

## Systematic Problems of Pollen Organs of the Genus *Permotheca* Zalessky from the Permian of Subangara

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**Abstract**—The species diversity of representatives of the genus *Permotheca* from the Middle Permian localities Kostovaty and Chepanikha of the Kama region is studied. A new species *P. ? musaformis* sp. nov. is described. The species *P. sardykensis*, *P. disparis*, and *P. vesicasporoides* are identified. New data on in situ pollen are obtained. Pollen grains *Vesicaspora* and *Piceapollenites* were found in the sporangia of *P. disparis*; the sporangia of *P. vesicasporoides* contain solitary *Pityosporites* pollen grains apart from *Vesicaspora* pollen grains. A new diagnosis is proposed for the genus *Permotheca* in the light of new data.

**Keywords:** Middle Volga region, peltasperm pteridosperms, systematics, microsynangia, pollen grains

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### INTRODUCTION

Zalessky (1929) proposed the name of the genus *Permotheca* for bunches of microsporangia of an uncertain systematic position from the Kazanian sediments of the Russian Platform. Gomankov and Meyen (1986) used this name in their study of a late Permian flora of the Russian Platform for microsynangia of peltasperms and angaropeltaceans, the sporangia of which fused at in their bases Naugolnykh (2007) proposed a new diagnosis of *Permotheca* including new characters such as architecture of fertile axes bearing synangia (simple and branching) and information on associations of the synangia with pollen *Vittatina* Wilson, 1962, *Protohaploxypinus* (Samoilovich) Hart, 1964, *Cycadopites* Wodehouse, 1933, *Falcisporites* (Leschik) Klaus, 1963, *Vesicaspora* Schemel, 1951 and leaves of peltasperm pteridosperms *Permocallipteris* Naugolnykh, 2014, *Lepidopteris* Schimper, 1869, *Psymophyllum* (Schimper) Saporta, 1878, *Mauerites* Zalessky, 1933, *Phylladoderma* Zalessky, 1913, *Pursongia* (Zalessky) Meyen, 1969, and *Tatarina* Meyen, 1969.

Currently, ten *Permotheca* species have been described: five species from the Kungurian Stage of the Cis-Urals region (Naugolnykh, 2007, 2013), one species from the Kazanian Stage of the Russian Platform (Zalessky, 1929), three species from the Severodvinian and Vyatkian Stages of the Russian Platform (Gomankov, Meyen, 1986), and one species from the Early Triassic of Australia (Retallack, 2002). The most

reliable criteria for identifying species of the genus *Permotheca* are morphology of pollen grains contained in sporangia and microsporoclad architecture. General morphology of synangia and sporangia can be used for species differentiation with care, due to high variability of these features, but the most common form of *Permotheca* preservation is as isolated synangia from which there is no possibility to extract pollen.

The first statement that *Permotheca* representatives may belong to Peltaspermales was given in the article of Gomankov and Meyen (1979) in which a coprolite with fragments of *Tatarina* cuticles and pollen grains of *Protohaploxypinus* type was described from the Severodvinian (Capitanian) sediments. Finds of *Permotheca striatifer* Meyen et Gomankov, 1986 sporangia with *Protohaploxypinus* pollen grains inside were mentioned in an association with the coprolites. Gomankov and Meyen (1979, 1986) during their study of *P. vesicasporoides* Meyen, Esaulova et Gomankov, 1986, *P. striatifer*, and *P. ? vittatinifera* Meyen et Gomankov, 1986 species provided strong evidence of relations between these species and peltasperm and angaropeltacean pteridosperms. Subsequently, assumptions of an affinity to peltasperm pteridosperms were also made for other species of *Permotheca*: *P. bifurcata* Naugolnykh, 2007, *P. disparis* (Zalessky) Naugolnykh, 1998, *P. colovratika* Naugolnykh, 2013, and *P. helbyi* Retallack, 2002 (Naugolnykh, 1998, 2007, 2013; Retallack, 2002). The main



Fig. 1. Chepanikha and Kostovaty localities in European Russia.

criterion for these assumptions was generally an association in a burial.

Nonetheless, a systematic affinity of the type species *Permothea sardyensis* Zalessky, 1929 and its relation to other organs of a parent plant remains unknown. In this work we undertook a study of the remains of representatives of the genus *Permothea*, including *P. sardyensis*, from the upper Kazanian sediments of Kama region localities.

## MATERIAL AND METHODS

The samples under study originate from two localities (Fig. 1): Kostovaty (Russia, Republic of Udmurtia, Votkinsky District, the right bank of the Votkinsk Reservoir in 1.5 km to north-east from the village of Kostovaty) and Chepanikha (Russia, Republic of Udmurtia, Zavyalovsky District; the left bank of the Rossokha River in 1 km to north-east from the village of Chepanikha). Compositions of plant and ostracod assemblages from the localities indicate the late Kazanian age (Gomankov, 2020). Gomankov (2012) proposed to identify the flora of these and some other localities close in age (Donauovo, Shikhovo-Chirkee, and Kargala mines) as the Kostovaty floristic

