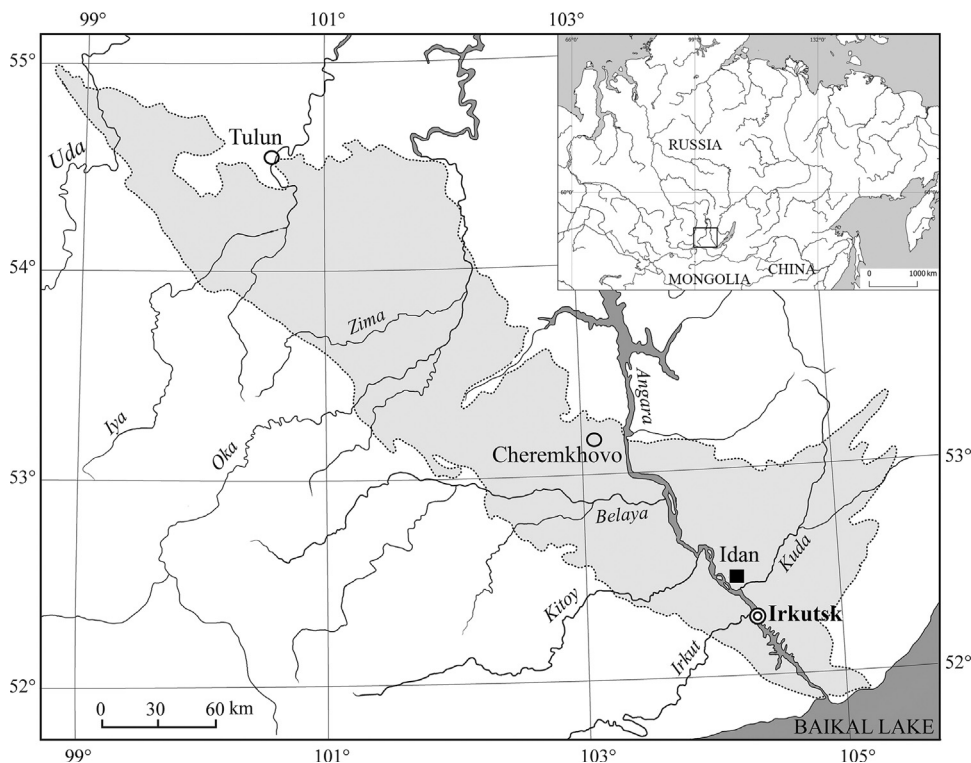
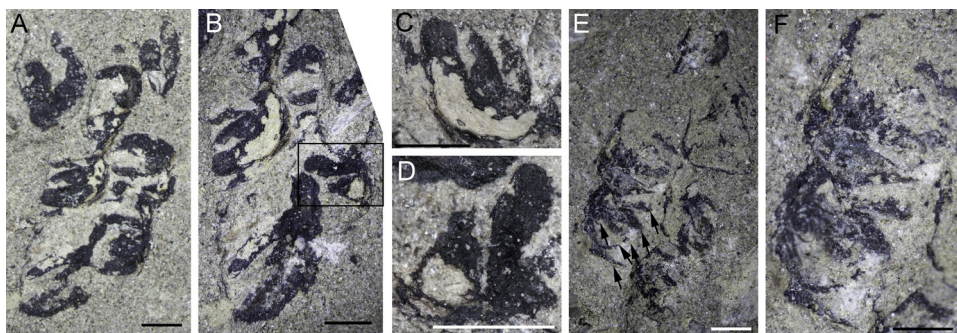


Fig. 1. Map of the Irkutsk Coal Basin (East Siberia) showing location of the Idan locality.



**Fig. 2.** Fragments of a pollen cone; Idan, Irkutsk Coal Basin, East Siberia, lower subformation of the Prisayan Fm. (Aalenian). **A–D.** Spec. BIN 1434/864-2a. **A:** fragment of the pollen cone; **B:** same pollen cone, with matrix partly removed with a needle; **C:** fragment of microsporophyll with four microsporangia (magnified from **B**); **D:** Microsporangium with round apex (magnified from **B**, black rectangle). **E, F.** spec. BIN 1434/864-3. **E:** fragment of the pollen cone (the arrows show six microsporangia on the microsporophyll); **F:** fragments of two microsporophylls (magnified from **E**). Scale bars: 1 mm.

### 3. Results

The structure of the pollen organ is unclear (Fig. 2(A, B, E)). A fragmentary pollen cone consists of several fragments of microsporophylls. Although we did not find any axes, the position of microsporophylls allowed us to suppose that they were attached to an axis and, therefore, we dealt with remnants of a strobile. Judging from the preserved fragments, each microsporophyll bore four to six microsporangia (Fig. 2(C, F)). The microsporangia are 1.0–2.2 mm long and 0.4–0.7 mm wide, elongated, oval to triangular with a rounded apex (Fig. 2(C, D)). Maceration yielded a thin cuticle of the microsporangium (Fig. 3(A, C)), clumps of pollen grains (Fig. 3(B, E, H, K), Fig. 4(A, F)), and several resin bodies 160–600  $\mu\text{m}$  in diameter (Fig. 3D).

