RESEARCH PAPER



First data on in situ pollen of *Permotheca sardykensis* Zalessky 1929 from the middle Permian of the Russian Platform

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Received: 9 January 2020 / Accepted: 29 March 2021 © Paläontologische Gesellschaft 2021

Abstract

Pollen grains were extracted from sporangia of the pollen organ *Permotheca sardykensis* for the first time. The material originates from the middle Permian deposits of the Kostovaty locality (Udmurt Republic, Russia). The pollen grains were studied with light, scanning, and transmission electron microscopy. The pollen grains are rounded to oval, protobisaccate, with a leptoma. The sacci are very small and difficult to see under transmitted light, but, in a scanning electron microscope, differ from the corpus region in their sculpture (they can be distinguished by their psilate surface versus verrucate corpus sculpture). The leptoma was distinguished in the transmission electron microscope only by a considerable thinning of the pollen wall. The pollen wall consists of two layers which may be interpreted as a thick ectexine without a clear subdivision into sublayers and a thin endexine. Outside the pollen grains, remnants of a thin probable tapetal layer are present. The observed results could arise from pollen wall deterioration during diagenesis or incomplete pollen wall development. The pollen grains from the sporangia of *P. sardykensis* strongly differ from in situ pollen types which were described from other *Permotheca* species earlier or were associated with Peltaspermales. This may indicate a heterogeneity of the genus *Permotheca*.

Keywords Exine ultrastructure · Peltaspermales · Pollen organ · Roadian–Wordian · Subangara

Introduction

The genus *Permotheca* Zalessky 1929, with the type species *P. sardykensis* Zalessky 1929, was described from the Kazanian deposits of the Russian Platform for pollen organs of unidentified affinity (Zalessky 1929). Later, eight more species were described from the Permian deposits of Subangara area (Gomankov and Meyen 1986; Naugolnykh 2007, 2013) and one from the Triassic of Gondwana (Retallack 2002). For some species (*P. striatifera* S. Meyen et Gomankov 1986, *P. vesicasporoides* Meyen, Esaulova et Gomankov in Gomankov et Meyen 1986, and *P.? vittatinifera* S. Meyen et Gomankov 1986), more or less convincing evidence of their peltaspermalean affinity was suggested (Gomankov

Handling Editor: Hans-Georg Herbig.

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² Laboratory of Paleobotany, Borissiak Paleontological Institute of Russian Academy of Sciences, Moscow, Russia and Meyen 1986). The peltaspermalean affinity has been hypothesized for some other species, which are *P. bifurcata* Naugolnykh 2007, *P. disparis* (Zalessky 1937) Naugolnykh 1998, *P. colovratica* Naugolnykh 2013, and *P. helbyi* Retallack 2002 (Naugolnykh 1998, 2007, 2013; Naugolnykh and Kerp 1996; Retallack 2002). These suggestions are mostly based on co-occurrence with peltasperm leaves or even less convincing circumstantial evidence. Nonetheless, nowadays, based on the previous research, there is a tendency to consider *Permotheca* as a peltaspermalean pollen organ (e.g., Naugolnykh 2007).

The Peltaspermales are seed ferns which are known almost worldwide (North America, South America, Europe, the Russian Platform, Southern Africa, India, and Australasia) from the Upper Carboniferous to the Upper Triassic (Anderson et al. 2007; Taylor et al. 2009). Some scientists suggest the Peltaspermales to be one of the basal groups of the Ginkgoopsida (Meyen 1984; Anderson et al. 2007), so the peltasperms are very important for understanding the evolution of the gymnosperms. Compared to the foliage and ovule-bearing organs, male reproductive organs which are ascribed to the Peltaspermales are very poorly understood. At least six pollen genera (*Falcisporites* Leschik emend.

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Klaus 1963; Cycadopites Wodehouse 1933; Ephedripites Bolkhovitina 1953; Protohaploxypinus (Samoilovich) Hart 1964; Vitreisporites (Leschik) emend. Jansonius 1962; and Vittatina Luber ex Jansonius 1962) were reported from pollen organs of the supposed peltaspermalean affinity (Balme 1995). Pollen grains of Falcisporites type were assigned to Vesicaspora Schemel 1951 by other authors (Gomankov, Meyen, 1986) or even Alisporites (s.l.) Daugherty 1941, if found dispersed (Naugolnykh 2013). It is an unusual case for the gymnosperms that so many different pollen types are associated with the same order. Among the peltaspermalean pollen organs, Permotheca is one of the most problematic genera. The synangia of *Permotheca* have a very simple morphology with few distinctive features. Taking this into account, in situ pollen from Permotheca assumes a great significance for the systematics of the genus. Pollen types which were earlier reported from the sporangia of Permotheca (Table 1) are Vesicaspora/Falcisporites (protobisaccate), Protohaploxypinus (bisaccate taeniate), and Vittatina (asaccate taeniate) (Gomankov and Meyen 1986; Krassilov et al. 1999a, b; Zavialova and Karasev 2015). The ultrastructure of in situ pollen grains from Permotheca was studied for Vesicaspora/Falcisporites (Krassilov et al. 1999a, b) and Protohaploxypinus (Zavialova and Karasev 2015). For P. sardykensis, no data on the in situ pollen have been available until now.