assemblage. The assemblage composition includes shoots of *Paracalamites* sp., leaves of *Ustyugia udmurtica* Gomankov, 2008, *Compsopteris* sp., *Ginkgophyllum rhipidomorphum* Gomankov, 2018, *Phylladoderma meridionalis* Meyen, 1971 (Meyen and Gomankov, 1971), fragments of pinnate leaves of *Pecopteris* (Brongniart) Sternberg, 1825 type, synangia of pteridosperms *Permothea* sp. and *P. vesicasporoides*, female fructifications of *Cardiolepis* sp. and *Krylovia* sp., and ovules *Nucicarpus piniformis* Neuburg, 1965 (Gomankov, 2020). New collections of fossil plants from Chepanikha and Kostovaty expanded the assemblage with the following additional elements: shoots and dispersed leaves of *Intia* aff. *variabilis* Neuburg, 1956, leaves of *Rhipidopsis* aff. *palmata* Zalessky, 1933, *Taeniopteris* sp., synangia of *Permothea sardyensis*, *P. disparis*, female fructifications of *Biarmopteris* sp. The female generative structures of *Krylovia* sp. should be designated as *Sashinia antiqua* Gomankov, 2010, based on the funicle curved to the abaxial side and the lack of sterile scales on polysperms (Forapono and Karasev, 2017, 2019).

The material under study is represented by imprints of leaves and generative structures with phytoliteims in some specimens. The synangia were examined under a

Leica M165c stereomicroscope and photographed using a Leica DFC420 camera. The phytollems were macerated according to a standard technique by a sequential placement of a phytollem first in hydrochloric acid, then in hydrofluoric acid, nitric acid, and thereafter in KOH solution. The macerated material was examined under a Zeiss AXIOPLAN-2 microscope with a Zeiss Axiocam 105 color digital camera. Scanning electron microscope (SEM) photos were taken using a TESCAN-Vega SEM (accelerating voltage 20 kV) at the Borissiak Paleontological Institute of the Russian Academy of Sciences (PIN RAS). The collections are kept at PIN RAS under nos. 5563 (Kostovaty) and 5564 (Chepanikha), holotypes are kept at the Geological Institute of the Russian Academy of Sciences (Moscow; GIN RAS) and Stuckenberg geological museum of Institute of Geology and Petroleum Technologies of Kazan Federal University (GM KFU).

# SYSTEMATIC PALEONTOLOGY

## DIVISION GYMNOSPERMAE

### (PINOPHYTA)

#### Incertae Sedis

#### Genus *Permotheca* (Zalessky) Forapontova et Karasev, emend. nov.

*Permotheca*: Zalessky, 1929, pp. 688–689; *Osnovy* ..., 1963, pp. 305–306; Gomankov and Meyen, 1979, p. 119–120; *Paleontologicheskii* ..., 1983, p. 92; Naugolnykh, 2007, pp. 146–149.

*Asterodiscus*: Zalessky, 1937, pp. 78, 80; *Osnovy*, 1963, p. 301.

*Anthicocladus*: Zalessky, 1937, pp. 81–82.

Type species. *Permotheca sardyensis* Zalessky, 1929, Kazanian Stage of the Kama region.

Diagnosis emended. Complexes of two or more (up to 20) microsporangia placed on short sporangiophore or fused at their bases. Synangia form racemose microsporoclad. Sporangia apically free. Sporangium outlines from linear with acuminate apices to broadly oval or obovate. Cells of sporangium wall arranged in longitudinal rows or rows up-tending helically.

Species composition. Apart from the type species, *P. vesicasporoides* Meyen, Esaulova et Gomankov, 1986 (Severodvinian–Vyatkian Stages of the Russian Platform), *P. striatifer* Meyen et Gomankov, 1986 (Severodvinian–Vyatkian Stages of the Russian Platform), *P. disparis* (Zalessky) Naugolnykh, 1998 (Kungurian–Kazanian Stages of the Cis-Urals and Kama regions), *P. colovratika* Naugolnykh, 2013 (Kungurian–Kazanian Stages of the Cis-Urals region and Kama region of Udmurtia), *P. deodara* Naugolnykh, 2007 (Kungurian Stage of the Cis-Urals region), *P. bifurcata* Naugolnykh, 2007 (Kungurian Stage of the Cis-Urals region), *P. fimbriata* (Zalessky) Naugolnykh, 2007 (Kungurian Stage of the Cis-Urals region), *P. vittatiner* Meyen et Gomankov, 1986 (Severodvinian–Vyatkian Stages of the Russian platform), *P. musaformis* sp. nov. (Kazanian Stage of the Kama

region of Udmurtia), *P. helbyi* Retallack, 2002 (Early Triassic of South-Eastern Australia).

Comparison. *Permotheca* differs from microsporoclad of peltasperm pteridosperms with pinnate microsporophylls [such genera as *Antevsia* Harris, 1937, *Townrovia* Retallack, 1981, *Schuetzia* Geinitz, 1863, *Dictyothalamus* Göppert, 1864, *Callipterianthus* Roselt, 1962, *Sobea indica* (Srivastava) Kumaran et Bonde, 1991] by racemose organization of a microsporoclad. *Sobea indica* also differs in that its sporangia are placed in rows on elongate microsporophylls rather than forming synangia. Racemose microstrobili of coniferophytes differ from *Permotheca* in the presence of an underlying bract and/or distal apophysis on synangiophores (Kumaran and Bonde, 1991).