The pollen grains are monosulcate,  $16.8\text{--}30.5 \times 29.1\text{--}39.8 \mu\text{m}$  in size,  $22 \times 35 \mu\text{m}$  on average (Fig. 3(F, G, I, J), Fig. 4(B, C)). The non-aperture surface is psilate to scabrate (Fig. 4(C, D)). The aperture membrane is folded (Fig. 4(E, G, H)). We suppose that the hemisphere bearing the aperture is distal and the non-aperture one is proximal.

All pollen grains show the same exine ultrastructure (Fig. 5(A–D)). The non-aperture ectexine is about  $0.7\text{--}0.81 \mu\text{m}$  thick (Fig. 5(B, C)) and composed of a thick solid tectum (ca.  $0.44\text{--}0.5 \mu\text{m}$  thick), a thin infratectum (ca.  $0.05\text{--}0.19 \mu\text{m}$  thick), and a thin foot layer (ca.  $0.07\text{--}0.17 \mu\text{m}$  thick). The infratectum includes one row of small rare alveolae between structural elements. The alveolae are stretched in the lateral direction: they are low, and the length largely exceeds the height (Fig. 5(B, C)). The supposedly poorly preserved endexine is thin (ca.  $0.07 \mu\text{m}$  thick) and appears grainy (Fig. 5D, white arrow). There are continuous areas of the ectexine that appear totally homogeneous, possibly because of the imperfect preservation of the material. The less altered structure of the infratectum is present in places, but more often in areas that are situated closer to the aperture than in the supposedly proximal exine. We think that areas with a better preserved infratectum have suffered less compression. The ectexine reduces greatly in the aperture area. There are only homogeneous ectexinal patches over the endexine (Fig. 5(A, D)).

### 4. Discussion

#### 4.1. The pollen organ under study

The unclear morphological features of the material did not allow us to supplement it with a taxon name. Male cones of

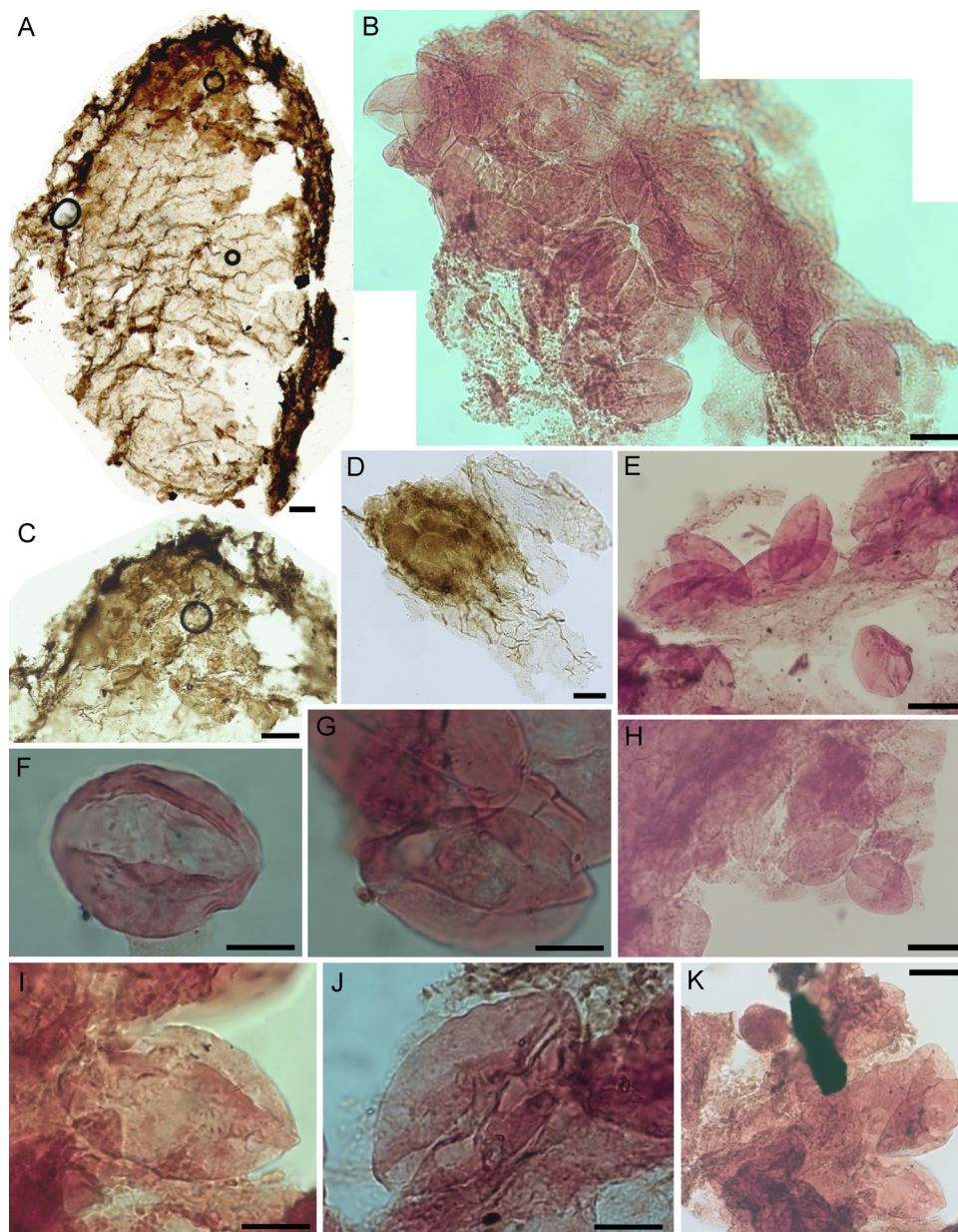
ginkgoaleans are sparse in the fossil record. All of them differ from the present material in number of microsporangia per microsporophyll. In particular, the Middle Jurassic male cone found in association with *Ginkgo huttonii* (Sternberg) Heer (Van Konijnenburg-van Cittert, 1971), the Middle Jurassic male cones of *Ginkgo hamiensis* Z.X. Wang et B.N. Sun (Wang et al., 2017), and the Late Cretaceous male cone of *Ginkgo* (Rothwell and Holt, 1997) have only two microsporangia at the abaxial side of the microsporophyll. Microsporophylls of the Early Cretaceous of *Ginkgo liaoningensis* Liu, Li et Wang bear two to four microsporangia (Liu et al., 2006). Male cones of *Stachyopitys preslii* Schenk from the Liassic of Germany consist of a main axis with several lateral stalks ending in distal clusters of radial microsporangia (Kirchner and Van Konijnenburg-van Cittert, 1994; Van Konijnenburg-van Cittert, 2010). The microsporangia under study do not form such a radial structure.