Materials and methods

A part of the studied material was kindly provided by Alexey Gomankov (Komarov Botanical Institute of Russian Academy of Sciences, Saint-Petersburg, Russia; BIN RAS). Additional material was collected in 2016 during a joint field trip of the laboratory of arthropods and laboratory of paleobotany of the Borissiak Paleontological Institute of Russian Academy of Sciences, Moscow, Russia (PIN RAS). The material comes from the Subangaran locality called Kostovaty (Udmurt Republic, Russia; N56.9, E54.1; Fig. 1). According to Gomankov (2012, 2019), this locality is a middle Permian (Roadian-Wordian) in age based on ostracod fauna. Gomankov (2019) reported the peltasperms Ustyugia udmurtica Gomankov 2008, Odontopteridium sp., and Compsopteris sp.; angaropeltaceans Phylladoderma (Phylladoderma) meridionalis Meyen in Meyen et Gomankov 1971, Cardiolepis sp., Nucicarpus piniformis Neuburg 1965, and Permotheca vesicasporoides; cordaitaleans Krylovia sp.; sphenophytes Paracalamites sp.; fern-like leaves of Pecopteristype; and incertae sedis leaves assigned to Ginkgophyllum rhipidomorphum Gomankov 2018 from Kostovaty and the nearby contemporaneous Chepanikha locality. Foraponova and Karasev (2019) supplemented the list of taxa with ovuliferous organs of early conifers Sashinia antiqua Gomankov 2010, leaves of mosses (cf. Intia variabilis Neuburg 1960), pollen organs of a probable peltaspermalean affinity Permotheca disparis, incertae sedis pollen organs Permotheca sardykensis, and incertae sedis leaves Rhipidopsis cf. palmata Zalessky 1932. Sporangia of Permotheca vesicasporoides and P. disparis contained pollen grains of the Vesicaspora/Falcisporites type (Foraponova and Karasev, in preparation).

Untreated specimens were studied under a Leica M165c stereomicroscope and photographed with a Leica DFC420 camera. Fragments of the sporangia of P. sardykensis were used for the research. The material first was treated with HCl for 15 min for depleting carbonates, and then, the material was washed with water and treated with HF for 2 h for resorption of non-organic particles. Afterwards, it was washed with water again, and then, the material was kept in HNO₃ (65%) for 20 min, washed from the acid and placed into distilled water. KOH (a pellet per ca. 20 ml of distilled water) was added by drops. Process of oxides resorption was controlled under a stereomicroscope. After the maceration stopped, the material was washed with distilled water again. The pollen grains were in clumps and superimpose each other, so that most of the details were not seen (Fig. 3a, e). For obtaining individual pollen grains, the author tried to disintegrate the clumps with an Elmasonic One ultrasonic bath (operating frequency 37 kHz) in 3 10-min cycles, at the Geological faculty of Lomonosov Moscow State University (Moscow, Russia; MSU). After each cycle, the clumps were checked for their disintegration. Only a few small pieces of the pollen masses which allowed to get more or less full information about the pollen morphology were obtained.

After the clumps were disintegrated into smaller pieces, they were studied under light microscopy (LM) with a Zeiss Axioplan 2 microscope and photographed with a Zeiss Axiocam 105 color camera. The pollen grains were studied under a scanning electron microscopy (SEM) with a TESCAN-Vega microscope at PIN RAS with accelerating voltage 20 kV. Ultrathin sections were obtained by standard techniques (after Zavialova et al. 2018) without any staining. The sections were studied via transmission electron microscopy (TEM) with a JEM-1011 microscope (accelerating voltage 80 kV) at the Electron Microscopy Laboratory at MSU. Three specimens of P. sardykensis were used in the study. From two specimens, 32 pollen grains were obtained and studied with LM, ten pollen grains with SEM, and ultrathin sections of three pollen grains were studied with TEM. Efforts to obtain pollen grains from the third specimen were not successful.