#### *Permotheca sardyensis* Zalessky, 1929

Plate 11, figs. 1–6

*Permotheca sardyensis*: Zalessky, 1929, p. 689, text-fig. 15

*Permotheca sardyensis*: Naugolnykh, 2007, p. 144, text-figs. 66A–66E.

Holotype. GM KFU, sp. no. 556/28(19) illustrated by Zalessky (1929, p. 689, text-fig. 15); Tatarstan, Sardy River, tributary of the Burets River, Kullarovo locality; Upper Kazanian Substage.

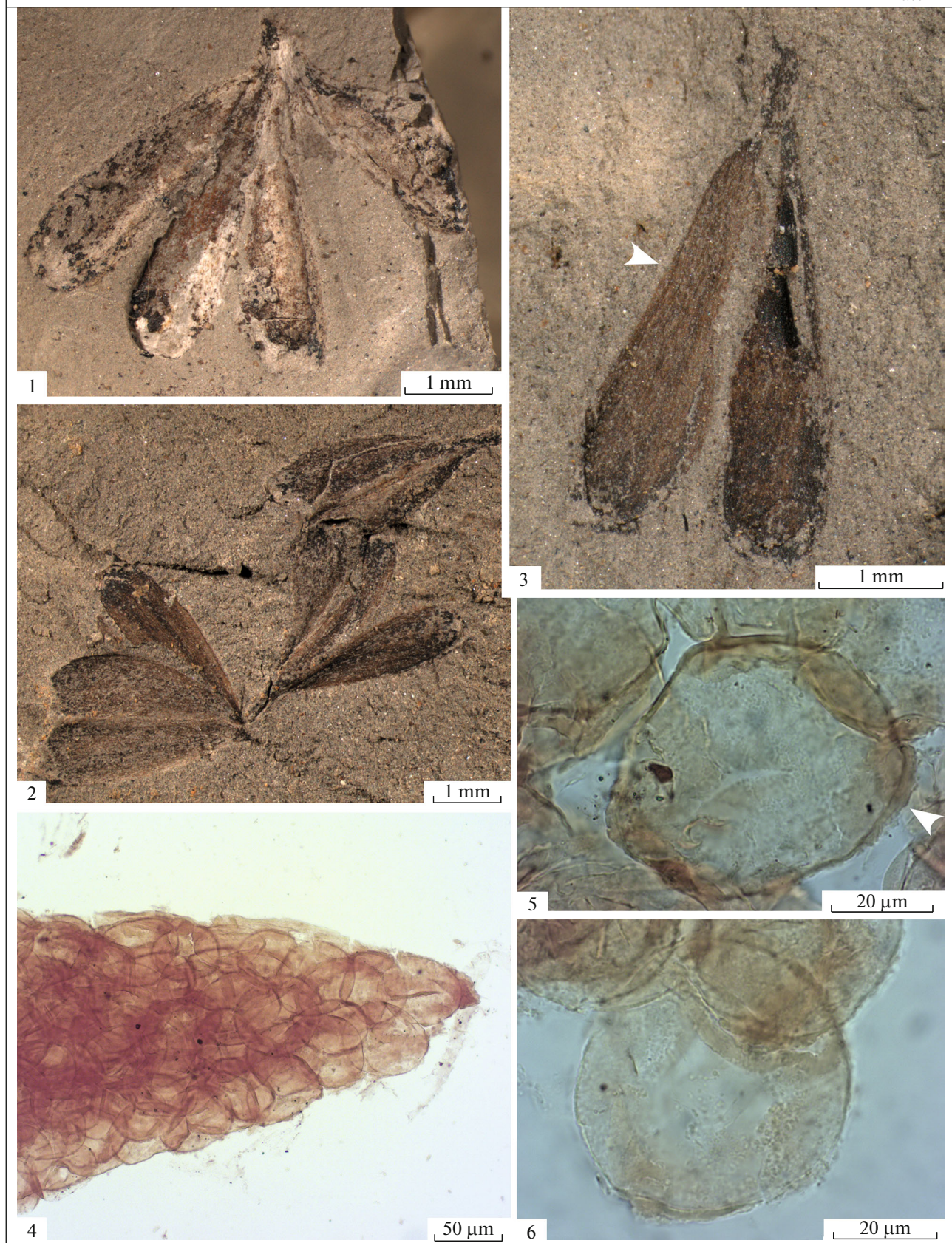
Description. Sporangia form bunches from two to four sporangia per bunch. Sporangia are oblong-clavate in outline (Pl. 11, figs. 1–3). The sporangium length is from 2.1 to 4.5 mm (3.4 mm on average), the width is from 0.8 to 1.3 mm (1 mm on average). On average, the sporangium length is 3.5 times the width, the widest part of a sporangium is displaced to its apex, sporangium bases are tapered. The sporangia are placed on a short branching sporangiophore, the sporangiophore branches grade into tapered bases of the sporangia (Pl. 11, figs. 1–3). The sporangium surface is covered with thin longitudinal wrinkles (Pl. 11, fig. 3).

In some sporangia, pollen grains were found (Pl. 11, figs. 4–6). The diameter of the pollen grains is 60 µm (54–68 µm). The corpus is circular, two poorly developed sacci are preserved on both sides of the corpus (Pl. 11, figs. 5, 6).

Comparison. *P. sardyensis* is different from the other species of the genus *Permotheca* in smaller size, clavate sporangia, branching sporangiophores, thin wrinkles on the sporangium surface, and a lack of fusion of sporangia into a synangium.

