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Mesofossils of an unrevealed affinity from the Jurassic of Siberia

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Abstract

Enigmatic mesofossils were obtained via maceration of a microsporangium detached from a ginkgoalean pollen cone of *Sorosaccus sibiricus* Prynada from the Aalenian Ust'-Baley locality in Irkutsk Coal Basin, Siberia. The organic-walled remains were constituted by rounded oval bodies of sporopollenin-like colour, overlapped with their margins and arranged in several layers. The bodies had jointed continuous walls of variable thickness, which bifurcated, fused and formed inseparable structures. LM, SEM and TEM observations showed that the find cannot be *in situ* ginkgoalean pollen or other remains of a ginkgoalean plant. The further comparison also excluded the possibility that these mesofossils were alien pollen or spores, trapped in an open sporangium or fossilized in its close vicinity. Some slight ultrastructural similarities were only revealed to cryptospores, which led the search to algae and bryophytes. However, although fresh-water colonial algae and bryophytes theoretically could have been present in these lacustrine deposits, they differ from the mesofossils by smaller cells, which are grouped differently and show dissimilar outlines and wall ultrastructure. There is a possibility that the find represents wall fragments of some resting stage of an unknown organism. So far, no close analogues to these mesofossils have been found.

Keywords: *Sorosaccus*, ginkgoalean pollen cone, lacustrine deposits, scanning electron microscopy, transmission electron microscopy

Introduction

Fossil plant assemblages from the Jurassic deposits of the Irkutsk Coal Basin of Siberia are a valuable source of new information regarding Jurassic vegetation, that allows one to advance in whole-plant reconstructions; however, they repeatedly provide scientists with fossils that are unexpectedly difficult to interpret, for example, *in situ* pollen grains with poorly preserved exine ultrastructure (Zavialova & Nosova, 2023; Zavialova *et al.*, 2023).

The material described in the present paper is a total puzzle, since we have not decided about the biological affinity of these mesofossils. We figured out what it was not, but did not find what it was, in spite of a spectrum of methods successfully applied to its study and a considerable bulk of information about its structure that was amassed. We document what we have learned about it in the hope that readers might recognize the objects, and that the affinity of our find will be clarified.

A fragmentary ginkgoalean pollen cone of *Sorosaccus sibiricus* Prynada from the well-known Jurassic Ust'-Baley locality was studied. Several fragments of the specimen that contained microsporangia enveloped in a small amount of the surrounding rock were macerated for *in situ* pollen. We found in products of maceration of one of the sporangia what we first identified as unseparated masses of pollen grains. However, further examinations showed that this conclusion was wrong.

Material and methods

Material

A single pollen organ was studied. The pollen organ (coll. BIN 1434, spec. 643-21) comes from the lower subformation (Aalenian) of the Prisayan Formation in the Ust'-Baley locality (52°37'47" N, 103°59'1" E), Irkutsk Coal Basin, Irkutsk oblast', the south-west of East Siberia, Russia (Fig. 1). The total thickness of the Prisayan Formation is up to 250 m. It consists of inequigranular sandstones with sublayers of gritstones and

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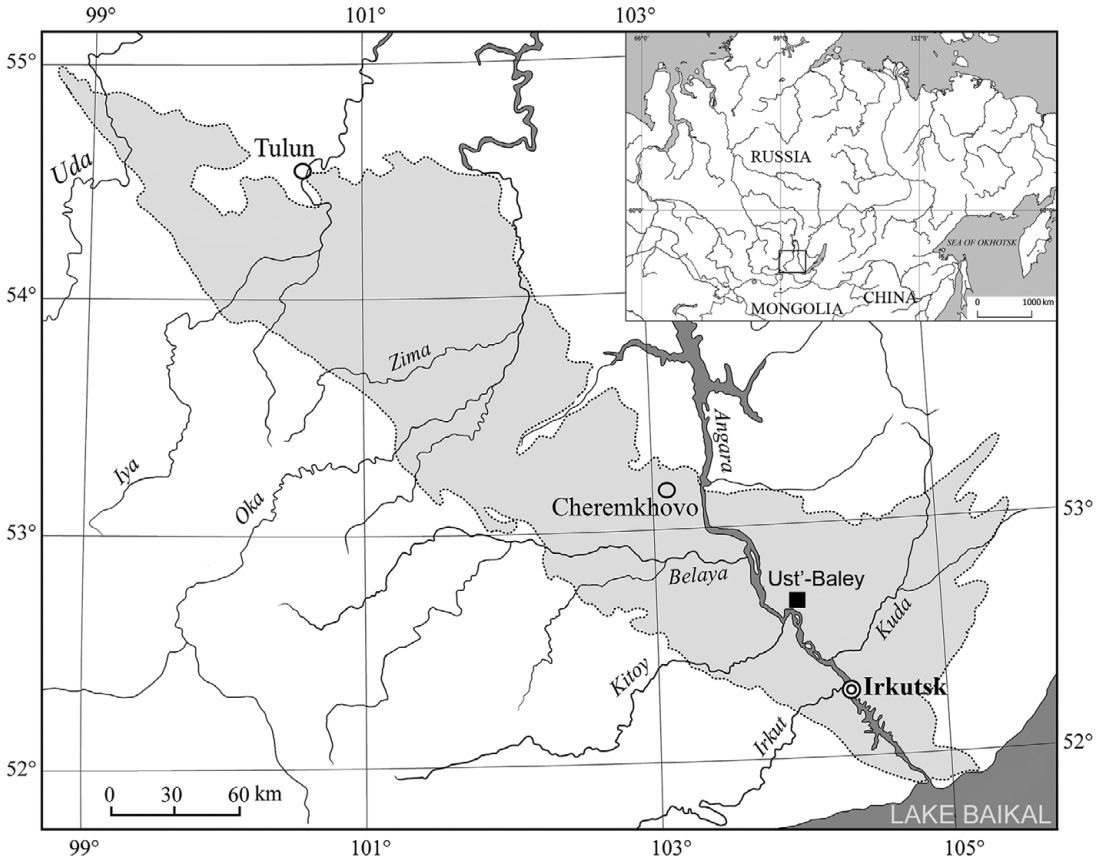