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

In situ pollen	Protohaploxypinus	Vittatina subsaccata	Vesicaspora	Falcisporites*
Permotheca	P. striatifera ¹	P.? vittatinifera ¹	P. vesicasporoides ¹ P. disparis ² , *P. colovratica ³	P. helbyi ⁴ , P. colovratica ³ , *P. vesicasporoides ⁵
Sacci	Bisaccate ⁶	Asaccate ^{8,9} or with small sacci, e.g. in <i>V. costabilis</i> ¹¹	Monosaccate, saccus bilobed	Bisaccate ¹⁶
Saccus type	$Protosaccate^7$	- ^{8,9} /Eusaccate in V. costabilis ¹¹	Proto-/Eusaccate ¹⁴	Proto- ^{15,16} /Eusaccate ¹³
Proximal surface	Striate ⁶	Striate ^{8,9}	Non-striate	Non-striate
Aperture-type	Leptoma ⁶	Leptoma (divided into two areas by transversal taenia) ^{8,9}	Leptoma ²	Sulcus ^{15,16}
Additional details	1	Equatorial rim; distal surface bears a transversal taenia and thickenings on the edges ^{8,9}	Equatorial strips can change position towards equatorial plane, thereby pol- len grains may look bisaccate in polar view ¹²	Sometimes sacci make contact ¹³
Proximal exine				
Tectum	Thick continuous ⁷	Continuous ^{8.9}	Thick continuous ²	Thin homogeneous ^{13,15} If stained, outer less electron dense homo- geneous layer with rare thin lacunae and a thin more electron dense layer occur ¹⁶
Infratectum	Thinner alveolar ⁷	Columellate ^{8,9} /granulate ¹⁰	Alveolate ²	
Foot layer	Continuous homogeneous ⁷		Continuous ²	
Endexine	Shows some layering ⁷	No data	More electron dense and lamellate ²	
Additional details	Between the ribs the sporoderm is represented by endexine or endexine and foot layer ^{7}	Taeniae with cavities inside ^{8.9}	1	In saccus region continuous tectum, sporopollenin units, thin basal layer, and a thin more electron dense layer were observed ¹⁶
Distal exine	Endexine only ⁷	No data In <i>V. connectivalis</i> ectexine homogene- ous, with a very thin alveolate layer; lamellate endexine ¹⁰	Thinner with reduced alveolae ²	Thin homogeneous ^{13,15} If stained, the outer less electron dense layer thins considerably, the inner more electron dense layer remains the same thickness as in non-apertural areas ¹⁶
Aperture region	No data	No data	Alveolate infrastructure is absent ²	Very thin nearly membraneous ¹⁵ . If stained, the outer light layer thins
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¹Gomankov and Meyen 1986; ²Krassilov et al. 1999a, b; ³Naugolnykh 2013; ⁴Retallack 2002; ⁵Balme 1995; ⁶Zavialova et al. 2001; ⁷Zavialova and Karasev 2015; ⁸Koloda 1986; ⁹Koloda 1997; ¹⁰Afonin 1999; ¹¹Gomankov and Tarasevich 2008; ¹²Gomankov and Meyen 1980; ¹³Osborn and Taylor 1993; ¹⁴Zavialova et al. 2001; ¹⁵Taylor et al. 1984; ¹⁶Zavada and Crepet 1985. ^{*}Ultrastructural data are for in situ pollen grains from Pteruchus (Corystospermales)

*The other possible interpretation of in situ pollen type

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Fig. 1 Location of Kostovaty locality

Results

Pollen organs

The pollen organs consist of 2–4 (up to 10) oblong claviform sporangia sitting on a short pedicle (Fig. 2a, b), which occasionally branch (see Zalessky 1929). The sporangia are 3.4 (2.1–4.5) mm long and 1 (0.8–1.3) mm wide. Usually, the sporangium length is 3.5 times larger than the width. The widest parts of the sporangia are shifted to the apical part and the sporangium bases are strongly pulled aside (Fig. 2c, d). The sporangium bases gradually pass into the branchlets of the pedicle. The sporangium surface is covered by tiny longitudinal wrinkles (Fig. 2b).

Pollen grains

Due to insufficient preservation, the morphology details are difficult to observe Fig. 4. The pollen grains are bisaccate and have a leptoma, $60 \mu m$ (54–68 μm) in size. They can be described as circular in outline (Fig. 3c, d), but because of a thin pollen wall, the pollen grains are easily crumpled appearing elliptical or irregular in the outline (Fig. 3b, f–i). The pollen grains are slightly diploxylonoid (Fig. 4). The corpus is nearly circular and represents the most part of

pollen grain. Small underdeveloped sacci appear crescentlike and distally inclined (Fig. 4b), and they slightly protrude over the corpus (Fig. 3b, d, h), but are easily damaged and often are not seen (Fig. 3c, f, g, i).

The corpus sculpture is scabrate in LM, and can be described as areolate (with insular ornamentation elements approximately 1 μ m in size) or verrucate with granulate suprasculpture elements at higher magnifications in SEM (Fig. 5b). The saccus surface is more or less psilate both in LM (Fig. 3b, d, h) and SEM (Fig. 5b). The leptoma was not observed in LM or SEM, which could be due to a small sampling size (10 pollen grains, photos of four pollen grains only were more or less informative). However, a probable leptoma region may be detected by verrucae that become smaller and smoother (Fig. 5c).