Remarks. The sacci of pollen grains appear as protosaccate in ultrathin sections. The leptoma region is not distinguished in transmitted light, however, it is well-defined in the ultrathin sections. Presumably, the pollen grains obtained from sporangia of *P. sardyensis* may be identified as *Piceapollenites* Potonie, 1931 (preliminary data).





*P. sardyensis* differs from the other species of the genus not only in morphology, but also in the found in situ pollen grains. The other *Permotheca* species were described as synangia, which is apparently usually the case. Sporangia fuse at their bases, remaining free for the most part of their length, however, it is obvious for the type-species *P. sardyensis*, that sporangia do not fuse. Also, an important point is that no other *Permotheca* species has a branching sporangio-phore, and the last important feature is the presence of the new type of pollen grains which was not described earlier in other *Permotheca* species. This complex of features implies that all the other *Permotheca* species may stand apart from *P. sardyensis* and might have belonged to another genus, however, the currently available data are inadequate to divide the genus correctly.

**Occurrence.** Kama region of Tatarstan and Udmurtia; Kazanian Stage.

**Material:** Kostovaty (17 specimens), Chepanikha (5 specimens).

*Permotheca disparis* (Zalessky, 1937) Naugolnykh, 1998

Plate 12, figs. 1–10

*Asterodiscus disparis*: Zalessky, 1937, pp. 78–80, text-fig. 45.

*Permotheca disparis* (Zalessky) Naugolnykh: Naugolnykh, 1998, p. 96, figs. 54B, 54G, 55; Krassilov et al., 1999, pp. 20–22, Pl. 1; Naugolnykh, 2007, pp. 154–155.

**Holotype.** Specimen illustrated by Zalessky (1937, text-fig. 45); Middle Cis-Urals region, Perm Region, lower reaches of the Sylva River, locality near Kazarinovskii settlement; Ufimian Stage, Sheshmian (?) Horizon. The depositary of the holotype is currently unknown (Naugolnykh, 2007).

**Description.** Synangia are composed of from three to nine microsporangia which fuse at their bases (Pl. 12, figs. 1–3, 5) with a rather small attachment disc in the center (Pl. 12, figs. 3, 4). No attached synangia were found.

Buried synangia were found in both lateral (Pl. 12, fig. 1) and abaxial (Pl. 12, figs. 2, 3, 5) positions. The number of sporangia per synangium varies from three to nine, with six being most common (14 specimens out of 38). On average, the sporangia are about 6 mm long and 2 mm wide, the sporangium size may vary significantly within the same synangium (Pl. 12, fig. 2). Sporangium outline is from obovate to elliptical, normally with a rounded, rarely slightly tapered apex. The most characteristic feature is the presence of conspicuous helical ribs on the sporangium surface,

the helix wraps along the longitudinal axis (Pl. 12, figs. 1, 2, 5).

Sporangia of different synangia contain pollen grains of several pollen types (*Vesicaspora*, *Piceapollenites*, *Alisporites*). The results were obtained based on the study of four synangia.

Pollen grains from the first synangium are almost haploxytonoid, of *Vesicaspora*-type (which is consistent with: Krassilov et al., 1999), with large lateral bladders of a saccus, which almost contact each other, and a rather small body (Pl. 12, fig. 6). The size of the four measured pollen grains was  $63\text{--}87 \times 44\text{--}57 \mu\text{m}$ . Pollen grains from the second synangium are of *Piceapollenites*-type, rather diploxytonoid, with body large, slightly quadrangular in outline and rather small, relatively narrow sacci (Pl. 12, fig. 8). Sizes of the two measured pollen grains were  $81 \times 61 \mu\text{m}$  and  $79 \times 58 \mu\text{m}$ . Large pollen grains of *Alisporites*-type (Pl. 12, fig. 7) obtained from the two other samples in most cases are severely deformed and often damaged. The pollen grains were found independently of cuticles or pollen masses. The pollen grains are diploxytonoid in outline, the body is usually larger than the sacci. Size of the pollen grains is  $114 \times 64 \mu\text{m}$  on average.

**Comparison.** *Permotheca disparis* is different from other *Permotheca* species in the presence of helical ribs on the sporangium surface. It differs formally from the closely related species *P. colovratika* which also has helically ribbed sporangium surface in number of sporangia per synangium: *P. colovratika* has four sporangia per synangium.

**Remarks.** Presumably, *P. disparis* belongs to Pelataspermaceae and is associated with leaves *Permocalipteris retesorium* (Zalessky) Naugolnykh, 2014 and peltoids *Peltsapermum* (Naugolnykh and Kerp, 1996; Naugolnykh, 1998).