FIGURE 1. Schematic map showing the geographic position of the Ust'-Baley locality, East Siberia, Russia.

pebbly conglomerates, siltstones and coaly argillites and coals (Akulov *et al*., 2015; Kiritchkova *et al*., 2017). The lithology of the Ust'-Baley deposits (finely alternating siltstones and silty sandstones) allows one to reconstruct a relatively quiet and still water body, most probably a lake. Indeed, the locality has yielded nymphs of stoneflies, dragonflies and mayflies, beetle larvae and fish remains (Kiritchkova *et al*., 2020).

Plant fossils from the Ust'-Baley locality include sparse bryophytes, lycophytes, and horsetails (*Hepaticites* sp., *Lycopodites tenerrimus* Heer, and *Phyllotheca sibirica* Heer) and diverse and abundant ferns and gymnosperms. Among the ferns there are *Hausmannia crenata* (Nathorst) Moeller, *Coniopteris murrayana* (Brongniart) Brongniart, *Cladophlebis argutula* (Heer) Fontain, *C. haiburnensis* (Lindley & Hutton) Seward, *C. whitbiensis* (Brongniart) Brongniart, and *Raphaelia diamensis* Seward. The gymnosperms are represented by the cycad *Nilssonia* cf. *kendallae* Harris, ginkgoaleans *Ginkgoites concinna* (Heer) Seward, *G. sibirica* (Heer) Seward, *Sphenobaiera czekanowskiana* (Heer) Florin, *Sorosaccus sibiricus* Pryn., and *Pseudotorellia ensiformis* (Heer) Doludenko, leptostrobaleans *Czekanowskia rigida* Heer, *Leptostrobus laxiflora* Heer, and *Ixostrobus heeri* Prynada, conifers *Elatocladus falcatus* (Heer) Prynada, *Elatides ovalis* Heer, *Samaropsis rotundata* Heer, and *Pityospermum* sp., and gymnosperms incertae sedis *Angarolepis odorata* Krassilov & Bugdaeva and *Aegianthus sibiricus* (Heer) Krassilov (Kiritchkova *et al*., 2020).

The collection BIN 1434 is stored at the Laboratory of Palaeobotany of the Komarov Botanical Institute of the Russian Academy of Sciences (BIN RAS) in Saint Petersburg, Russia.

Methods

The hand specimen was photographed with a Canon EOS-60D digital camera. Since the microsporangia in the pollen cone under study were incompletely preserved, they cannot be extracted from the specimen without capturing some of the surrounding rock. Taken in this way fragments of the specimen were cleaned with HF for about one day, followed by maceration in Schulze's reagent (HNO_3 catalysed with $KClO_3$) for about 3 h. Then the material was rinsed with water and then treated in 10% solution of KOH for a few minutes.

Among products of maceration of one of the sporangia we found seven pieces of what we originally supposed were clumps of pollen grains. They were photographed 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). For scanning electron microscopy (SEM), they 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. The stub was tilted to take some images. Ultrawave vacuum cleaning was applied in a (futile) attempt to disintegrate these fragments into monads. For transmission electron microscopy (TEM), the material was 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.

Results

The collection contains a fragmentary pollen cone on an axis (Fig. 2E). The basal part of the main axis does not bear microsporophylls. It is at least 13 mm long and 1–1.2 mm in diameter and has a faintly striated surface. The pollen cone is elongated cylindrical, at least 21 mm long and 7 mm wide. The microsporophylls are numerous. The poor preservation of this cone does not allow us to study the microsporophyll structure in detail; in particular, the number and position of microsporangia remain unknown. The microsporangium is oval, and the distal lamina ends with an acute apex commonly bending upward. This cone resembles other pollen cones of *Sorosaccus sibiricus* from the same locality, the morphology of which was studied in detail (Nosova *et al*., 2018).

Several fragments of what we originally supposed were clumps of pollen grains were obtained via maceration of one of the several treated microsporangia enveloped in a small amount of the surrounding rock (Figs. 2C, D, F, 3A–C). The largest of the fragments reached about 267 μm long and 217 μm wide (Fig. 2D). The pieces seemed torn around the entire perimeter; we did not notice any margins that would have appeared intact (Fig. 2A, B). These remains were constituted by rounded oval bodies, which overlapped with their margins and were arranged in more than one layer (Figs. 2A–D, F, G, 3A–D). There were about a dozen of such bodies per the length of the largest fragment and about 7 or 8 per width (Fig. 2D). They were yellowish-brown in transmitted light, 28.6–(35.9)–48.1 μm wide and 34.0–(49.3)–67.8 μm long. We managed to discern boundaries of 27 bodies in transmitted light, to measure them; others were either partly torn or covered by other bodies in a way that their boundaries cannot be traced with certainty. A granulate pattern was visible in places (Fig. 2G). A few of the bodies appeared as if they possessed trilete scars with unusual curving rays (Fig. 2B), but observations at different focal depths revealed that these were margins of overlying or underlying bodies. Apparent sulci that were partially visible on a few other bodies (Fig. 3G) also resulted from such overlapping or from folding of the bodies: we have never detected a complete 'sulcus', with a closed contour, but merely one of the extremities. We have not found any other features that are normally present on pollen grains or spores.