TEM data were obtained from three pollen grains from a single synangium. The pollen grains were parts of the small pollen clumps obtained after the ultrasonic bath treatment. The sections show some differences in the pollen grains ultrastructure. One pollen grain shows a bilayered pollen wall (Fig. 6a). The outer layer is quite thick, homogenized, without a clear subdivision into sublayers. It can be described as tectate-granular. It varies in thickness over the corpus region, being 0.5–0.7 μ m on average. At places, the inner surface shows invaginations (Fig. 6a,



Fig. 2 Sporangia of *Permotheca sardykensis*. **a**, **b** Morphology of a cluster of sporangia sitting on a pedicle, reflected light. **a** specimen no. 5563–219 (collection of PIN RAS); **b** specimen no. 5563-226A.

c, **d** Sporangium in LM and SEM, specimen no. 5563–229. **e** Surface of the same sporangium supposedly damaged by fungi



Fig. 3 Pollen morphology in LM. **a** Piece of sporangium, specimen no. 1853–308 (collection of BIN RAS). **b–d** Pollen grains from specimen no. 1853–308. **e** Piece of sporangium of specimen no. 5563-

226A (collection of PIN RAS). **f-i** Pollen grains from specimen no. 5563-226A deformed and damaged in different ways. Arrowheads show underdeveloped sacci



Fig. 4 Pollen morphology under LM. **a** Pollen grain from specimen no. 1853–308. **b** The same pollen grain with approximate line drawing, showing the main features of the pollen grain

c). The inner layer is thin (about 0.06–0.07 μ m thick) and homogeneous, slightly less electron dense than the outer layer, detached from it, and absent in some sections. No essential differences between the proximal and distal exine are seen (Figs. 6c, d, 7e, f) except the leptoma area. The leptoma is easily detected by a distinct thinning of the exine down to about 0.15 μ m (Fig. 6b, d). Outside the pollen grain, a fragmented poorly preserved layer is present. It is about 0.03–0.05 μ m thick and less electron dense than the outer exine layer.

Two pollen grains show a one-layered pollen wall (Fig. 7). The outer contour of the pollen wall is wavy (Fig. 7c, d, e). Thick protosaccate regions filled with narrow and small alveolae are present in probable saccus regions (Fig. 7b, f). Ubish bodies are present too (Figs. 5a, 7a, f). In the leptoma region, waving is also present (Fig. 7c, e), but it is unclear whether it is different from those in the corpus or not.

Discussion

Interpretation of the results

The pollen grains under study can be assigned to *Piceapollenites* Potonié 1931, though this assignment is provisional because of the poor preservation and supposed not completely mature state of the pollen grains.

The outermost layer is not a part of the pollen wall. Probably, this layer is probably represented by tapetal remnants. The outer layer of the pollen wall seems to be a globular ectexine, and differences between the pollen wall ultrastructure in Figs. 6 and 7 may reflect the consecutive steps of the pollen wall development, with Fig. 6 showing a later stage. The wavy contour of the pollen wall of the pollen grains in Fig. 7 probably corresponds to the verrucae and resulted from globulae formation. The invaginations in Fig. 6 probably could be formed after the globulae fusion. The innermost layer is most likely an endexine, but may be a foot layer too. It is difficult to say which layers are present in the aperture region, though both ectexine and endexine may be present, inasmuch as in the pollen grains in Fig. 7, the exine is represented by the ectexine only and the aperture region is clearly distinguishable.

Diagenesis and treatment effects on the studied pollen preservation

Probably, during fossilization and diagenetic processes, the pollen grains were transformed or the sporangia were exposed to decomposer fungi. The fact that there could be exposure to fungi can be deduced from SEM photos of the sporangial surface (Fig. 2d, e). The surface is strongly corroded, cell boundaries can be seen neither with LM (Fig. 2c) nor with SEM (Fig. 2e). This transformation of the sporangium cuticle might have caused such tight adhesion of the pollen grains and some changes in the pollen wall ultrastructure. Experiments accomplished by Rowley et al. (1990) showed that pollen wall deterioration most often occurs by pollen wall thinning, which may develop in several ways: formation of tunnels through the ectexine zones and destruction of inner parts of an ectexine, an endexine separation and loss, or formation of "ball-like protrusions". Nonetheless, surficial erosion or etching of the exine surface does not occur. Such thinning can partly explain the differences between the pollen wall ultrastructure in Figs. 6 and 7, e.g., the absence of the inner layer in pollen grains from Fig. 7. However, such a thinning is a bad explanation for differences in ectexine outer contours, and the tunnels were not observed in pollen walls. Nonetheless, it is not inconceivable that the process could have



Fig. 5 Pollen morphology in SEM. **a** General view on pollen grains from Fig. 3c with orbicules. **b** Enlargement of Fig. 5a showing verrucate surface of the corpus and psilate surface of the saccus. **c** Pollen

grain showing probable leptoma region with reduced vertucae. ap?– probable aperture region, *orb* orbicules, *sc* saccus, *srf* surface of pollen grain

taken place in a different way. Thus, the real reasons for the cuticle corrosion remain unknown.