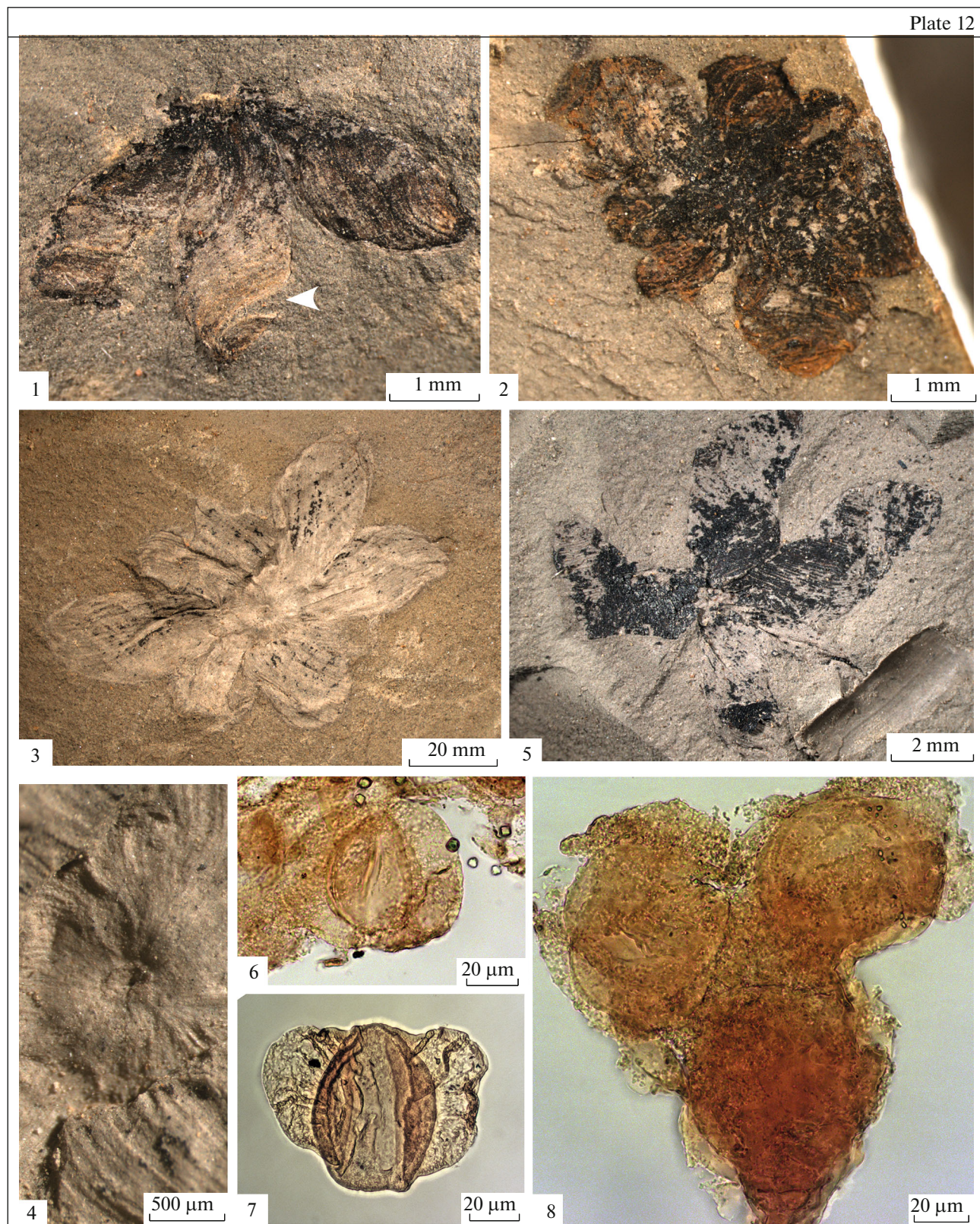
The described specimens of *Permotheca disparis* are the most recent finds of this species. In some cases, a break of sporangium wall may be observable along the ribs on the sporangium surface ribs, what may indicate a method of dehiscence (Pl. 12, fig. 1).

Three specimens from our material fit the diagnosis of *P. colovratika* (Pl. 12, fig. 5). They consist of four (in one case—three) sporangia fused at their bases. It became clear in comparison, that there are no distinct differences between *P. disparis* and *P. colovratika*: both species have comparable helical ribbing on sporangium surface and sporangia of these species contain pollen grains of related pollen morphotypes (see Discussion), additionally these specimens fit the collected monotypic sampling. Taking these facts into

Explanation of plate 11

**Figs. 1–6.** Morphology of pollen organs *Permotheca sardyensis* Zalessky and pollen grains extracted from it: (1, 2) general view of synangia: (1) specimen PIN RAS, no. 5564/6, (2) specimen PIN RAS, no. 5563/219; (3) thin longitudinal wrinkles (arrow) on sporangium surface, specimen PIN RAS, no. 5563/226A; (4) pollen grains in a sporangium, specimen PIN RAS, no. 5563/226A; (5, 6) pollen grains with underdeveloped sacci (arrow), specimen PIN RAS, no. 5563/226A; Udmurtia, Kostovaty (coll. no. 5563) and Chepanikha (coll. no. 5564) localities; upper part of the Kazanian Stage.







account, *P. colovratika* may be a junior synonym of *P. disparis*.

The pollen grains of *Alisporites*-type extracted from the sporangia of *P. disparis* are apparently contamination, and belonged to another plant.

The pollen grains *Vesicaspora* and *Piceapollenites* were found in connection with the cuticles and are most likely *in situ* pollen grains. The reason why sporangia of one species contain pollen grains of two different types has yet to be explained. It is unlikely that *Piceapollenites* pollen grains are immature *Vesicaspora* pollen grains or their preservation form, as far as body size of *Piceapollenites* pollen grain is substantially larger than that of *Vesicaspora* pollen grains. It is probable that *P. disparis* is a collective species. Nonetheless, more extensive material of *in situ* pollen is required before reliable conclusions can be drawn.

