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# *Pseudoschizaea* sp. from the Early Jurassic of Italy: Fine Structure and Comparison

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**Abstract**—The dispersed palynomorph *Pseudoschizaea* sp. of unknown affinity from the Jurassic of Italy was studied under transmitted light, confocal, fluorescent, scanning, and transmission electron microscopy. A comparison with spores of mosses and fungi, algal cysts and resting eggs of worms has been conducted. Similar sculpture pattern and size range are observed in some algae and fungi. A cross striation of the wall, discovered for this taxon, is so far unknown among algae and fungi studied with a transmission electron microscope, but channels similar to those of *Pseudoschizaea* are observed in some particular wall layers of some algae. The possible relationships and ecology of the producers of such palynomorphs are discussed.

**Keywords:** Jurassic, *Pseudoschizaea*, wall ultrastructure, algal cysts, fungal spores

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## INTRODUCTION

Spheroidal and ellipsoid flattened palynomorphs ca. 35–40 in size with a distinctive concentric plicate surface pattern are represented in sediments of different natures, geographic areas and age (from the Paleozoic almost to the present day). These palynomorphs are unified under the generic name *Pseudoschizaea* Thiergart et Frantz ex R. Potonie emend. or under a group of genera *Pseudoschizaea*, *Circulisporites* de Jersey, *Concentricystes* Rossignol, and *Chomotriletes* Naumova. Despite this, these palynomorphs have so far been studied mostly under transmitted light (LM), rarely by means of scanning electron microscopy (SEM), and assumptions about their relationships are rather speculative. This appreciably reduces the level of interpretation of the sediments where these remains can be found (considering their widespread occurrence), and the understanding of ecology and evolution of the organisms which could have produced the palynomorphs. Possible interpretations of the palynomorphs by different authors include spores of higher plants, algal cysts, fungi spores, eggs of a number of invertebrate groups (e.g., see review in: Scott, 1992). For precise interpretation of the palynomorphs, a detailed investigation by means of light and electron microscopy was required, to obtain maximum information. This was the aim of this study.

## MATERIAL AND METHODS

The samples studied originate from sediments of the Rotzo Formation outcropping near Bellori village (Verona Province, Northeastern Italy) (Fig. 1). The formation belongs to the Calcari Grigi Group; fossil remains of mollusks, foraminifers, plants and amber, and dinosaur footprints have been described from the formation (Wesley, 1956, 1958; Bosellini and Broglio Loriga, 1971; Clari, 1975; Avanzini et al., 2006; Neri et al., 2017). The age of the two coal-clay layers containing *Pseudoschizaea* is Pliensbachian (for more detail see: Neri et al., 2017, 2018; Fig. 2). The composition and proportions of the pollen assemblage were given by Neri et al. (2017). Samples for palynomorphological study were processed according to standard techniques, macerated and treated with HCl, HF, and $HNO_3$. The residue obtained after washing and sifting (sieving?) was embedded in glycerin for further investigation. Palynological analysis of the sample revealed the presence of psilate and ornamented spores of pteridophytes, and pollen grains Circumpolles.

The sample was studied under an Olympus CX41 light microscope, and palynomorphs *Pseudoschizaea* that were found were individually moved to a new slide in a glycerin drop. Further preparation for LM, SEM and transmission electron microscope (TEM) followed the techniques described by Zavialova et al.

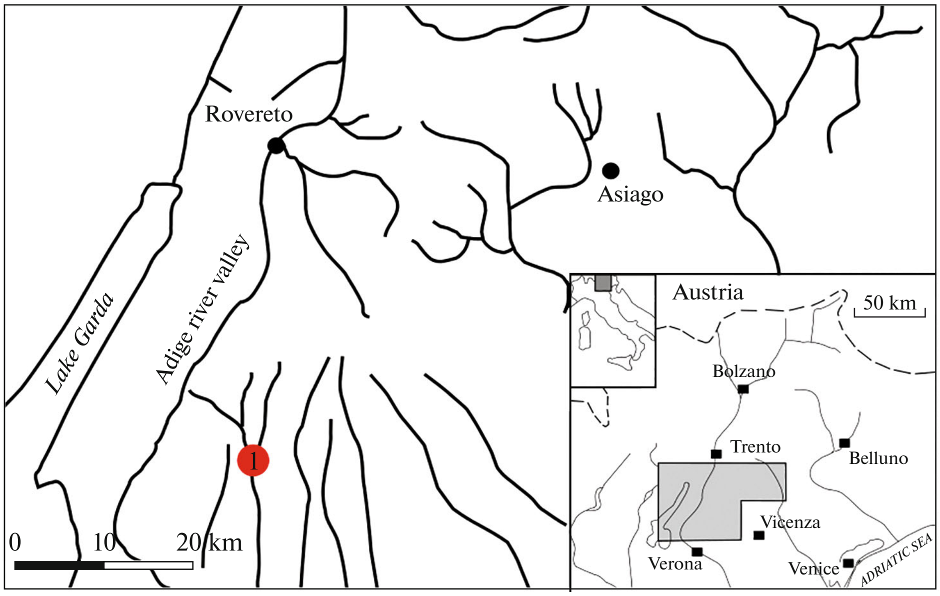


**Fig. 1.** Map showing the Bellori village locality (1).

(2018). A SEM stub with pollen grains was coated with gold and studied using SEM TESCAN VEGA-II XMU (accelerating voltage 30 kV). Ultrathin sections were made using a Leica UC6 ultramicrotome. Some sections were additionally stained with lead citrate and uranyl acetate and studied using TEM, Jeol 100 B and Jeol 1011 (accelerating voltage 80 kV). Other parts of the sections were studied without additional staining, using the same microscopes. The pollen grains were also studied with an LSM 780 confocal (CLSM) microscope [technique described by Gavrilova et al. (2018)]. Altogether 15 palynomorphs were studied with LM, SEM, and TEM.