Also the chemical and ultrasound treatment could affect the pollen ultrastructure and damage the pollen walls. Chemical oxidation during the maceration was done with HNO_3 but not Schulze solution, because HNO_3 is a less active oxidizer than Schulze solution. Still, there remained a possibility that it could disrupt the pollen surface. In addition, during the ultrasound disintegration, many pollen grains were broken due to the strong adhesion to each other.

Ontogeny effect on the pollen ultrastructure

The sacci in the pollen grains are small, what causes a question if it is a character of the mature pollen or this state is caused by the unfinished pollen development. Nowadays, we know very little about the pollen development of fossil plants, so we can only approximate with some confidence our knowledge about modern plants on their fossil relatives.

Deringer

Though the pollen grains passed the tetrad stage (they are not aggregated in tetrads), they are somewhere within the free-spore stage and it is unclear whether they are completely mature.

Saccus formation begins during the tetrad phase under a callose wall within the microspore outline and continues after releasing from tetrads. Protuberation of sacci over the corpus outline occurs at different stages in different species, e.g., in *Pinus banksiana* Lamb. 1803, it happens after releasing from the tetrads (Dickinson and Bell 1970), but in *Abies concolor* (Gord. et Glen.) Lindl. sacci begin to protuberate at the end of the tetrad phase already (Kurmann 1989). Unfortunately, in the light of this information, the degree of sacci development of the pollen grains under study does not allow to form an opinion whether the pollen grains are mature.

Probably, the pollen development can partly explain the differences between the sections of the pollen grains in Figs. 6 and 7 which were taken from a single synangium. In Fig. 7, the vertucate structure is more distinct. Probably,



Fig.6 Sporoderm ultrastructure in TEM. **a** Section of pollen wall showing homogenized granular ectexine and thin endexine and supposed remnants of tapetum outside the pollen wall. **b** Section through aperture region. **c**, **d** Sections through pollen clump showing sections

of a intact (to the left) and damaged (to the right) pollen grains. In Fig. 6d, section goes through the aperture region. *ap* aperture, *ect* ect-exine, *en* endexine, *tap* supposed remnants of tapetum



Fig.7 Sporoderm ultrastructure in TEM. **a** Part of sporoderm and orbicules. **b** Protosaccate region. **c**, **d** Section of the pollen wall showing verrucate sculpture. **e** Section through the whole pollen grain, aperture region is visible in the middle part. **f** Section through the

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whole pollen grains; to the left, the same pollen grain as in Fig. 7e, but sectioned in a non-apertural region; to the right transverse section of the other pollen grain with protosaccate region in the upper part. *ap* aperture, *orb* orbicules, *ver* vertucae

the pollen grains from Fig. 7 represent an earlier stage of the free-spore phase, and the pollen grain from Fig. 6 represents a pollen grain after further globulae fusion. Vasil (1978) stated that the pollen development in a single synangium in extant gymnosperms can be asynchronous, and probably in fossil gymnosperms, this could occur too. However, pollen wall deterioration is a more probable explanation for the observed results.

Comparison

The comparison below aims at understanding the relation of *P. sardykensis* to the other *Permotheca* species in light of palynological data, though the possibility should be kept in mind that the differences are due to the incompletely mature state of the pollen grains.

Pollen grains are known from the sporangia of *Permotheca disparis* (Krassilov et al. 1999a, b), *P. colovratica* (Naugolnykh 2013), *P. vesicasporoides* (Gomankov and Meyen 1986), *P. striatifera* (Gomankov and Meyen 1986), *P. striatifera* (Gomankov and Meyen 1986), and *P. helbyi* (Retallack 2002). The pollen types are *Vesicaspora* (*P. colovratica*, *P. disparis*, and *P. vesicasporoides*), *Falcisporites* (*P. helbyi*), *Protohaploxypinus* (*P. striatifera*), and *Vittatina* (*P.? vittatinifera*). All the above *Permotheca* species are associated with the order Peltaspermales (e.g., Gomankov and Meyen 1986; Retallack 2002) with varying degrees of confidence.