#### 4.2. Ginkgoalean features in the pollen morphology and ultrastructure

On the other hand, the morphology and ultrastructure of the *in situ* pollen grains are indicative of the ginkgoalean affinity of the remains under study. The boat-shaped monosulcate pollen grains under study closely resemble pollen grains of *Ginkgo biloba* by the exine ultrastructure (Table 1). In particular, they have the same ratio of ectexine sublayers: a thick homogeneous tectum, a thin infratectum of one row of structural elements, and a thin foot layer. Zavialova et al. (2011) assessed published data on the exine ultrastructure of *G. biloba*, restudied it with emphasis on the nature of the ectexine elements, and concluded that its infratectum is constituted of pillars, most of which hang from the inner surface of the tectum into the infratectal cavity and reach the foot layer; some pillars arise from the foot layer. Keeping in mind that the fossil exines are strongly flattened, we think that the infratectum of the pollen grains under study, when it was unaltered, was arranged in the same way as that in modern *G. biloba* pollen.

Earlier studied pollen grains extracted from presumably ginkgoalean seeds of *Allicospermum budantsevii* showed the same ratio of ectexine sublayers and the same type of infratectum (Zavialova et al., 2014). The aperture ultrastructure is similar: the exine reduces greatly, and the sublayers are indistinguishable; only homogeneous patches of the ectexine are present over the endexine. This similarity between the exine ultrastructure of pollen grains of *G. biloba* on the one hand, and that of the pollen grains under study and pollen grains from *A. budantsevii* on the other hand, proves that the ginkgoalean ultrastructure of the modern type already existed as early as the Middle Jurassic.