Spores and algal cysts from Jurassic deposits of Russia, and Devonian sediments of Poland, were used for comparison in the study of cell wall autofluorescence with a fluorescence microscope (FM). An Axioplan 2 imaging MOT microscope, AxioCam HRc digital camera, and AxioVision 4.7 software (Zeiss, Germany) were used to study autofluorescence. Fluorescence was excited with a mercury lamp. To analyze the fluorescence, we used different sets of filters. Autofluorescence excitation appears in the range 540–552 nm, detection is possible at wavelengths > 590 nm, which are applied in registration of autofluorescence of sporopollenin walls of modern and fossil pollen and spores (Matveyeva et al., 2012). Measurements of the studied palynomorphs were made under LM, SEM, and TEM. In the article, the terminology of Hesse et al. (2009) is used. Facilities of the Center for collective use of the Borissiak Paleontological institute of the Russian Academy of Sciences (PIN RAS; LM, SEM), Faculty of Biology of Moscow State University (MSU; TEM, FM), and Komarov Botanical Institute (BIN RAS; CLSM) at the Core Centrum "Cell and Molecular Technologies in Plant Science" of BIN RAS were used.

The studied sample no. C1 is housed at the Institute of Geosciences and Earth Resources, Padova, Italy.

## RESULTS

**LM.** Palynomorph ellipsoid (Figs. 3a, 3b, 3d) or spheroidal (Figs. 3c, 3e, 3f), 37.3 (30.7–44.8) × 47.0 (42.3–50.8) µm, flattened. The surface is represented by a distinctive concentric plicate pattern, 'wrapped' around an ellipsoid (rarely circular) region in the central area. Rare, in some cases quite large, irregularly spaced holes (Figs. 4a–4f) can be observed on the surface. No signs of an aperture or any similar structure were found. The wall is relatively thick, one-layered.

**SEM.** Size of the palynomorph in SEM is 35.9 (30.4–41.4) × 47.2 (42.8–52.2) µm. Surface sculpture is plicate with rare, in some cases quite large, irregularly spaced holes (Figs. 4a–4f), width of the ribs varies from 0.14 to 0.21 µm (Figs. 4g–4i).

**TEM.** The wall is unequal in thickness along the perimeter (Figs. 5a–5d), 1.35 (0.2–4.1) µm thick on average. The wall ultrastructure consists of one homogeneous layer of unequal thickness with 'denticles' on both outer and inner sides. The largest thickness is usually observed in the lateral regions of the palynomorph (Figs. 5e–5g). The outer 'denticles' coincide with the plicate pattern of the surface, the inner 'denticles' are continuations (opposite ends) of the outer 'denticles'. In some areas a striation through the wall thickness is observed (Figs. 5e–5g). The width of the 'denticles' is 0.3 (0.2–0.4) µm; prevalently, they can