Vesicaspora/Falcisporites

Different authors identify the pollen from *P. vesicasporoides*, P. disparis, P. colovratica, and P. helbyi synangia as Vesicaspora (e.g., Gomankov and Meyen 1986), Falcisporites (Balme 1995; Retallack 2002) or Alisporites (Naugolnykh 2013). Gomankov and Meyen (1986) attributed the pollen from P. vesicasporoides synangia to Vesicaspora, but Balme (1995) supposed that it would be more correct to assign the pollen to Falcisporites; still, he made a point that in some pollen grains, the protosacci are joined by narrow equatorial strips, as in Vesicaspora, which is protomonosaccate, by contrast with Falcisporites, which is protobisaccate. Furthermore, Gomankov and Meyen (1980) studied variability of dispersed Vesicaspora ex. gr. magnalis, associated with Phylladoderma, as P. vesicasporoides, and concluded that the equatorial strips can change position towards the equatorial plane to the distal or proximal side. Thereby protomonosaccate pollen grains after the flattening in equatorial plane may look like protobisaccate if the equatorial strips were displaced to the distal side. Osborn and Taylor (1993) studied in situ pollen from Pteruchus-like pollen organs, which Balme (1995) attributed to *Falcisporites* to *Alisporites* (s.1.). Osborn and Taylor (1993) showed that the sacci of the studied pollen grains sometimes make contact in lateral equatorial sections. Krassilov et al. (1999a, b) studied the pollen and its ultrastructure from P. disparis synangia, and noted that this pollen apparently belongs to the same type as found in P. vesicasporoides. They identified this pollen as Vesicaspora due to its alveolar sporoderm. Pollen grains from P. colovratica (Naugolnykh 2013) are very similar to pollen from P. disparis, studied by Krassilov et al. (1999a, b). Naugolnykh (2013) attributed them to Falcisporites type, compares them with Alisporites and Vesicaspora, and mentioned a transition from protomonosaccate to protobisaccate state within the one sporangium. Still, there is some uncertainty on the independence of P. colovratica species. This species differs from *P. disparis* in the pollen type, what may be disputed, and the number of sporangia: four per synangium in P. colovratica (Naugolnykh 2013) and from six to ten per synangium in P. disparis (Naugolnykh 2007). Still, the number of sporangia is a very variable character. All other characters are identical in these two species. The other problem is that P. colovratica is described using six specimens only: four from three different localities and two figured by M.D. Zalessky (Naugolnykh 2013). Therefore, there is a possibility that P. colovratica may be a junior synonym of P. disparis.

P. helbyi with in situ *Falcisporites australis* pollen grains (Retallack 2002) stands apart all other *Permotheca* species, because of the huge stratigraphic and geographic gap and unclear relation between *P. helbyi* and all other *Permotheca* species (it was described from the Triassic of Australia). Nonetheless, Retallack (2002) mentions a close resemblance between the in situ pollen grains of *P. helbyi* and *P. vesicasporoides*.

Summing up, all the studies mention a strong resemblance between the pollen from sporangia of *P. disparis*, *P. colovratica*, *P. vesicasporoides*, and *P. helbyi*. There is a transition from protomonosaccate to protobisaccate state, which can be observed both in *Vesicaspora* and *Falcisporites* pollen types. Unfortunately, only pollen grains from *P. disparis* were studied ultrastructurally, and it is alveolar as in *Vesicaspora* (rather than homogeneous, as in *Falcisporites*; see below). The ultrastructure of pollen from sporangia of *P. colovratica* and *P. vesicasporoides* is known, so supposedly, it would be more correctly to identify the pollen as *Vesicaspora/Falcisporites* type until a new data on in situ pollen from these *Permotheca* species will be obtained.

Vesicaspora

In situ *Vesicaspora* from *Permotheca disparis* from the early Permian deposits of the Russian Platform was studied by Krassilov et al. (1999a, b). The TEM ultrathin sections showed that the proximal ectexine consists of three layers: a

thick continuous tectum, an alveolate infratectum, and a continuous foot layer; the endexine is more electron dense and lamellate. On the distal side, the sporoderm gets thinner with reduced alveolae. The absence of the alveolate infrastructure marks a leptoma area. The pollen grains from Permotheca vesicasporoides were ascribed to Vesicaspora magnalis Hart 1965 (Gomankov and Meyen 1986). The upper Permian dispersed pollen grains of Vesicaspora ex. gr. magnalis were studied with TEM by Zavialova et. al. (2001) and showed the same structure of the sporoderm. Based on the obtained data, the authors concluded that the sacci of Vesicaspora ex. gr. magnalis may demonstrate a transition from the proto- to the eusaccate condition unless this structure was the result of preservational flattening of the pollen grain. The threelayered structure of the ectexine is absent in the pollen grains from P. sardykensis. The granular infratectum may be analogous to the alveolate layer of Vesicaspora; by contrast to the Vesicaspora pollen, the foot layer is absent and the ectexine is not subdivided into sublayers. However, the presence of a leptoma and protosaccate regions and the absence of striae in the sporoderm of the P. sardykensis pollen show some similarity to pollen of Vesicaspora type.