SEM confirmed that the surface is granulate in places (Fig. 3D, F, I). Observations of a tilted stub allowed us to look at the objects sideways, where the granulate pattern on more inner bodies was also detected and the multilayered arrangement of the find became obvious (Fig. 3E, G). However, the number of layers was difficult to count accurately, because the bodies did not have closed contours. The walls that formed them dichotomized, fused, and folded, and these folds became compressed (Fig. 3G–I). This is why it was impossible to detach individual bodies from the clumps: in fact, there were no independent separable bodies. We have not noticed any differentiation between the outermost and inner walls of the studied objects. The thickness of the walls varied significantly (Fig. 3G, H).

We roughly calculated about 11 layers of walls per the total thickness of the fragment observed on a tilted SEM stub (Fig. 3E) and 5 to 8 walls in fragments observed under TEM (Fig. 4B, C). If we suppose that each constituting body had upper and lower walls within the mesofossil, then there were from two to five layers of constituting bodies within it.

Ultrathin sections showed that the thickness of the walls varied from 0.1 to 1.4 μm (Fig. 4A–E), reaching 2.6 μm in bifurcations (Fig. 4B, C). Long thicker areas alternated with long thinner areas (Fig. 4B, C). Thicker areas often had even margins (Fig. 4D); thinner areas often had crenate margins (Fig. 4E). The ultrastructure was homogeneous and, in places, nearly homogeneous. Lacunas and ruptures were rare and mostly present in points of bifurcations. Ruptures might have mimicked a proximal scar ray as it should appear in sections, but the ridge over this 'ray' gradually continued into a wall of another compartment (Fig. 4A–C). Grainy material was present on thinner portions of the walls (Fig. 4A). The crenate margins and grainy material corresponded to the granulate pattern visible in LM and SEM. We roughly counted about a dozen of compartments per ultrathin section and there were two to four of them, for which closed contours were traced (Fig. 4C). However, portions of their walls served as walls of other compartments