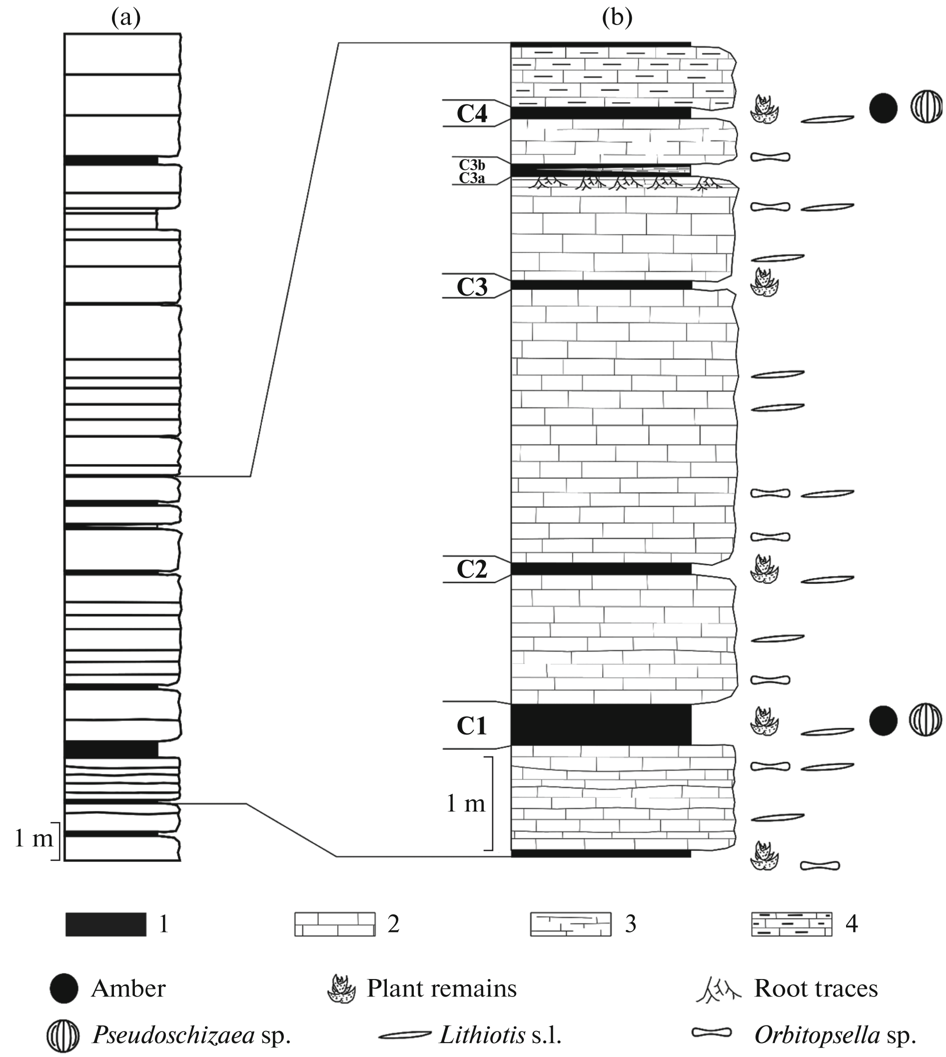


**Fig. 2.** Studied part of the section: (1) clay rich in organic matter and carbon, (2) gray to yellow massive limestone, (3) fine-grained limestone, (4) marly limestone. C1–C4—collected samples, C1—studied sample.

be distinguished in folds in the lateral regions, other areas of the wall look homogeneous. In some regions fragments of an unstructured layer are observed on the inside of the wall, probably an unpreserved inner layer of the wall, or an artifact (Figs. 5e, 5g).

**CLSM.** The palynomorphs are ellipsoid or spheroidal, flattened, the surface is plicate, the ribs are thin. The small circular holes in the wall of some palynomorphs were observed in LM (one or two per palynomorph); it was suggested that these holes are a kind of aperture. However, it was revealed during the CLSM study of the serial optical sections (Figs. 6a–6e) that the holes are splits divaricating in different directions and visible on the fold of the fossilized wall (Figs. 6n, 6o). The splits are often found in the palynomorph wall (Figs. 6h, 6i, 6l). The palynomorphs are unevenly flattened, a cavity can be often seen inside (Figs. 6j, 6k). The palynomorph images reconstructed from the sections demonstrate a plicate surface; the ribs are thin, long, mostly unidirectional, quite densely placed. CLSM shows all the surface characters (Figs. 6f, 6g), available to explore using SEM. CLSM was also used to help solve one further issue—a reconstruction of inner surface of the wall (Fig. 6h). On the inner surface of the reconstructed palynomorph, ‘denticles’ are sometimes observed (Fig. 6h), ‘cross striation’ of the wall (Figs. 6l–6n) is also observed in some palynomorphs, this may indicate that the wall is formed by a number of narrow strips, closely adjoined to each other. However, at other times the wall is homogeneous, probably when the section was made along the strips.

**FM.** In the autofluorescence study, the *Pseudoschizaea* fluoresced weakly in different filters (Figs. 7a, 7d). The fossil spores and pollen grains studied for comparison (Figs. 7b, 7e) as well as algae [*Endoscrinium* (Klement) T.F. Vozzhennikova, *Fromea* Cookson et Eisenack, *Pareodinia* Deflandre,

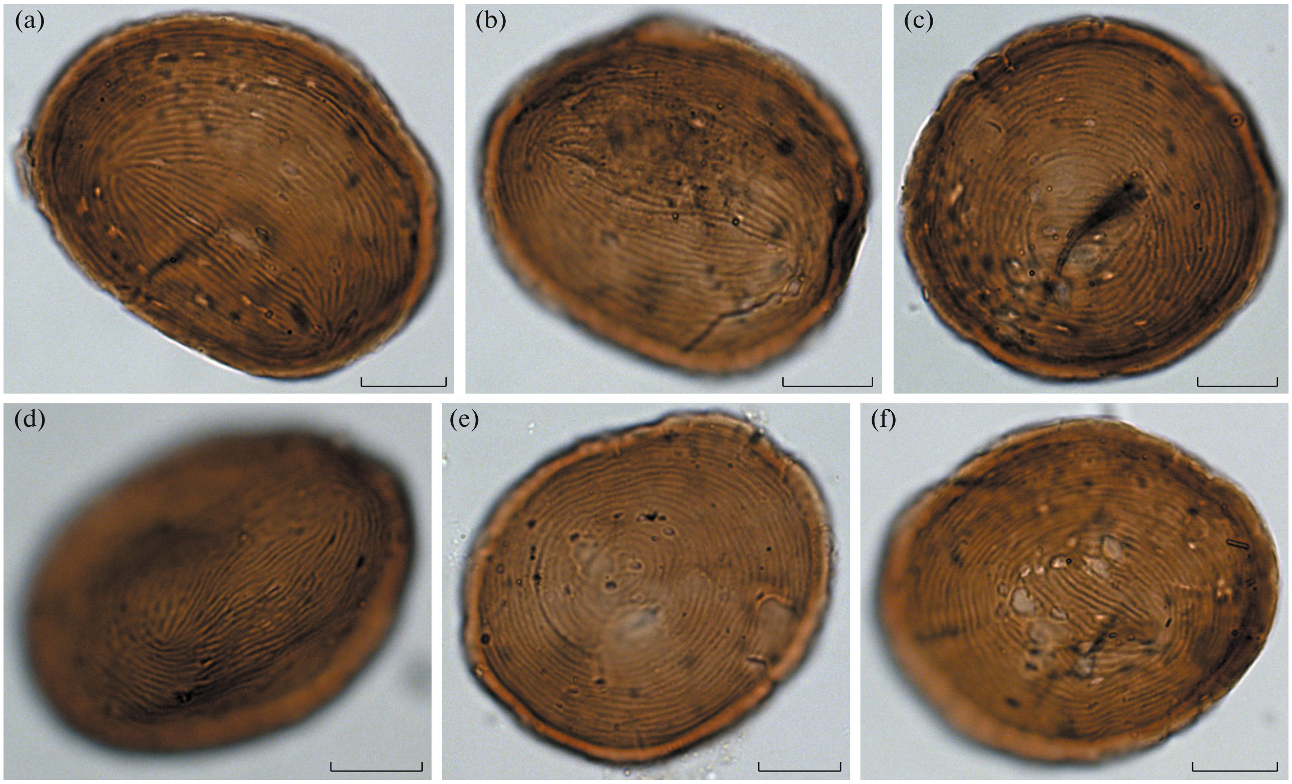


**Fig. 3.** *Pseudoschizaea* sp., sample no. C1, LM: (a, b, d) ellipsoid form; (c, e, f) spheroidal form. Scale bar 10 μm.