Falcisporites (and Alisporites)

Some in situ bisaccate sulcate pollen grains of Corystospermales (Peltaspermales sensu Meyen; Meyen, 1987) were studied by Taylor et al. (1984), Zavada and Crepet (1985), and Osborn and Taylor (1993). All authors did not attribute the pollen grains to any genera of dispersed pollen but likened them to *Alisporites* or *Pteruchipollenites*. Balme (1995) assigned the pollen grains to *Falcisporites* or *Alisporites*. Still, the information on the exine ultrastructure of *Falcisporites* or *Alisporites* of Peltaspermales is unknown to me.

Taylor et al. (1984) studied in situ pollen from sporangia of Pteruchus dubius Thomas 1933 from the Middle Triassic of Argentina. The sacci of the pollen grains are represented by thick sporopollenin units separated by narrow, irregularly spaced lacunae. The sporoderm is thin and homogeneous on both sides of the corpus, with gradual thinning towards the proximal pole and a very thin nearly membranous sulcus. Zavada and Crepet (1985) studied pollen from the type material of three species of Pteruchus from the Triassic of South Africa: P. africanus Thomas 1933, P. dubius, and P. papillatus Thomas 1933, which are palynologically very similar. The pollen grains for TEM were stained in KMnO₄. The exine sculpture of the pollen grains is psilate mostly. The sacci are formed by a homogeneous tectum, irregularly shaped "processes" separated by lacunae, a thin basal layer, and a thin more electron dense staining layer, which underlains the basal layer. The corpus exine consists of the outer less electron dense staining homogeneous layer with rare thin lacunae and a thin more electron dense layer. The less electron dense layer thins in the apertural region. Osborn and Taylor (1993) studied in situ three-dimensionally preserved pollen grains from *Pteruchus*-like sporangia from the Triassic of Antarctica. The pollen grains are eusaccate. The sporoderm is homogeneous, up to 1 μ m thick in the cappa and thins towards the sulcus. In the regions, where the sporoderm layers separate to form sacci, it changes to tectate–alveolate. The authors interpret the pollen grains as eusaccate, but mention that they may be protosaccate. Sacci are laterally attached and make contact in lateral equatorial section.

Summing up, all three studies show different pollen ultrastructures, there is no agreement on the pollen assignment, and this question requires additional research. Still, the pollen under study from *P. sardykensis* differs from the pollen from *Pteruchus* in the saccus ultrastructure (protosaccate, not eusaccate or filled with sporopollenin units). The corpus exine shows some similarity to the corpus exine of the pollen studied by Taylor et al. (1984) and Osborn and Taylor (1993) in its simple ultrastructure and sufficient differences from the exine ultrastructure studied by Zavada and Crepet (1985).

Protohaploxypinus

Protobisaccate pollen grains of *Protohaploxypinus* were extracted from the sporangia of *Permotheca striatifera* (Gomankov and Meyen 1986). More strictly, these pollen grains could be identified as *Protohaploxypinus dvinensis* (Sedova 1956) Hart 1964 (Zavialova et al. 2001). *Protohaploxypinus* pollen grains also have a leptoma, but differ from the pollen under study in having well-developed sacci and striae on the proximal surface (Zavialova et al. 2001).

Protohaploxypinus pollen grains from Permotheca striatifera were studied with SEM and TEM by Zavialova and Karasev (2015). The pollen grains are characterized by a complex sporoderm which differs on the proximal and distal sides. On the distal side, it is presented by an endexine only. On the proximal side in ribs, the exine consists of an ectexine with an outer well-developed continuous layer, a thinner alveolar layer, and an inner layer and of the more electron dense endexine. In the grooves between the ribs, the exine is represented by the inner homogeneous layer of the ectexine and the endexine or of the endexine alone. Moreover, the endexine may show some layering. The sacci are supposed to be protosaccate. Dispersed pollen grains of Protohaploxypinus from the Permian of Subangara were studied by Zavialova et al. (2001). Sections obtained in these studies do not show any principal differences from the in situ material. Pollen grains of Protohaploxypinus perfecta (Naumova) Samoilovich 1953 which were extracted from a gut of the Permian booklouse Parapsocidium uralicum Zalessky 1939 (Krassilov et al. 1999b) still show nearly the same exine ultrastructure. The ultrastructure of the *Permotheca* sardykensis pollen grains strongly differs from that of the *Protohaploxypinus* pollen: there are no principal differences between the proximal and the distal sporoderm, no regions represented by the endexine only; the endexine is less developed and often absent. An alveolar layer is presented in the sacci regions only.