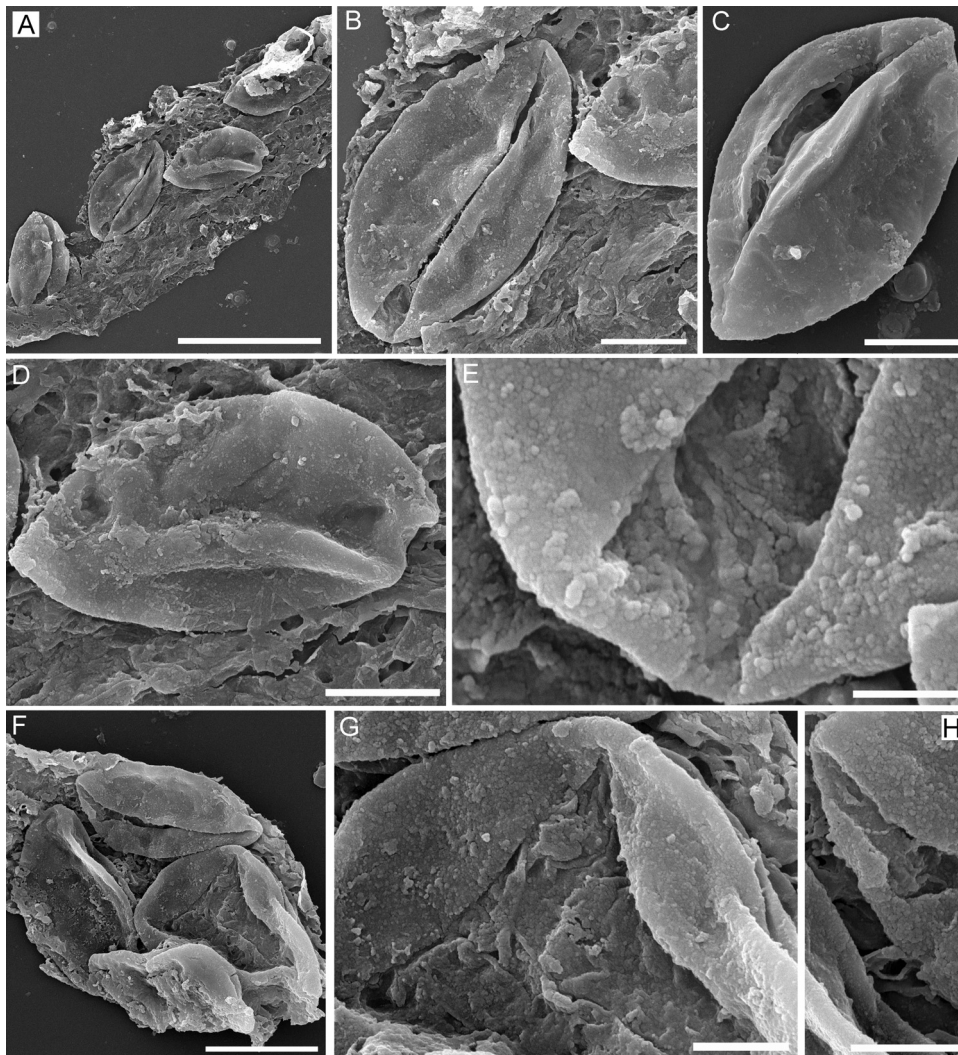


**Fig. 3.** LM, spec. BIN 1434/864–2a; Idan, Irkutsk Coal Basin, East Siberia, lower subformation of the Prisayan Fm. (Aalenian). **A.** Cuticle of the pollen sac with pollen grains. **B, E, F–K.** Pollen grains on the cuticle; monosulcate state of most of the pollen is evident. The ultrastructure of pollen grain F is shown in Fig. 5. **C.** Enlargement of A. **D.** A resin body. Scale bars: 50  $\mu\text{m}$  (A, C, D), 20  $\mu\text{m}$  (B, E, H, K), 10  $\mu\text{m}$  (F, G, I, J).

The exine ultrastructure under study is also similar, though to a lesser degree, to that of dispersed pollen grains from the Cretaceous of the Russian Far East (Zavalova et al., 2011) and to a pollen grain associated with a seed of *Ginkgo gomolitzkyana* N. Nosova from the Jurassic of Uzbekistan (Zavalova et al., 2016). The boat-shaped monosulcate pollen grains from the Russian Far East dominated in a palynological assemblage that came from a coal bed exclusively constituted by ginkgoalean foliage. Other possible producers of monosulcate pollen grains are very rare in coeval deposits of the region. On that ground, it was hypothesized that the pollen grains most probably derived from a ginkgoalean parent plant (Zavalova et al., 2011). A pollen grain was obtained in course of maceration of a seed of *G. gomolitzkyana*, suggesting its probable ginkgoalean affinity (Zavalova et al., 2016). The dispersed pollen grains from the Russian Far East and the pollen grain associated with the seed of *G. gomolitzkyana* turned to be relatively similar by their exine ultrastructure. In comparison to the present material,

the dispersed pollen grains have a similar tectum/ectexine ratio and aperture ultrastructure, but differ by an infratectum with a row of granules. The pollen grain associated with the seed of *G. gomolitzkyana* shows the same aperture ultrastructure and granules in the infratectum, but a different tectum/ectexine ratio. It is understandable that the diversity of such a long-living group as ginkgoaleans is also reflected in the diversity of their exine ultrastructure.

The endexine in pollen grains of modern *Ginkgo biloba* is usually reported as lamellate, but often the lamellae are discernible only in areas adjacent to the aperture; the lamellae are better visible in slightly immature pollen grains and can be indistinguishable in mature pollen grains (Zavalova et al., 2011). It would be pertinent to compare the endexine of the pollen grains under present study with that of pollen grains of modern *G. biloba* as well as fossil pollen grains of the presumed ginkgoalean affinity, but the endexine of the pollen grains under study seems