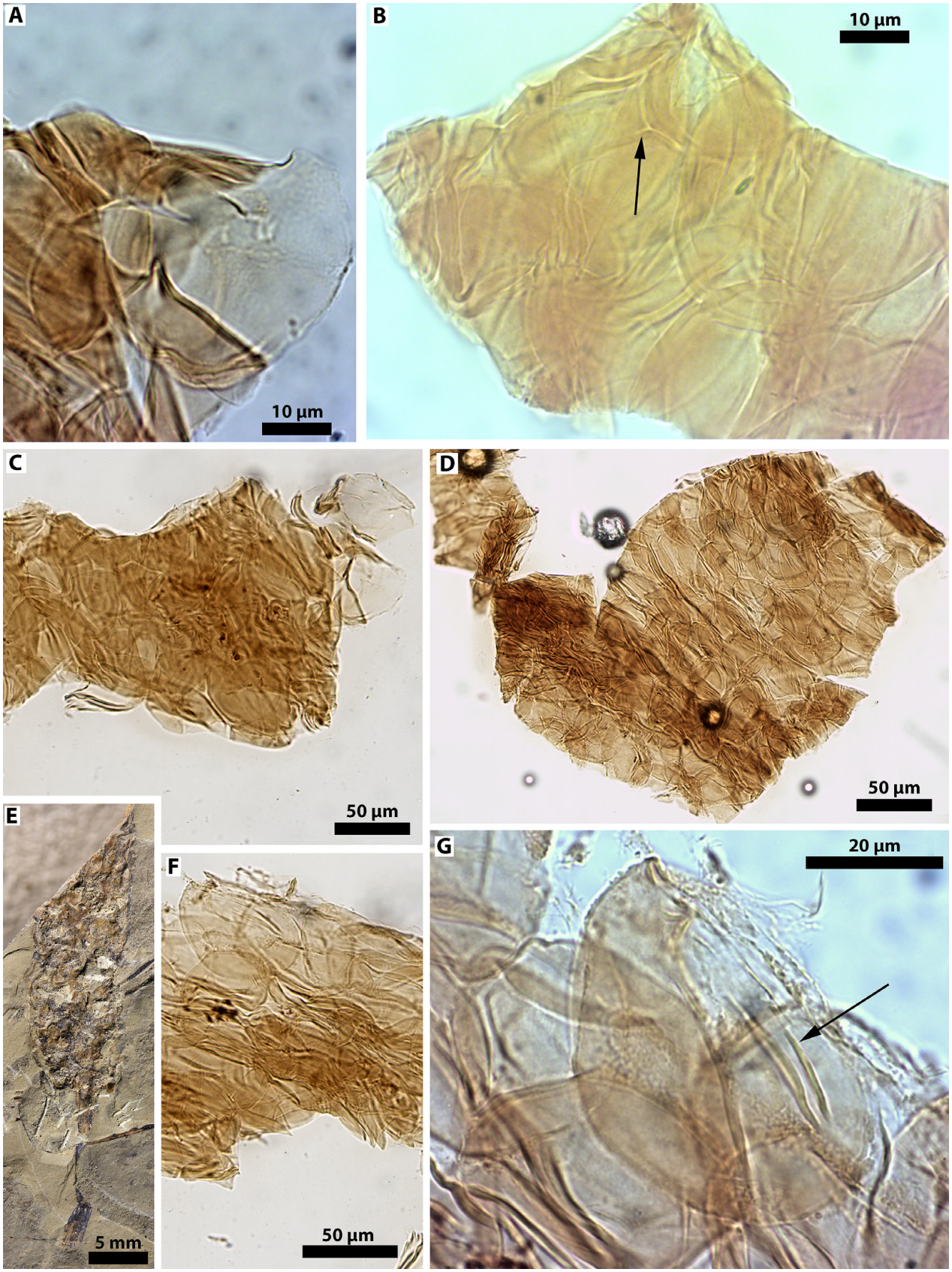

FIGURE 2. Mesofossils under study in transmitted light (**A**–**D**, **F**, **G**) and a strobile of *Sorosaccus sibiricus* Prynada in reflected light (**E**), LM, Ust'-Baley locality in East Siberia, Russia, Aalenian. **A**, Enlargement of Fig. 2**C**, partially torn body is visible (compare with Fig. 4**C**, lower right of the figure, arrow). **B**, Apparent "trilete scar" with curved "rays" (arrow) in reality results from overlapping oval bodies. **C**, **D**, Mesofossils with torn margins. **E**, Fragmentary strobile. **F**, Constituting bodies near the margin of a mesofossil. **G**, Enlargement of Fig. 2**F**, granulate pattern is visible, apparent "sulcus" is indicated with an arrow.