**Occurrence.** Kungurian—Kazanian Stage of the Cis-Urals and Kama regions of Udmurtia.

**Material.** Kostovaty (38 specimens), Chepanikha (11 specimens).

*Permotheca vesicasporoides* Meyen, Esaulova et Gomankov, 1986

*Permotheca* sp.: Meyen, 1982, p. 36, Pl. 6, figs. 45–47, text-fig. 15c.

*Permotheca vesicasporoides* Meyen, Esaulova et Gomankov: Gomankov and Meyen, 1986, p. 122–123, Pl. 14, figs. 5, 6, 10–15, text-fig. 64a.

**Holotype.** GIN, no. 3981/60b–17 (Gomankov and Meyen, 1986: pl. 14, figs. 5, 6, 10–15; text-fig. 64a); Mutovino (=Isady), Severodvinian Stage, upper Permian.

**Description** (Fig. 2). Microsporangia are fused at their bases in synangia. In most cases the synangia are found in lateral position (Figs. 2a–2c). The number of sporangia per synangium varies from four to seven. The sporangium surface is usually smooth, may sometimes be covered with longitudinal irregular thin wrinkles (Fig. 2c), in some rare cases the wrinkles may be quite deep. Sporangium length varies from 2 to 6 mm. However, it is only slightly variable within the same synangium.

Two morphological types can be distinguished, and occasional transitional forms (Fig. 2d). The first morphotype is represented by compact synangia, in which the sporangia are compactly pressed to each other (Figs. 2a, 2c). The sporangia are usually elliptical with

slightly obtuse apices. The synangia are sessile, attached to a strobilus axis with a wide base. The second morphotype is represented by laxer synangia (Fig. 2b). The sporangium apices are apiculate, frequently tapered.

More reliable and consistent features are cuticular and palynological features. The cuticle of sporangium walls is thin, usually bright. The periclinal cell walls bear large papillae 20–30  $\mu\text{m}$  in diameter (Fig. 2e), from which only circular holes of a regular shape may remain on the cuticle.

Pollen grains of *Vesicaspora*-type [*V. ex. gr. magnalis* (Andreeva) Hart, 1965] were found in sporangia. The pollen grains are usually haploxytonoid, elliptical in outline, monosaccate; The saccus has two bladders, the bladders are connected by thin bridges in equatorial region (Fig. 2f). The body is elliptical, rather small. We have measured 13 pollen grains preserved in polar view. The average size of the pollen grains is 74.2  $\mu\text{m}$  (varies from 46 to 118  $\mu\text{m}$ )  $\times$  49.6  $\mu\text{m}$  (from 25 to 80  $\mu\text{m}$ ). On average, the ratio of a general pollen grain length to its width is equal to 1.5 (varies from 1.2 to 1.9). Morphological variability in pollen grain structure is observed. One clearly diploxytonoid pollen grain with a diminished body belonging to type *Pityosporites* (Seward) Manum, 1960 (Fig. 2f) was found among pollen grains of *Vesicaspora*-type, its size was 64.5  $\times$  37.6  $\mu\text{m}$ .

**Comparison.** *P. vesicasporoides* differs from other *Permotheca* species in smooth surface, relatively small number of sporangia and *in situ* pollen grains of *Vesicaspora*-type.

**Remarks.** Microsynangia of *P. vesicasporoides* are associated with leaves *Phylladoderma*, cupules *Cardiolepis* Neuburg, 1965 and seeds *Nucicarpus* Neuburg, 1965 of family Angaropeltidaceae (Gomankov and Meyen, 1986).

The collected material is not enough to evaluate frequency of occurrence of *Pityosporites*-type pollen grains among pollen grains of *Vesicaspora*-type in sporangia of *P. vesicasporoides*. It can be both aberrant pollen grains and occurrence of natural polymorphism.

The collection includes one specimen (imprint with counterpart) representing a thick axis near to which a synangium of *P. vesicasporoides* was buried (Fig. 3). Probably, it is a part of a microsporoclad on

#### Explanation of plate 12

**Figs. 1–8.** Morphology of pollen organs *Permotheca disparis* (Zalessky) Naugolnykh and pollen grains extracted from it: (1) synangium in lateral position with a break of sporangium wall along the ribs (arrow), which may indicate a method of sporangium dehiscence, specimen PIN RAS, no. 5563/23; (2) synangium in adaxial position demonstrating a high variability of sporangium size within a synangium, PIN RAS, no. 5563/74; (3, 4) specimen PIN RAS, no. 5563/73: (3) synangium in abaxial position, (4) attachment scar; (5) synangium of *P. disparis* (Zalessky) Naugolnykh fitting the diagnosis of *P. colovratika* Naugolnykh, specimen PIN RAS, no. 5563/20; (6) pollen grain of type *Vesicaspora* Schemel, extracted from specimen PIN RAS, no. 5563/60; (7) probably, contaminant pollen grain of type *Alisporites* Daugherty, extracted from specimen PIN RAS, no. 5563/20; (8) pollen grains of type *Piceapollenites* Potonie, extracted from specimen PIN RAS, no. 5563/77; Udmurtia, Kostovaty and Chepanikha localities; upper part of the Kazanian Stage.