*Tubotuberella* Vozzhennikova] (Figs. 7c, 7f) showed a similar intensity response. The palynomorphs and cuticle fragments differed notably in their autofluorescence intensity in different filters. The cuticles are brightly fluorescent, specifically at wave-lengths more than 590 nm in both of studied specimens (Figs. 7e, 7f).

## DISCUSSION

Similarities of *Pseudoschizaea* to spores of Schizaeaceae, noted previously and referred to in the name, does not reflect their relationships. The similarity is expressed in the sculpture pattern of the palynomorph surface, however, a laesura (or any other aperture) is absent in *Pseudoschizaea* and the wall ultrastructure differs markedly. In Schizaeaceae the striation and inner 'denticles' peculiar to *Pseudoschizaea* are never observed (Tryon and Lugardon, 1991; Skog, 1993; Parkinson, 1994, 1995; Ramos Giacosa et al., 2015; Ramos Giacosa and Barakat, 2018). The same applies to the majority of other spore-bearing plants and all seed plants: the complex of features of the sporoderm structure (absence of an aperture pronounced morphologically or ultrastructurally; distinctive wall striation; ribbing, observed on both the outer and inner sides of the wall) unambiguously excludes the material from being attributed to spore-bearing or seed plants. Following many researchers (e.g., Christopher, 1976; Scott, 1992), we describe the surface of *Pseudoschizaea* as plicate; some other authors (e.g., Milanesi et al., 2006) sometimes call it striate. A plicate surface often includes several layers of an ectexine or even all layers of an ectexine, whereas in contrast a striate surface includes a tectum or part of one. In our situation, of these two terms, "plicate surface" is more suitable for describing *Pseudoschizaea*. However, taking into consideration inner 'denticles' of the wall of *Pseudoschizaea*, it is obvious that another non-palynological term is needed here, for example, banded, string-like surface. In the present case, the 'denticles' appear on both the outer and inner surfaces of the *Pseudoschizaea* wall. It can be assumed that a development of a wall of this type with layers perpendicular to the surface should happen a little differently than in spore-bearing and seed plants, in which the wall layers are formed parallel to the surface. Though, this is impossible to prove for the moment, and additional data are needed for interpretation of a wall of this type.

The most viable candidates for comparison, which were also reviewed by the previous *Pseudoschizaea* researchers, are spores of mosses, algal cysts, spores of fungi and eggs of invertebrates.

**Comparison of the palynomorph under study with bryophytes.** Bryophytes include three main groups: hornworts, liverworts, and mosses. Hornworts are a small group of plants producing spores of medium size (10–80 μm), mostly monads (tetrads are known in a