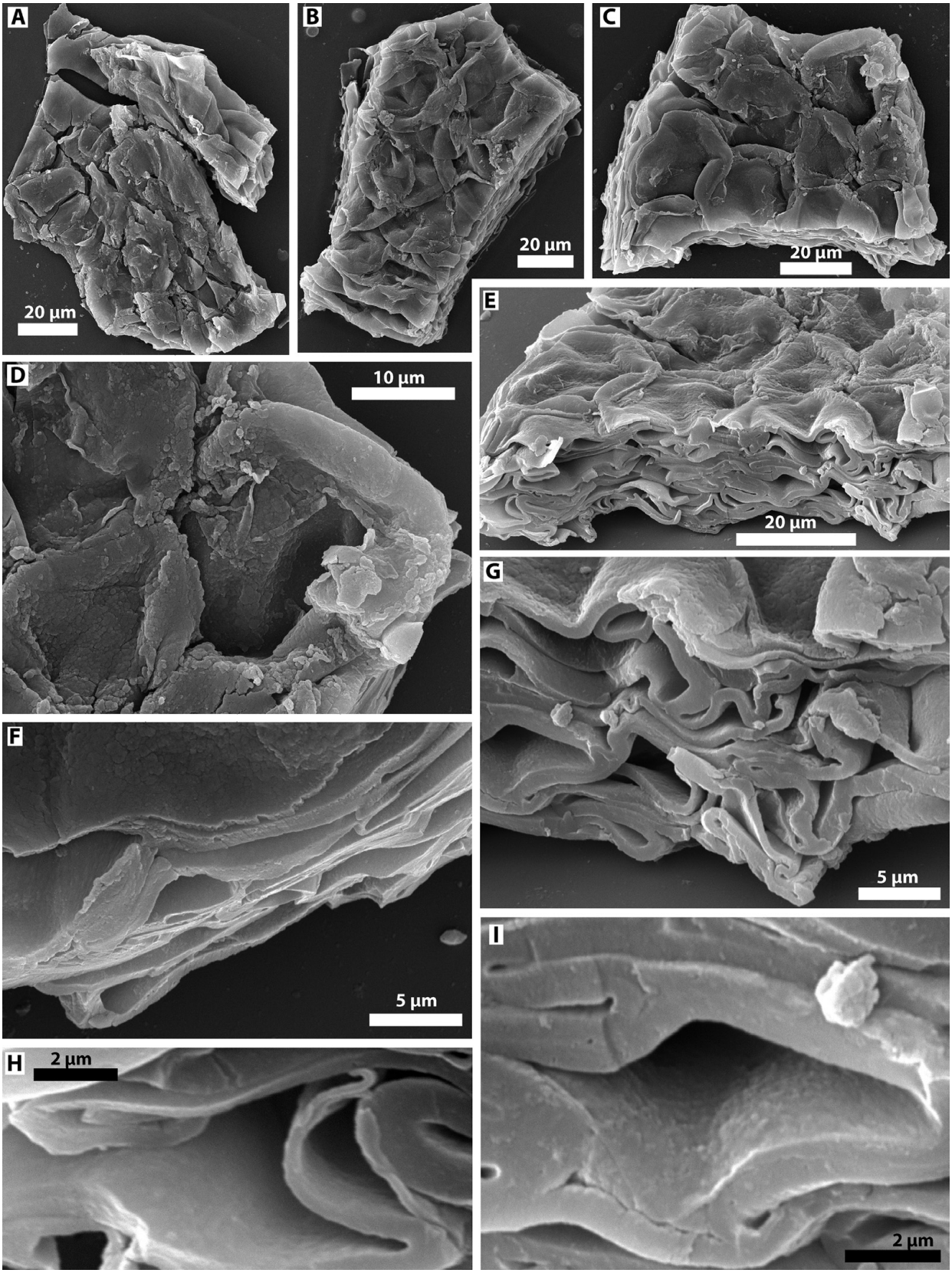

FIGURE 3. Surface pattern and inner structure of mesofossils under study, SEM, Ust'-Baley locality in East Siberia, Russia, Aalenian. **A**–**C**, Mesofossils showing overlapping constituting bodies. **D**, Granulate pattern is visible. **E**, Multilayered arrangement is evident, SEM stub was tilted. **F**, Multilayered arrangement of the mesofossil. **G**, Enlargement of the area shown in Fig. 3**E**, walls vary in thickness, granulate pattern is occasionally present on internal walls as well. **H**, **I**, Greater enlargement of Fig. 3**E. H**, Note that the walls significantly vary in thickness. **I**, Note the bifurcations of the walls and also the occurrence of the granulate pattern even on one of the internal walls.

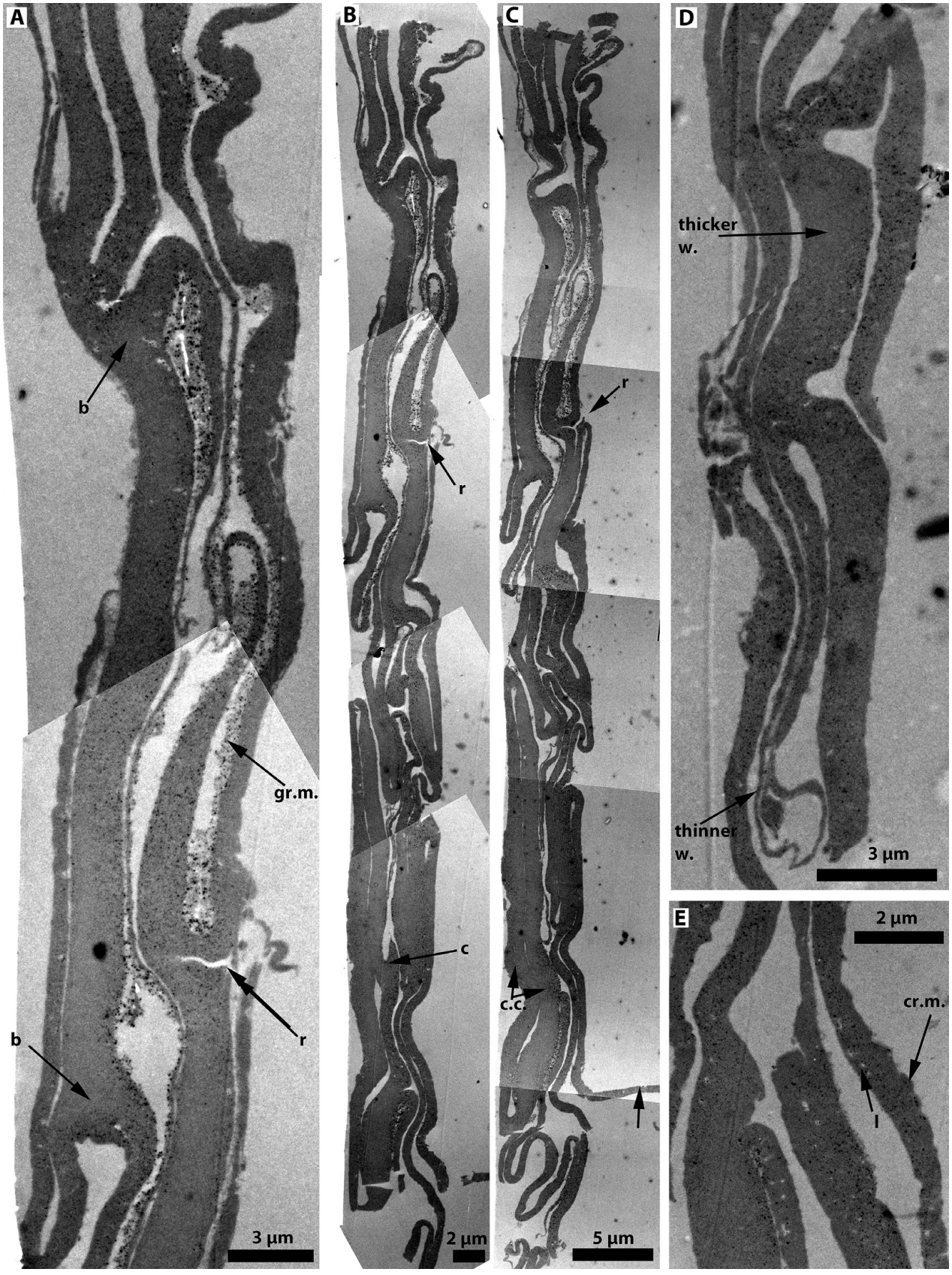

FIGURE 4. Ultrathin sections of mesofossils under study, TEM, Ust'-Baley locality in East Siberia, Russia, Aalenian: (b) bifurcation, (gr.m.) grainy material, (r) rupture, (c.c.) closed contour, (c) continuation of the wall into the wall of adjacent compartment, (thicker w.) thicker wall, (thinner w.) thinner wall, (cr.m) crenulate margin, (l) lacuna. **A**, Enlargement of **B**. **B**, Composite image of an ultrathin section. **C**, Composite image of an ultrathin section that passed at a deeper level than that shown in Fig. 4**B**. **D**, Folding slightly resembles elevations over rays of the proximal scar. **E**, Some lacunae are visible within the wall.