**Fig. 2.** Morphology of pollen organs *Permotheca vesicasporoides* Meyen, Esaulova et Gomankov and pollen grains extracted from it: (a) compact synangium in lateral position with flat attachment scar, fitting the description of the first morphotype, specimen PIN RAS, no. 5563/33; (b) lax synangium with apiculate sporangium apices and poorly defined attachment place, fitting the description of the second morphotype, specimen PIN RAS, no. 5563/34; (c) synangium with thin longitudinal irregular wrinkles on sporangium surface, fitting the description of the first morphotype, specimen PIN RAS, no. 5563/84; (d–f) specimen PIN RAS, no. 5563/69: (d) synangium of transitional morphotype; (e) papillae on sporangium surface, SEM; (f) pollen grains from sporangium of *P. vesicasporoides*: pollen grain of type *Pityosporites* (Seward) Manum (Pt) on the left, pollen grain of type *Vesicasporea* Schemel (Ves) on the right; Udmurtia, Votkinsky District, Kostovaty locality; upper part of the Kazanian Stage.

which sessile synangia of *P. vesicasporoides* were placed, but it is impossible to establish the arrangement of synangia, based on the available material. It is likely that the synangia could have been arranged in a helix, as depicted on a reconstruction of *P. disparis* (Krassilov et al., 1999; Naugolnykh, 2007).

**Distribution.** Middle and late Permian of the East European Platform.

**Material.** Kostovaty (22 specimens), Chepanikha (10 specimens).

*Permotheca? musaformis* Foraponova et Karasev, sp. nov.

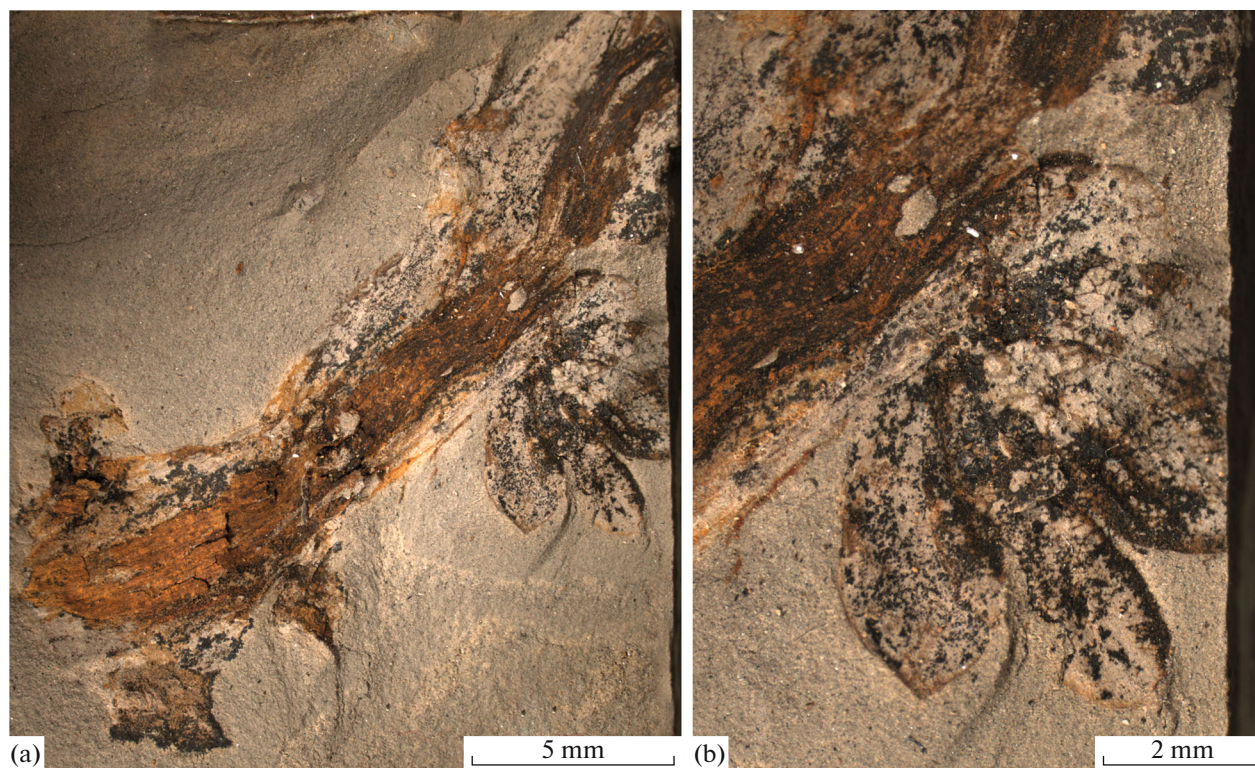
**Etymology.** From the generic name *Musa* L. and the Latin *formis* (similar, resembling).

**Holotype.** PIN, no. 5563/3, synangium composed of six sporangia; Russia, Udmurtia, Votkinsky District, Kostovaty village (Kostovaty locality), south-

ern part of the western bank of the Votkinsk Reservoir; middle Permian, uppermost Kazanian Stage; designated here (Figs. 4a, 4b).