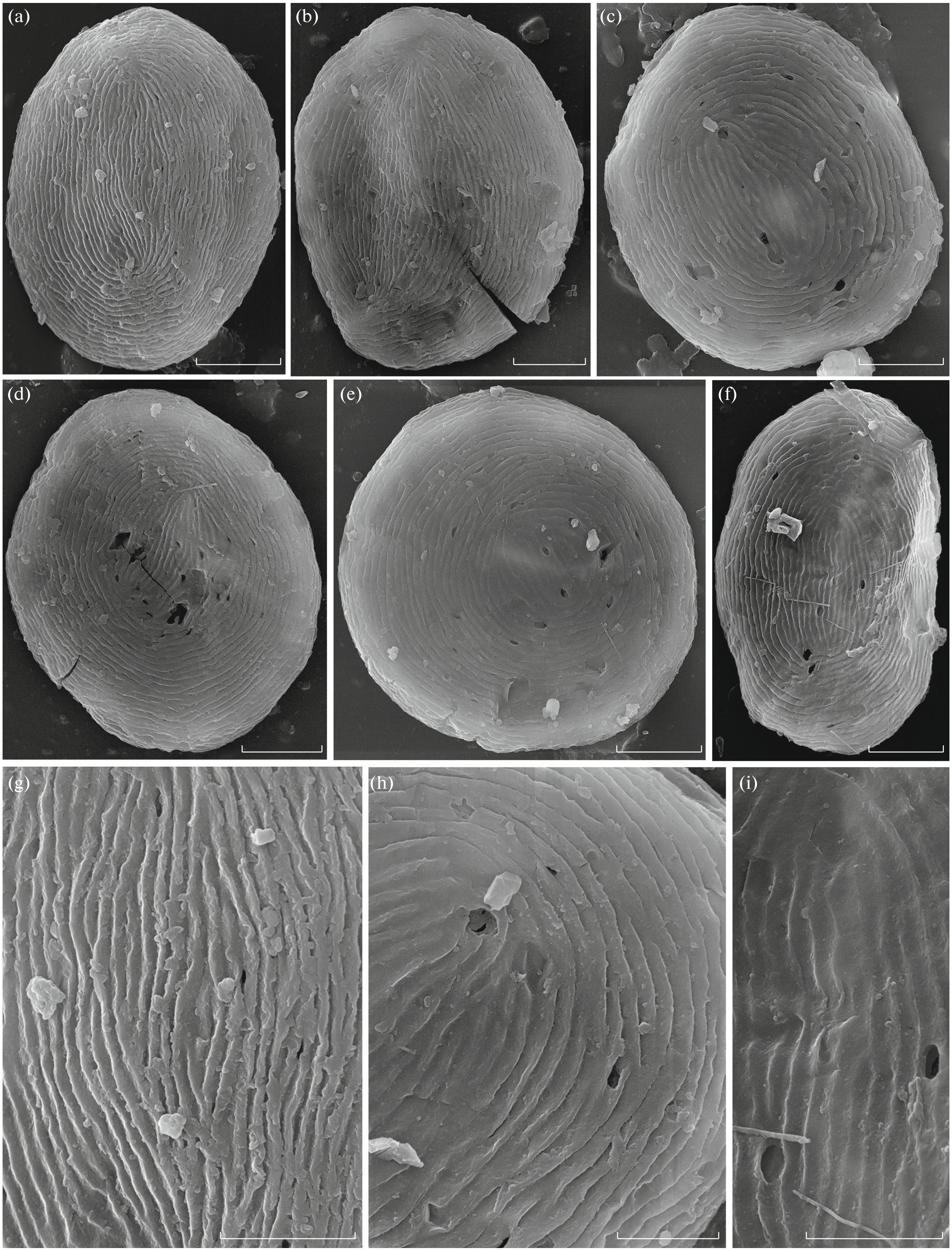


**Fig. 4.** *Pseudoschizaea* sp., sample no. C1, SEM: (a–f) general view of the palynomorph; (g–i) surface areas under higher magnification, ribs and small holes visible. Scale bar is: (a–e) 10; (g–i) 5 μm.

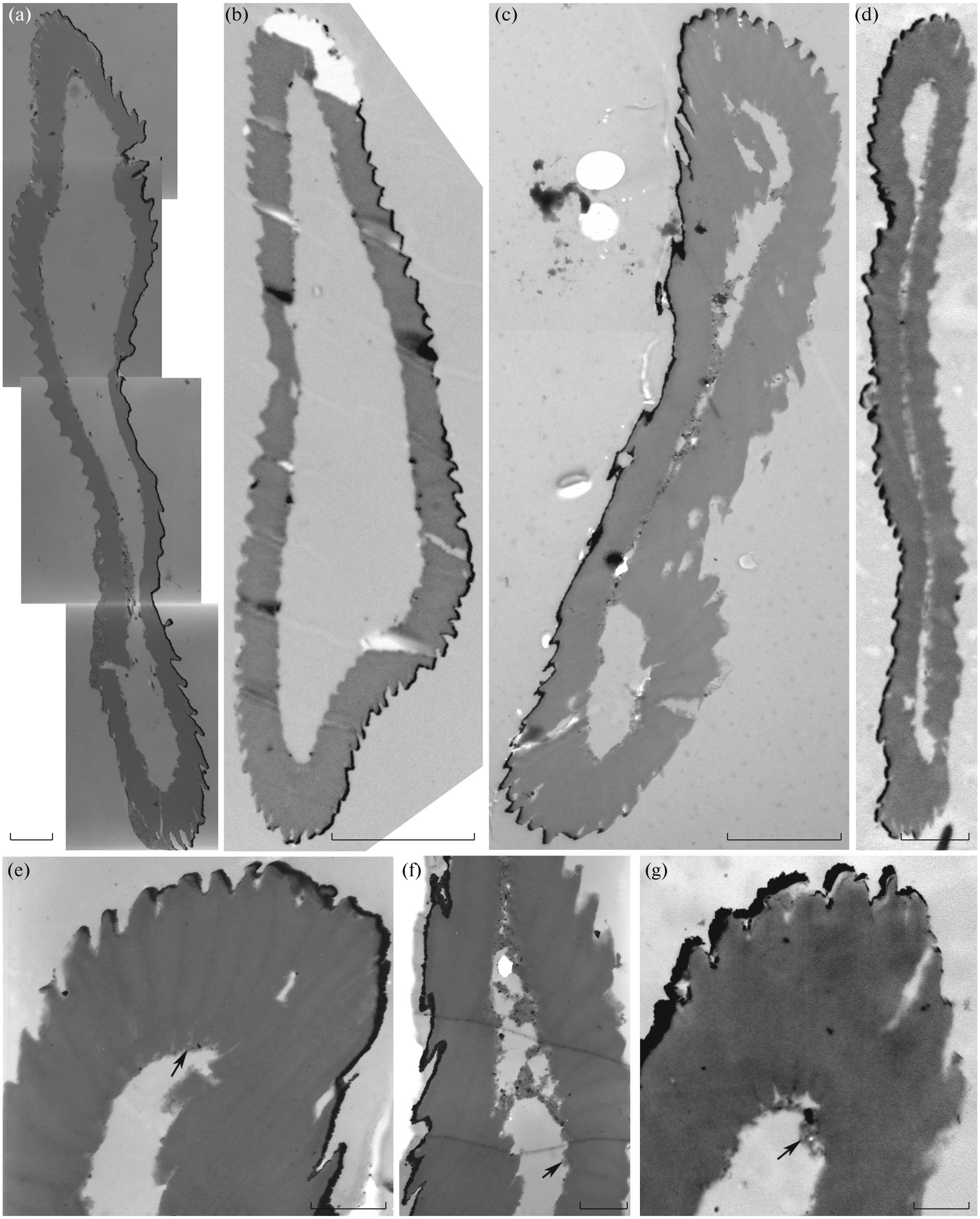


**Fig. 5.** *Pseudoschizaea* sp., sample no. C1, TEM: (a–d) sections through the palynomorph, general view; (e–g) wall regions, cross striation and poorly preserved inner layer (arrow) are visible. Scale bar is: (a, e, f) 1.25; (b, c) 5; (d) 2.5; (g) 0.5 μm.