(Fig. 4B). Therefore, TEM observations confirmed our earlier SEM observations that there were no independent separable bodies in the fragments under study.

Discussion

We attempted bulk maceration of microsporangia of the ginkgoalean *Sorosaccus sibiricus* (Fig. 2E) with the aim to obtain *in situ* pollen grains. The preservation of the strobile was far from perfect: it was preserved as a very flat structure; the walls of microsporangia (epidermis, endothecium and tapetum) were absent. A small amount of the surrounding rock inevitably accompanies sporangia in course of maceration of such a material, and the scientist cannot be totally sure whether the products of maceration came from inside of the sporangium or were attached to its surface or present in the rock. Thus, a small input of alien pollen very often cooccurs with *in situ* pollen, and the scientist differentiates between them by the expected morphology, prevalence of one of the morphological types, and preservation of *in situ* pollen in clumps—not by direct observation of *in situ* pollen grains inside the sporangium. So, as these remains were yielded via bulk maceration of a microsporangium, we expected them to be *in situ* ginkgoalean pollen. Indeed, they survived HF treatment and showed sporopollenin-like colour. In transmitted light, we observed numerous rounded to oval bodies that fit the pollen size range and were similar to each other. They were grouped in aggregations (Fig. 2D), similar to fossil *in situ* pollen grains or spores that often are difficult to disintegrate into monads (*e.g.*, Zavialova *et al.*, 2021, fig. 3a, c; Nowak *et al.*, 2023, fig. 2a). We failed to detect any characteristic features of palynological objects (such as apertures, sacci, an equatorial girdle, striation, or a trilete or monolete scar), but the supposed pollen grains were superimposed on each other in layers that strongly hampered light-microscopical observations. Some structures that resembled trilete scars were occasionally observed, but they turned out to be a result of superposition of the constituting bodies (Fig. 2B). Folds that could have been taken for a sulcus turned out to be interrupted and did not form complete ‘sulci’.

We needed to detach individual elements from the aggregations to evaluate their general morphology, so we tried to separate them mechanically, with dissecting needles, and via ultrawave vacuum cleaning, which occasionally helps in such cases (*e.g.*, Taylor *et al.*, 1987), but failed. Nonetheless, we switched to the electron-microscopical stage of the work, still thinking that we were dealing with pollen or at least spores and hoping to understand their morphology with help of SEM. However, electron microscopies revealed that we dealt with an inseparable structure; and no pollen or spore characteristic features were detected as well (Figs. 3C, E, 4A). TEM results were particularly revealing. The matter is that even strongly compressed fossil *in situ* pollen and spores show traceable closed contours of sporoderms of individual pollen grains or spores in ultrathin sections (*e.g.*, Osborn *et al.*, 1991, fig. 4; Zavialova *et al.*, 2021, fig. 5b). Contrariwise, these bodies demonstrated jointed continuous walls, instead of individual ones. Rare, closed contours that we detected showed bifurcations and continuity with other walls in subsequent sections (Fig. 4B, C). Therefore, we realized that these fossils were not clumps of ordinary *in situ* pollen grains or spores, which were monads in living state, but could have represented some multicellular structure, and, therefore, we should have examined them as entities. For example, the mutual arrangement of the constituting bodies and dimensions and outlines of intact fossils could have been meaningful for interpretation. We attempted to macerate additional materials from the cone, but failed.

As the fossils under study were yielded via maceration of a *Sorosaccus* cone, theoretically they could have been remains of its parent plant. The most expectable remains are ginkgoalean *in situ* pollen grains, but our objects, as we concluded, were not *in situ* pollen grains, and additional attempts of maceration did not give us pollen grains. Speaking about remains of the same plant, but other than *in situ* pollen grains, there is some resemblance to the sporangial wall of the modern *Ginkgo* (*e.g.*, Mundry & Stützel, 2004, fig. 6f; Lu *et al.*, 2011, fig. 7d), such as comparable sizes of the cells and number of cell layers. However, the cells of the sporangial walls are polygonal (by contrast to rounded–oval bodies constituting our objects), they touch each other with their margins (by contrast to overlapping bodies of our objects), the thickness of their walls is more or less constant (by contrast to the walls of the bodies that are highly variable in thickness), and the outer cell layer differs from the underlying layers (whereas no differentiation between layers of external and more inner bodies was revealed in our objects). In addition, in all probability, the cuticle is the only part of the sporangial wall that can fossilize, and it is a one-layered structure, and the outlines of cells that it retains are very different from the outlines of the bodies that constitute our mesofossils (*e.g.*, Wang *et al.*, 2017, fig. 6.1, 6.2). The same is true for any foliar remains of the parent plant, which, if preserved, would be represented merely by cuticles.