Vittatina

Vittatina subsaccata f. connectivalis Samoilovich 1953 pollen grains were obtained by Gomankov and Meyen (1986) from the sporangia of P.? vittatinifera, which had earlier been associated with Peltaspermopsis buevichiae Gomankov et Meyen 1986 (Gomankov and Meyen 1979). Vittatina strongly differs from the pollen grains under study by its morphology. According to Koloda (1986, 1997), in pollen grains of Vittatina sensu stricto, an equatorial rim is present, the proximal surface is striate, and the distal surface bears a transversal taenia and thickenings on the edges. A leptoma on the distal surface is divided into two areas by the transversal taenia. Koloda (1986, 1997) reported for Vittatina subsaccata Samoilovich 1953 an exine with a continuous tectum, a columellate layer and taeniae having cavities inside. Afonin (1999) studied pollen grains identified as Vittatina connectivalis (Sauer) Warjuchina 1971 ex Utting 1994 with the exine showing different structures on the proximal and distal sides. The proximal sporoderm consists of thick taenia regions with thin stria regions between them. The taenia regions are represented by thick homogeneous taeniae with four-to-six granules at the bases, and the stria regions are presented by a bent thin homogeneous exine. The endexine was poorly preserved on the proximal side. On the distal side, the exine consists of an ectexine which looks homogeneous, but includes a very thin alveolate layer, and of a lamellate endexine with five or six lamellae. Gomankov and Tarasevich (2008) studied Vittatina costabilis Wilson 1962 and a verrucate form of the same pollen species (Gomankov and Tarasevich 2011), which they proposed to name Vittatina costabilis f. verrucata. They reported that the proximal exine of these pollen grains consists of a homogeneous tectum, a granulate-columellate infratectum, and a thick continuous foot layer, and there are no principal differences between the verrucate and non-verrucate forms. Moreover, according to their photos, the underdeveloped sacci are eusaccate, and the authors report that they have the same nature as the cavities in the taeniae (Gomankov and Tarasevich 2008). Summing up all of the above, the Vittatina pollen grains have the complex sporoderm with the alveolae in the taeniae and differ from the pollen grains under study in having three well-defined layers of the ectexine and the well-developed endexine. Still, the granulate-collumelate layer of the Vittatina exine may show some similarities to the granular infratectum in the pollen grains under study, but the differences between these two types of pollen grains remain remarkable.

Conclusion

The pollen grains from the sporangia of P. sardykensis differ from the pollen species which were reported from the sporangia of Permotheca from the Permian of Angaraland earlier (Protohaploxypinus, Vesicaspora/Falcisporites, and Vittatina). The pollen grains under study have the underdeveloped sacci as some species of Vittatina, but they are protosaccate as, e.g., in Vesicaspora or Protohaploxypinus and not eusaccate as in Vittatina (Gomankov and Tarasevich 2008). The studied pollen grains have no taeniae or striae as Protohaploxypinus and Vittatina, but share a leptoma-type aperture with all the above pollen types. However, a leptoma is quite usual for the gymnosperms. In addition, what is also important, the pollen grains from Permotheca sardykensis have a much more simply organised sporoderm comparing to any other pollen from *Permotheca*. The sporoderm of *P*. sardykensis pollen grains is uniform except in the leptoma region and can be presented by two layers, which may be interpreted as a thin endexine and a homogenized granular ectexine without a clear subdivision into sublayers. Outside the pollen grains, remnants of subsidiary structures (e.g., a tapetal layer) may occur. Though, there is no certainty that the pollen grains under study were mature and that the observed differences were not caused by incomplete pollen development.

The obtained palynological data give one more argument to an idea that probably *Permotheca* may be a heterogeneous genus. Four species are attributed to the Peltaspermales more or less convincing (among them one, *P. ? vittatinifera*, is not surely a *Permotheca*, and the other, *P. helbyi*, is the only *Permotheca* species not from the Permian of Angarida, but from the Triassic of Gondvana); for the others, the associations are not established or established by the co-occurrence only or even less convincing evidence. Supposedly, there is a possibility that *Permotheca* actually unites several similar groups of pollen organs which are not related to each other, and the author would not dare to bind all *Permotheca* species with Peltaspermales, including *P. sardykensis*.

Acknowledgements The author would like to thank Dr. A.V. Gomankov (Komarov Botanical Institute, St-Petersburg, Russia), who kindly provided his material for this study, Dr. N.E. Zavialova (Borissiak Paleontological Institute, Moscow, Russia) and Dr. E.V. Karasev (Borissiak Paleontological Institute, Moscow, Russia) for their invaluable help and advice at all stages of the paper preparation, Dr. M.V. Tekleva (Borissiak Paleontological Institute, Moscow, Russia) for her comments on the text, N.I.Gabaraeva (Komarov Botanical Institute, St-Petersburg, Russia), and S.V. Polevova (Lomonosov Moscow State University, Moscow, Russia) for their help. Additional thanks to H. Nowak (Museum of Nature South Tyrol, Bolzano, Italy), E. Kustatscher (Museum of Nature South Tyrol, Bolzano, Italy), and anonymous reviewers for their comments, thanks to which article was significantly supplemented, and M. Reich (Bavarian State Collection of Palaeontology and Geology, Munich, Germany) for his corrections. The study was supported by the Russian Foundation for Basic Research, project no. 19-04-00498 a and PaISIRP Sepkoski Grant 2018.

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