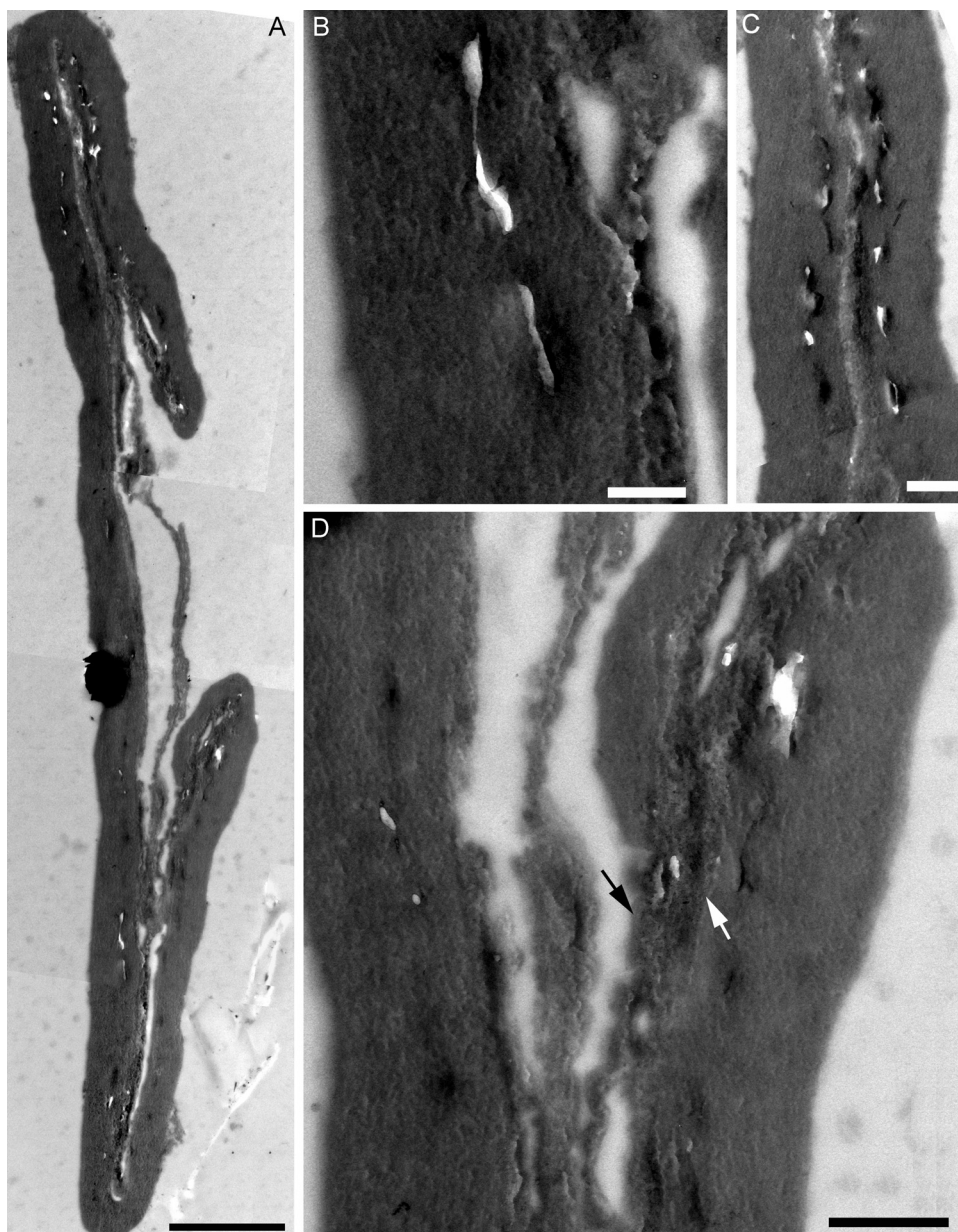
**Fig. 4.** Pollen surface, SEM, spec. BIN 1434/864-2a; Idan, Irkutsk Coal Basin, East Siberia, lower subformation of the Prisayan Fm. (Aalenian). **A, F.** Pollen grains on the cuticle. **B.** Enlargement of A showing the supposedly distal surface of a pollen grain. **C.** Pollen grain, supposedly distal surface. **D.** Enlargement of A showing the supposedly proximal surface of a pollen grain. **E, G, H.** Aperture membrane; E is enlargement of B; G, H are enlargements of F. Scale bars: 50  $\mu\text{m}$  (A), 10  $\mu\text{m}$  (B–D), 2  $\mu\text{m}$  (E), 20  $\mu\text{m}$  (F), 5  $\mu\text{m}$  (G, H).

poorly preserved. The endexine is also described as poorly preserved and occurring only at places in dispersed pollen grains of the presumed ginkgoalean affinity from the Russian Far East (Zavalova et al., 2011). By our experience, the endexine is often more poorly preserved than the ectexine; in addition, it often shows significant variability in the preservation in the same pool of specimens (Zavalova et al., 2010). The ectexine ultrastructure appears to be a more reliable and useful feature to characterize a fossil taxon.

The surface patterns, although quite indistinct, are also not identical in pollen grains of ginkgoaleans (Table 1). Thus, the proximal surface of pollen grains of *Ginkgo biloba* is rugulate with rare granules and rare small perforations; the equatorial area shows the same but less distinct sculpturing; and the aperture area bears low small verrucae (Zavalova et al., 2011). The pollen grains under study are psilate to scabrate in non-aperture areas; the exine in the aperture area is folded. Pollen grains from the Russian Far East are psilate in non-aperture area; the aperture area remained unstudied with SEM, but the presence of ectexinal patches revealed with TEM in this area suggests that some sculpturing was present in this area (Zavalova et al., 2011). The same is probably true for pollen grains from seeds of

*Allicospermum budantsevii*, which are characterized by a nearly psilate non-aperture pattern and a more distinct aperture pattern (Zavalova et al., 2014). The exine surface of the pollen grain associated with a seed of *Ginkgo gomolitzkyana* is nearly smooth, with rare perforations in non-apertural regions and smooth in the apertural region (Zavalova et al., 2016). It is unfortunate that pollen grains from *Stachyopitys preslii* Schenk (Kirchner and Van Konijnenburg-van Cittert, 1994; Van Konijnenburg-van Cittert, 2010) cannot be studied with SEM: judging from light-microscopy images, it seems that the pollen grains bear a distinct, probably granulate or verrucate sculpture. So far, the surface pattern observed in pollen grains of modern *G. biloba* has not been registered in any fossil pollen grains of the presumed ginkgoalean affinity. We think that surface patterns will probably be useful for differentiation between low-rank taxa within the ginkgoaleans, such as species or genera, as soon as more information becomes available. Similarly, differences in the surface sculpture of pollen grains were observed between species of cycadalean *Androstrobus* Schimper (Hill, 1990; Zavalova and Van Konijnenburg-van Cittert, 2012, 2016); exine surface characters were shown to be important for characterization of the bennettitalean *Williamsoniella coronata* Thomas (Zavalova et al., 2009).