When the cone was still attached to the parent (most probably wind-pollinated) plant, it could have served as a trap for foreign pollen or spores from the air (Polevova & Tekleva, 2018). When the cone fell into the lake, it also could have caught foreign pollen or spores as well as other relatively small living objects that fell into the

same water pool or lived in it. These are conceivable explanations how the mesofossils under study cooccurred with a ginkgoalean cone, although they were not relevant to ginkgoaleans.

We have just ruled out the possibility that our find was *in situ* pollen grains or spores. The same arguments are applicable to an option that the cone was contaminated by dispersed pollen grains and spores, which were deposited as monads, since they similarly should have shown closed contours of their walls in sections. Although most often pollen grains are dispersed during pollination as monads, there are seed plants that shed their pollen grains as dyads, tetrads, and polyads and in massulae and compact pollinia (Pacini & Franchi, 1999, fig. 1). They may have some peculiarities of the ultrastructure differentiating them from 'ordinary' pollen grains due to their unusual mode of dissemination; therefore, we think it is worthwhile to evaluate them in relation to our find.

One can hypothesize that our find is not clumps of pollen grains that stuck to each other during fossilization, but aggregations of pollen grains that were disseminated in groups when they were still alive, during pollination. We do not know such cases for ginkgoaleans, but tetrads are known in other gymnosperms, such as, for example, tetrads of *Classopollis*, which were shed by cheirolepidiaceous conifers (*e.g.*, Zavialova, 2003). However, closed contours of the exines of individual pollen grains are evident in such tetrads in ultrathin sections (*e.g.*, Zavialova *et al.*, 2010, pls. 36.4, 36.7).

Pollen grains are shed in compound dispersal units in a list of modern angiosperm families, most prominent of those is Orchidaceae (Pacini & Franchi, 1999; Purgina *et al*., 2024). Obviously, we do not expect to discover remains of zoophilous angiosperms in Jurassic deposits, but are merely looking for suitable modern analogues for our find, for lack of anything better. However, these dispersal units appear very different from our find. Pollen grains within them have their own walls, with closed contours of the walls of individual pollen grains, by contrast to the jointed and bifurcating walls in our find. No alternations of thick and thin regions, as in our find, were observed in such pollen grains. Their outlines are polygonal (*e.g.*, Freudenstein & Rasmussen, 1997, fig. 1d–f), unlike rounded to oval outlines of the bodies that constitute our fossils. The pollen grains are held together by various means, such as pollenkitt, viscin, or elastovistin. Little is known about the chemistry of these substances. Some of them are known not to withstand acetolysis and, thus, most probably are not able to fossilize, whereas others most probably contain sporopollenin (Wolter & Schill, 1985; Pacini & Franchi, 1999) and are able to fossilize; however, those that have potential for fossilization form threads, and we did not observe any threads in our material. Speaking about sporopollenin, it is distributed unevenly in outer and inner members of pollinia, and walls of inner pollen grains nearly or totally devoid of it (*e.g.*, Purgina *et al*., 2024), that deprives them of a chance of fossilization (Wolter & Schill, 1985). In sum, our find is too different from compound dispersal units of pollen grains of seed plants.

Although there are rare cases, spores of homosporous ferns are also known to disperse in groups. Thus, 16 spores of the sporangium of the polypodiaceous *Lecanopteris mirabilis* (C.Chr.) Ching are held together by perisporal strands (Walker, 1985, pl. Ib–d; Tryon & Lugardon, 1991, fig. 118). Tetrads of fossil lycophytes are reported as *sporae dispersae* and *in situ* (*e.g.*, Looy *et al.*, 2005, figs. 4, 7; Nowak *et al*., 2023, fig. 6c). These compound dispersal units have the same dissimilarities from our find as those outlined above for pollen grains.

Heterosporous water ferns *Salvinia* and *Azolla* (Salviniaceae) disseminate microspores in massulae, where the microspores are embedded in the episporial tissue (Tryon & Lugardon, 1991). The ferns prefer stagnant or quiet water (Tryon & Tryon, 1982), that fits the presumed lake, where our cone was deposited. As massulae are constituted by epispore, microspores are covered by exospore and both epispore and exospore contain sporopollenin, there is a good chance to find fossil salviniaceous massulae. Indeed, they are reported in a list of papers on fossil members of the Salviniaceae (*e.g.*, Collinson, 1980; Vanhoorne, 1992; Collinson *et al*., 2013) and their relatives (Rothwell & Stockey, 1994). However, TEM observations reveal sharp differences from our find. Walls of microspores show distinct closed contours, which are smaller than the bodies constituting our mesofossils. The ultrastructure of salviniaceous microspores is typical of fern spores; the distinct proximal scar shows the *Blechnum*-type of the exospore ultrastructure (Tryon & Lugardon, 1991). The epispore that forms massulae is spongy and a bit reminiscent of our find, but the compartments do not quite fit by sizes: most of them are smaller, and they are much more variable in size than the bodies that constitute our mesofossils. The partitions are different by the ultrastructure from the walls of our bodies. In addition, the known geological history of the Salviniaceae starts in the Campanian and the ancestors of the family are believed to be not much older than an early Late Cretaceous (Hall, 1975), whereas our material is dated to the Middle Jurassic.