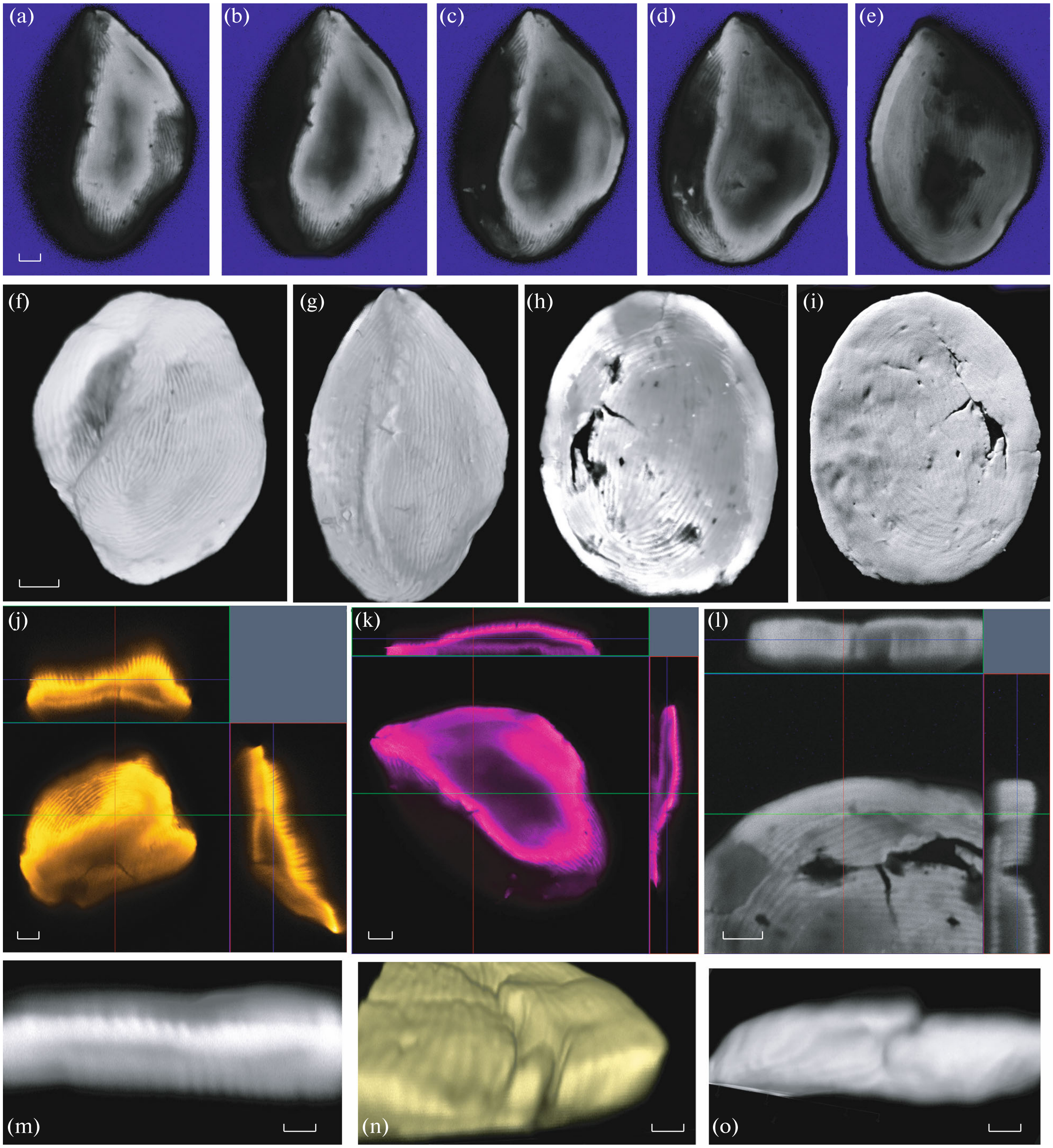


**Fig. 6.** *Pseudoschizaea* sp., sample no. C1, CLSM: (a–e) series of optical sections through a palynomorph; (f, g, i) general view of reconstructed palynomorphs; (h) inner surface of the palynomorph "i"; (j–l) "ortho"-mode (projection of three-dimensional objects on a two-dimensional surface): sections through three palynomorphs (f, g, i), respectively, showing the optical section and two projections of it; (m) virtual section the reconstructed palynomorph perpendicular to long axis of palynomorph and ribs on its surface, (n, o) reconstructed parts of palynomorphs showing breaks of the wall. Scale bar is: (a–e, j–l) 5; (f–i) 10; (m–o) 2 μm.

single representative of genus *Leiosporoceros* Hässel—*L. dussii* (Stephani) Hässel de Menéndez), trilete (monolete are known in *L. dussii*). The sculpture may be echinate, papillate, coarse, verrucate, reticulate, rarely striate (in *Hattorioceros striatisporus* (J. Haseg.) J. Haseg.) or psilate (in *L. dussii*). The exosporium is usually thick, granular, but representatives with quite a thin exosporium (0.4–1.0 μm) exist too. *Hattorioceros striatisporus* (J. Haseg.) J. Haseg is the only representative of the group which can be compared with *Pseu-*