**Fig. 5.** Exine ultrastructure, TEM, spec. BIN 1434/864-2a; Idan, Irkutsk Coal Basin, East Siberia, lower subformation of the Prisayan Fm. (Aalenian). **A.** Transverse section through the aperture. **B.** Enlargement of A showing several alveolae between structural elements of the infratectum. **C.** Lateral area of the pollen grain. **D.** Enlargement of A showing ectexine patches (black arrow) in the aperture area; white arrow points on a supposedly poorly preserved endexine. Scale bars: 2  $\mu\text{m}$  (A), 0.25  $\mu\text{m}$  (B), 0.5  $\mu\text{m}$  (C, D).

#### 4.3. Comparison with fossil monosulcate pollen grains of non-ginkgoalean affinities

A considerable bulk of ultrastructural information has been accumulated on Mesozoic monosulcate pollen, which can be attributed to several gymnosperm groups with different degrees of reliability (Table 1). Although some data sound contradicting, a few trends are traceable, and we believe that some day we will be able to differentiate between monosulcate-producers by the exine ultrastructure of their pollen grains. Zavialova and Van Konijnenburg-van Cittert (2012, 2016) named several characters that can be used to differentiate cycadalean pollen from similar pollen grains. In particular, the surface of cycad pollen grains often is foveolate or fossulate. Cycads are known to have monosulcate and inaperturate pollen; the latter is known only in cycads among gymnosperm producers of boat-shaped pollen grains. If a non-saccate and boat-shaped pollen lacks an aperture, this is an indication of possible

cycadalean affinity. Elongated ectexinal alveolae situated mostly in one row, arranged perpendicular to the exine surface and covered by a thin tectum is an unequivocal cycadalean character. Poorly preserved cycad pollen grains often show an alternation of alveolate and homogeneous regions in the exine, with predominance of homogeneous regions. Areas with the original alveolate ultrastructure of cycadalean type can be found by tracing numerous sections. This mode of preservation can be used as a hint of cycadalean affinity. Although pollen grains of many cycads are characterized by a thin tectum, a thicker tectum is also known. In some members, alveolae are grouped in two or three rows. In oblique sections, their outlines appear rounded, but cross sections reveal that they are elongated and situated perpendicularly to the exine surface. Irregularly distributed rounded alveolae and elongated alveolae situated perpendicularly to the exine surface revealed in different sections of a monosulcate pollen grain testify the cycadalean affinity of the pollen (Table 1). However, Zavialova

**Table 1**Comparison between monosulcate pollen grains found *in situ* and associated with plant mesofossils and studied with SEM and TEM (modified from Zaviialova et al., 2011, 2014, with additions).