The literature search has revealed similarities to our find in unexpected microfossils, which are separated from the Jurassic by a huge time gap. Strother *et al*. (2017) described cryptospores of an unknown affinity from the Ordovician of the USA, preserved as tetrads, dyads, irregular clusters and planar sheets of spore dyads, and discussed them in relation to the origin of the plant sporophyte in the streptophyte lineage. Some specimens

of these 'thalli' are constituted by rounded overlapping spore-bodies (Strother *et al*., 2017, fig. 3e), similar to our find and distinctive from any multicellular structures we used in the comparison, since all of them are formed by polygonal cells. Their ultrastructure does not resemble our find (Strother *et al*., 2017, fig. 5b), but there are some other cryptospores, which are less similar in general morphology, but more similar in the ultrastructure. Thus, Taylor and Strother (2009) reported dyads, tetrads and clusters of cryptospores from the Cambrian of the USA. In TEM, they show alternations of thicker and thinner areas of the walls (Taylor & Strother, 2009, *e.g*., fig. 21). Alternations of thicker and thinner regions of the walls as well as their bifurcations are seen in ultrathin sections of cryptospores from the Ordovician of Saudi Arabia (Taylor *et al*., 2017, figs. 1, 5) and from the Silurian of the USA (Taylor, 2002, pl. I (2)).

Cryptospores were produced by algae or first terrestrial plants, or their intermediates (Strother & Beck, 2000), that has directed our search of suitable analogues to the world of algae and to bryophytes, all the more so because remains of both groups are able to occur in lacustrine deposits like those that are hypothesized for the Ust'-Baley locality.

For instance, colonies of the green alga *Botryococcus* Kützing have been known since the Precambrian, or, by other estimations, since the Palaeozoic, to modern days primarily in freshwater environments (Guy-Ohlson, 1992; El Atfy *et al*., 2024). They survive maceration and occur in palynological slides, due to a chitin-like polymer, which is present in the sheaths and allows fossilization (Guy-Ohlson, 1992, 1998). Smaller colonies are nearly spherical and larger ones may branch. Smaller colonies (with rounded individual cells) show a superficial resemblance to our find, but both the cells, which range from 5 to 15 μm, and the colonies, which range 10 to 100 μ, are much smaller than our find. There is nothing similar to opened caps of *Botryococcus* in our material; the bodies that constituted our find, whatever they were, were always closed. Fossil remains of *Botryococcus* from deposits of various geological ages are very stable by their morphology (Guy-Ohlson, 1992, 1998). Observations with a confocal laser scanning microscope revealed that cells of *Botryococcus* have walls of a rather constant thickness and with multilayered inner structure (Stasiuk, 1999, fig. 2d), that additionally differentiates them from our find. There are other algae that are slightly reminiscent of our find (Batten, 1996; Prasertsin & Peerapornpisal, 2015). Among them is the streptophyte *Coleochaete* Brebisson that was shown to have autofluorescent and acetolysis-resistant cell walls and was compared to some Cambrian microfossils (Graham *et al*., 2012). However, its cells are significantly smaller than constituting bodies of our find and the walls reveal a layered ultrastructure (Graham *et al*., 2012). The chlorophyceous alga *Pediastrum* Meyen has been repeatedly reported from palynological assemblages since the Early Cretaceous (Zamaloa & Tell, 2005). Its members differ from our find by smaller cells, their angular outlines and the fact that the cells are arranged in the coenobium in one layer (Zamaloa & Tell, 2005, pls. 1, 2).

We have remarked something similar to our find in fossil bryophytes. For example, Ignatov *et al.* (2023, 2024a, 2024b) described Upper Permian mosses and provided the TEM data. A leaf apex of *Arvildia obtusifolia* Ignatov showed rounded overlapping cells (Ignatov *et al*., 2023, fig. 4c), which look quite similar to our find. Although other mosses show polygonal cells, there are similarities to our find at the ultrastructural level, such as bifurcations of the walls (*e.g*., *Gomankovia latifolia* Ignatov in Ignatov *et al*., 2024a, fig. 5d and *A. elenae* Ignatov in Ignatov *et al.*, 2024b, fig. 11j, k). However, leaves of bryophytes are most commonly formed by a single layer of cells. More than one layer may be present in costae, but another dissimilarity becomes evident in such areas: outer walls are always thicker than the inner ones in bryophytes (*e.g*., *Servicktia undulata* Ignatov in Ignatov *et al*., 2024b, fig. 7e), and this is not the case of our find (Fig. 4A–D). In addition, the cells of these mosses are smaller than the bodies that constitute our find.

Products of maceration of lacustrine deposits may contain not only plant but also animal remains. For example, clitellate annelid cocoons are found associating with other remains of terrestrial and marine biota since the Triassic (*e.g*., Manum *et al*., 1991; Steinthorsdottir *et al*., 2015; McLoughlin *et al*., 2016). Similarly to our object, they withstood HF treatment and showed a multilayered arrangement. However, their layers are constituted of numerous threads, which do not form any compartments (Manum *et al*., 1991; Steinthorsdottir *et al*., 2015; McLoughlin *et al*., 2016).

Conclusion

The mesofossils that we have found do not represent pollen or spore masses and they are not related to the ginkgoalean cone from which they were macerated. They are multicellular structures, but we are unaware of any higher plant tissue that would have looked like that. Colonial algae seem less dissimilar to it than remains of land plants, but we have not found any close analogue among them as well. There is a possibility that the object under study represents portions of walls of some resting stages of an unknown organism. As we are more knowledgeable in botanical objects and failed to find suitable analogues among them, it is possible that the clue

lies in the world of zoology. We will be thankful for ideas that could help us to interpret our find.

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