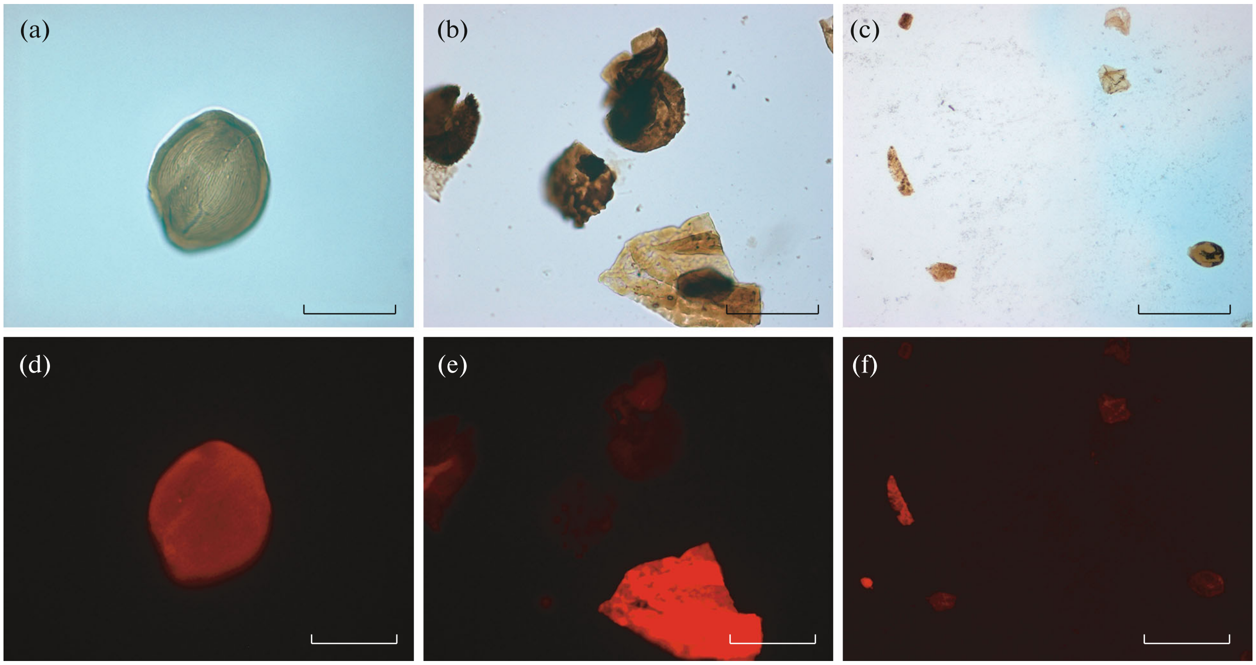


**Fig. 7.** (a–c) LM, (d–f) FM: (a) *Pseudoschizaea* sp., sample no. C1; (b) dispersed spores and cuticle remains from Devonian sediments of Poland; (c) cuticle remains and algae (*Tubotuberella* and *Fromea*) from Jurassic sediments of Russia; (d) *Pseudoschizaea* sp., sample no. C1; (e) dispersed spores and cuticle remains from Devonian sediments of Poland; (f) cuticle remains and algae (*Tubotuberella* and *Fromea*) from Jurassic sediments of Russia. Scale bar: (a, b, d, e) 30 μm; (c, f) 100 μm.

*doschizaea*. *Pseudoschizaea* and *H. striatisporus* are similar in wall sculpture, but spores of *H. striatisporus* are appreciably smaller (around one third of the size), and the ultrastructure of the wall has not been studied yet (Zhang et al., 2011).

Liverworts are a very diverse group, they produce spores, which are monads or tetrads, large, in some cases small (from 17 to 30 μm), but always both spores and elaters are represented in the spore-bearing capsules (except Sphaerocarpales). A tetrad mark is usually clearly seen. Sculpture can be very different, echinate and granulate, projections are often very curious, can be united by ridges or form a reticulum. The sporoderm is thick (if measured with echini), consisting of many layers, moreover, from the beginning it is formed as lamellate, and this lamellation is always preserved in mature walls. Spores of all representatives of this group differ markedly from the studied palynomorph *Pseudoschizaea*.

Mosses are the largest group among Bryophyta. Their spores are diverse, usually monads, sometimes aggregated into tetrads, the sizes are from tiny to very large (6–310 μm), in some species with a tetrad mark. The spore surface can be represented by different types: from psilate or granulate to verrucate or echinate, or even reticulate-baculate. Ultrastructure of the spore walls can be complex, multilayered, involving lamellate, homogeneous, or granular layers. Basal groups of mosses (Sphagnopsida, Andreaeopsida) are characterized by the most complex ultrastructure of spore walls. Usually the sporoderm is quite thin, represented by granules of the outer perispore and a homogeneous exosporium. Thickening of the endosporium is often marked in the region of an obscured laesura, which cannot be observed with either LM or SEM. A perine often has a wavy inner surface, but the perine is always loose, more or less granular, usually not forming a continuous layer, looks like aggregated granules. The perine is only well-developed in mosses. The inner surface of the *Pseudoschizaea* sections is most similar to what is observed in *Andreaea* Hedw. (Brown et al., 2015). As in *Pseudoschizaea*, a cross striation is sometimes observed in mosses [e.g., *Oedipodium griffithianum* (Dicks.) Schwägr.; Polevova, 2015] in the exosporium, the striation resembles slits between fused granules. The inner exosporium is thicker and more homogeneous. By contrast with the walls of the spores of the mosses, in *Pseudoschizaea* the whole layer is pierced with narrow cavities, which appear like coalescent plates forming the relief of the outer and inner surfaces.