Taxon	Affinity	Pollen size, $\mu\text{m}$	Pollen shape	Presence of aperture	Surface of non-apertural areas	Surface of aperture	Thickness of proximal ectexine, $\mu\text{m}$	Distinct lower boundary of tectum	Proximal tectum/ectexine ratio	Infratectum	Diameter of granules	Foot layer	Geography	Geological age
? <sup>1</sup>	pollen grains from a supposedly ginkgoalean pollen organ	22.0 × 35.0	boat-shaped	+	psilate to scabrate	folded?	0.70–0.81	–	0.62–0.63	one row of rare narrow horizontally stretched alveolae	n.a.	+	Russia	M. Jur.
<i>Ginkgo biloba</i> <sup>2</sup>	Ginkgoales	16.4 × 28.1	boat-shaped (in non-hydrated state), with pointed apices	+	rugulate	finely verrucate	0.74	+	0.50–0.80	pseudocolumellae, some appear as granules in sections	0.25–0.30	+	Russia	Rec.
<i>Allicospermum budantsevii</i> <sup>3</sup>	pollen from a supposedly ginkgoalean seed (pollen chamber)	18.9 × 35.4	ellipsoidal	+	nearly smooth	finely verrucate?	0.63	–	0.64–0.67	one row of alveolae, which are more or less horizontally stretched	n.a.	+	Uzbekistan	M. Jur.
<i>Ginkgo gomolitzkyana</i> <sup>4</sup>	pollen grain associated with a ginkgoalean seed	20.9 × 38.2	boat-shaped	+	nearly smooth, with rare perforations	smooth	1.1–1.24	+	0.30–0.34	one row of granules, many of them are fused to the tectum	0.20–0.40	+	Uzbekistan	M. Jur.
<i>Ginkgocycadophytus</i> sp. <sup>2</sup>	supposedly ginkgoalean dispersed pollen	21.2 × 37.7	boat-shaped, with slightly pointed apices	+	smooth	finely verrucate?	1.20	+	0.71–0.76	one row of big and widely spaced granules	0.07–0.33	+	Russia	E. Cret.
<i>Antevsia zeilleri</i> <sup>5</sup>	Peltaspermales	33.1 × 47.4	ellipsoidal	+	scabrate	scabrate	0.57–0.73	+	0.69–0.88	pseudocolumellae; a rim surrounds the aperture	n.a.	+	Germany	L. Tr.
<i>Cycadeoidea dacotensis</i> <sup>6</sup>	Bennettitales	12.0 × 25.0	irregular outlines, often folded	+	punctate	smooth	0.50	+	0.28	irregularly distributed fine granules, up to homogeneous appearance	0.06	–	USA	E. Cret.
<i>Leguminanthus siliquosus</i> <sup>7</sup>	Bennettitales	13.0 × 23.0	ovoid	+	smooth	smooth	0.70	–	0.62	very densely packed granules	0.07	+	Switzerland	L. Tr.
<i>Williamsoniella coronata</i> <sup>8</sup>	Bennettitales	16.5 × 24.5	ovoid	+	verrucate	smooth	0.20–0.30	–	n.a.	homogeneous	n.a.	–	UK	M. Jur.
<i>Sahnia laxiphora</i> <sup>9</sup>	Pentoxylales	23.0 × 26.0	ovoid	+	smooth	smooth	0.80–1.10	–	? infratectum grades gradually into tectum	medium-sized and densely packed granules	0.12	–?	Australia	E. Cret.
<i>Androstrobus balmei</i> <sup>10</sup>	Cycadales	17.7 × 24.3	ovoid	+	foveolate	finely rugulate	0.62	+	0.33	elongate alveolae	n.a.	–	UK	M. Jur.
<i>Androstrobus manis</i> <sup>11</sup>	Cycadales	29.3 × 36.5	oval to subcircular	+	foveolate-fossulate	wrinkled	0.74–0.99	–	0.26	irregularly distributed rounded alveolae or elongated perpendicular to the surface	n.a.	+	UK	M. Jur.
<i>Androstrobus patagonicus</i> <sup>12</sup>	Cycadales	28.0 × 34.0	circular to subcircular	–?	smooth	n.a.	1.00	–	0.17	alveolae in two or three rows?	n.a.	+	Argentina	E. Cret.
<i>Androstrobus rayen</i> <sup>12</sup>	Cycadales	19.5 × 25.0	ellipsoidal to circular	+	scabrate	?	1.00	–	0.36	rounded alveolae; alternation of alveolate/homogeneous regions	n.a.	–	Argentina	E. Cret.
<i>Androstrobus prisma</i> <sup>13</sup>	Cycadales	23.8 × 29.7	nearly rounded to more elongate	–	indistinctly verrucate	n.a.	0.14–0.73	–	0.17–0.27	perpendicular to the surface alveolae; alternation of alveolate/homogeneous regions	n.a.	–?	UK	M. Jur.
<i>Cycandra profusa</i> <sup>14</sup>	Cycadales	20.1 × 25.2	nearly rounded to more elongate	–	foveolate?	n.a.	0.20–1.00	–	0.14	elongate alveolae; alternation of alveolate/homogeneous regions	n.a.	–	Georgia	L. Jur.
<i>Allicospermum angrenicum</i> <sup>4</sup>	pollen grains associated with a ginkgoalean? cycadalean? seed	24.7 × 39.1	oval	+	nearly smooth, with rare depressions	folded	0.74–0.88	–	0.39–0.47	irregularly distributed rounded alveolae or elongated perpendicular to the surface	n.a.	+	Uzbekistan	M. Jur.
<i>Sphenobaiera angrenica</i> <sup>4</sup>	pollen grains associated with ginkgoalean leaves	30.0 × 40.0	oval	+	?	?	1.1	–	0.13–0.45?	irregularly distributed rounded alveolae or elongated perpendicular to the surface	n.a.	?	Uzbekistan	M. Jur.

References: <sup>1</sup>: present paper; <sup>2</sup>: Zaviialova et al. (2011); <sup>3</sup>: Zaviialova et al. (2014); <sup>4</sup>: Zaviialova et al. (2016); <sup>5</sup>: Zaviialova and Van Konijnenburg-van Cittert (2011); <sup>6</sup>: Osborn and Taylor (1995); <sup>7</sup>: Ward et al. (1989); <sup>8</sup>: Zaviialova et al. (2009); <sup>9</sup>: Osborn et al. (1991); <sup>10</sup>: Hill (1990); <sup>11</sup>: Zaviialova and Van Konijnenburg-van Cittert (2016); <sup>12</sup>: Archangelsky and Villar de Seoane (2004); <sup>13</sup>: Zaviialova and Van Konijnenburg-van Cittert (2012); <sup>14</sup>: Tekleva et al. (2007). Caption: +: character present; –: character absent; n.a.: not applicable; ? : no data.

et al. (2016) discovered pollen grains with unequivocal cycad ultrastructure in a seed of an unclear affinity (ginkgoalean or cycadalean) and attached to ginkgoalean leaves (Table 1: *Allicospermum angrenicum* Nosova and *Sphenobaiera angrenica* (Samylina) Nosova). We think that in this case the exine ultrastructure unequivocally points to the cycadalean affinity of these pollen grains.

Far less information is available about the exine ultrastructure of bennettites (Table 1). Osborn and Taylor (1995) studied pollen grains of *Cycadeoidea dacotensis* (McBride) Ward and revealed a granular infratectum with small, numerous, and irregularly scattered granules, a tectum/ectexine ratio much lower than in the pollen grains under study, and no foot layer. Ward et al. (1989) studied pollen grains of *Leguminanthus siliquosus* Kräusel et Schaarschmidt, with a smooth thick tectum, an infratectum of coarse and densely packed granules, apparently fused into a foot layer. Pollen grains of *Williamsoniella coronata* showed a distinctly verrucate surface pattern and a homogeneous ectexine (Zavialova et al., 2009). So far, it is not possible to list the ultrastructural characteristics of pollen of bennettites as a whole group; however, the pollen grains under present study are different by their exine ultrastructure from pollen grains of any of the three bennettites studied so far. This is also true for the Pentoxylales, with a dense and nearly homogeneous ectexine of their pollen grains (Osborn et al., 1991). The Late Triassic peltasperm *Antevsia zeilleri* (Nath.) Harris is indeed similar to ginkgoaleans in pollen morphology and ultrastructure, which could testify to the relationships between the two groups (Table 1; Zavialova and Van Konijnenburg-van Cittert, 2011). However, pollen grains of *A. zeilleri* differ from the pollen grains under study by the presence of lateral extensions surrounding the aperture.

No information has been so far available about the fine morphology of czezanowskialean pollen grains (Balme, 1995). In addition, dispersed monosulcate pollen grains are quite diverse in terms of the exine ultrastructure, and at least some of their ultrastructural types have not been reported from *in situ* materials (Meyer-Melikian and Zavialova, 1996; Zavada and Dilcher, 1988; Zavada, 2004). As more data will be accumulated, our ideas about characteristics of the exine ultrastructure of the above-discussed gymnosperm groups will inevitably be refined.

#### 4.4. Comparison with coeval monosulcate pollen grains from the Irkutsk Basin

A comparison with dispersed pollen grains from the same beds would have been suitable, but the palynological assemblage from the Idan locality has so far remained unstudied. Iljina (1985) named two monosulcate pollen types from deposits of the Prisayan Fm. of the Irkutsk Basin: *Cycadopites dilucidus* (Bolch.) Iljina and *Ginkgocycadophytus* Samoilovich. She acknowledged that differences between the two genera, if any, are unclear and also decided not to define species within the latter genus. Pollen grains of *C. dilucidus* are  $55\text{--}70 \times 30\text{--}45 \mu\text{m}$ ; their exine shows a grainy appearance in transmitted light (Bolchovitina, 1956). Iljina (1985) believed that pollen grains of *Ginkgocycadophytus* which occurred in Jurassic deposits of Siberia are smaller ( $20\text{--}40 \mu\text{m}$ , rarely  $50 \mu\text{m}$ ), with a psilate or grainy exine pattern. Kiritchkova et al. (2017b) described the so-called Angarsko-Zimniy palynological assemblage from the Prisayan Fm. of the Irkutsk Basin and provided a list of characteristic members of the assemblage, based on a study of several (other than Idan) localities of the Irkutsk Basin. Among monosulcates, they named *Ginkgocycadophytus*, *C. dilucidus*, and *C. medius* (Bolch.) Iljina. Pollen grains of the last species are larger ( $80\text{--}102 \mu\text{m}$  long and  $38\text{--}51 \mu\text{m}$  wide), with a thick and densely verrucate exine, as was originally described by Bolchovitina (1956) in transmitted light. The pollen grains under

present study fit better to Iljina's perception of *Ginkgocycadophytus* from the Siberian Jurassic. Of interest is that our ongoing study of the *in situ* material from the Irkutsk Basin revealed monosulcate pollen grains with a granulate pattern of the exine.

## 5. Conclusions

Although the pollen organ is fragmentary, the morphology and ultrastructure of the pollen grains are indicative of the ginkgoalean affinity of the remains under study. The pollen grains resemble greatly in their exine ultrastructure pollen grains of modern *Ginkgo biloba* and pollen grains from the presumably ginkgoalean seeds of *Allicospermum budantsevii* from the Middle Jurassic of Uzbekistan, indicating that the ginkgoalean ultrastructure of the modern type already existed as early as the Middle Jurassic. To a lesser degree, they are similar to presumably ginkgoalean dispersed pollen grains from the Cretaceous of the Russian Far East; the main dissimilarity is the type of infratectal elements. It seems that the diversity of ginkgoaleans is also reflected in their exine ultrastructure. Among pollen characters, ectexine peculiarities are most reliable for the differentiation of ginkgoalean pollen grains from similar boat-shaped pollen grains; the endexine is often poorly preserved and difficult to interpret. Surface patterns will probably be useful for differentiation between low-rank taxa within the ginkgoaleans as more information becomes available. To the present knowledge, ginkgoalean pollen grains can be differentiated from similar boat-shaped monosulcate pollen of other affinities by a certain ratio of ectexinal sublayers (a thick homogeneous tectum, a thin infratectum of one row of structural elements, and a thin foot layer) and by an ectexine that is greatly reduced in the aperture region. However, additional data on the exine ultrastructure of pollen grains from unequivocally ginkgoalean pollen organs are strongly needed.

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