**Comparison of the palynomorph under study with algae.** There is much less information on the ultrastructure of spores of fungi and algal cysts. Among algae, prevalently cysts and spores (having different names in different groups), gyrogonites (fossil calcareous shells of charophyte algae), and rarely cell walls (for some representatives of green algae) are discussed. Most researchers assign *Pseudoschizaea* to algae after Rossignol (1962) and Thiergart and Frantz (1962).

Principally, Zygnemataceae (e.g., Zippe, 1998; Scafati et al., 2009 and others) are discussed, in particular, *Debarya* Wittrock. However, the sculpture pattern and shape of *Debarya* zygospores differ markedly from those in *Pseudoschizaea*, but the fine structure of the wall has not yet been studied (Van Geel and Van der Hammen, 1978; Head, 1992; Kołackzek et al., 2012). Besides, species similar to *Pseudoschizaea,* in particular in features of the general morphology of the cell wall and cysts, can be found among representatives of Chrysophyceae and Chlorellaceae. A plicate spore surface occurs in some representatives of Oedogoniaceae and Characeae (Van Geel and Van der Hammen, 1978; Zippe, 1998; Tiss et al., 2019). Cyst sizes and wall thickness are also comparable with those in *Pseudoschizaea*. However, the plicate pattern is markedly different from that in the palynomorph studied, and the wall ultrastructure also differs in the studied representatives (Van Geel and Van der Hammen, 1978; Zippe, 1998; Domozych et al., 2010; Tiss et al., 2019). The surface sculpture of cysts, most similar to that in *Pseudoschizaea*, can be found among euglenids (e.g., Hindak et al., 2000; Leander and Farmer, 2000). The cyst sizes and wall thickness in euglenids are comparable to those in *Pseudoschizaea*. In euglenids, as in *Pseudoschizaea*, holes are observed on the wall surface (pellicle pores, e.g., Leander and Farmer, 2000), however, the holes in the studied species are not as regularly spaced as in euglenids, and there are fewer of them. The fossil palynomorph *Moyeria* Thusu, with similar surface sculpture, is also close to euglenids (Gray and Boucot, 1989). Strother et al. (2019) studied the wall ultrastructure of two *Moyeria* specimens: *Moyeria* sp. and *M. uticana* Thusu, from the upper Silurian of Scotland, and assigned of the corresponding palynomorphs to euglenids. The wall ultrastructure of *Moyeria* they illustrated is unilayered, as in *Pseudoschizaea*, however, the distinctive cross striation and 'denticles' inherent to the palynomorph under study are absent in *Moyeria*. However, considering the diversity of euglenids demonstrated in the modern material, it cannot be ruled out that *Pseudoschizaea* could belong to this group too. The cross striation of the wall distinctive to *Pseudoschizaea* was found in some layers of the wall of the fossil taxon *Tasmanites* Newton (Arouri et al., 2000; Vigran et al., 2008; Telnova, 2012), which is presumed to belong to algae; however, the morphology of *Tasmanites* contrasts markedly with the morphology of *Pseudoschizaea*.

**Comparison of the palynomorph under study with spores of fungi.** Spores of fungi are overwhelmingly characterized by considerably smaller size; however, remarkably similar wall structure was found in many representatives, especially in ascospores of species of *Neurospora* Shear et B.O. Dodge (Ascomycota) (e.g., Byrne, 1975). Furthermore, a plicate surface was noted for a number of taxa, e.g., *Ascobolus* Pers., *Caryospora* Leger (Ascomycota) [see a short review on spores of fungi with a plicate surface in Gray and Boucot (1989) and review on fossils of Ascomycota in Taylor et al. (2015)]. The only spores of fungi of a size which is close to *Pseudoschizaea* are urediniospores, which are characterized by an echinate sculpture (e.g., Baka et al., 2004). Wall ultrastructure is simple, usually homogeneous, and in general terms, it can be said that it is similar to the wall of *Pseudoschizaea* and a number of representatives, however, such cross striation and wavy inner surface were not observed in any of the discussed variants.

**Comparison of the palynomorph under study with the resting eggs of invertebrates.** Among invertebrates, eggs of Collembola, Nematoda, Trematoda, and Rotifera are the most promising for comparison with the palynomorph under study. The wall ultrastructure of eggs of the known representatives makes a comparison with Rotifera and Collembola not very effective due to a significant difference in their structure; the size of eggs of representatives of these groups are often larger too, and their sculpture demonstrates a different structure (e.g., Gilbert and Wurdack, 1978; Wurdak et al., 1978). Wall structure in number of worm taxa (especially, Trematoda) is though mostly homogeneous, but is of similar thickness, while egg sizes are comparable to the size of *Pseudoschizaea* (e.g., Bird and McClure, 1976; Swiderski et al., 2010, 2014; Conn et al., 2018). Badly preserved remnants of a layer on the inside of the wall of *Pseudoschizaea* also resemble a granular layer on the outer wall of representatives of worms. However, the surface usually observed in resting eggs of worms is psilate, unlike that of *Pseudoschizaea*.

Autofluorescence does not help to clarify interpretation of *Pseudoschizaea*. All palynomorphs fluoresce weakly in contrast with fossil cuticles, which does not exclude comparisons with spores of land plants and algae. It is possible to expect that fossil walls of invertebrate eggs will differ from palynomorphs as much as cuticles do.

Thus, individual features of the sculpture of *Pseudoschizaea* resembled one representative of mosses, and a number of fungi; its overall general morphology resembled cysts of a number of algae. Some cysts and spores of algae and mosses show similar features of the wall ultrastructure. Currently, the hypothesis that *Pseudoschizaea* belongs to algae, but euglenids rather than the previously proposed Zygnemataceae, seems least controversial.

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