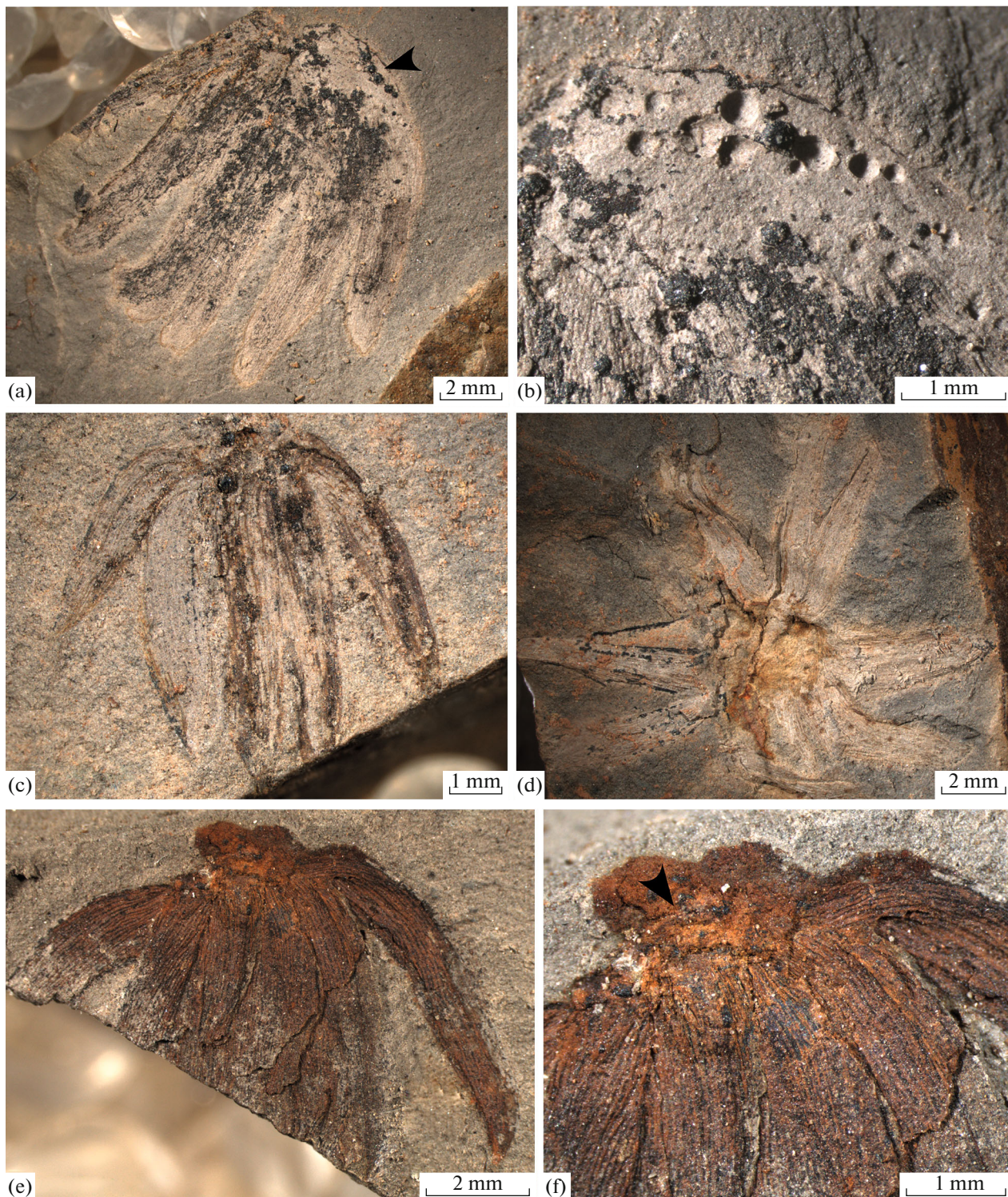
**Diagnosis.** Microsynangia (?) of gymnosperms, consist of 4–10 sporangia. Sporangia strongly elongated, nearly linear, at about 8.0 mm long and 1.5 mm wide, with slightly acute apices. Surface of sporangia covered with thin longitudinal ribs, sometimes bifurcating. Short chains of resin bodies, of different sizes, occur in synangium base. In situ pollen unknown.

**Description** (Fig. 4). Theynangia are quite large, the number of sporangia per synangium varies from four to ten. The sporangia themselves are highly elongated, cigar-shaped in outline, ca. 8.0 mm long and 1.5 mm wide (Fig. 4a). The apices are slightly apiculate, free, the sporangia are tightly fused at their bases. At the base of the sporangia, around their fusion



**Fig. 3.** Thick axis and synangium *Permotheca vesicasporoides* Meyen, Esaulova et Gomankov, specimen PIN RAS, no. 5563/91B: (a) general view; (b) point of contact between the synangium and axis; Udmurtia, Votkinsky District, Kostovaty locality; upper part of the Kazanian Stage.





**Fig. 4.** Morphology of *Permotheca? musaformis* sp. nov.: (a, b) holotype PIN RAS, no. 5563/3: (a) general view of synangium with a chain of resin bodies (arrow) preserved at the base; (b) resin bodies in the synangium base and imprints of resin bodies which fell out; (c) general view of synangium, specimen PIN RAS, no. 5563/6; (d) synangium in adaxial view, specimen PIN RAS, no. 5563/5; (e, f) specimen PIN RAS, no. 5563/7: (e) general view of synangium; (f) synangium base with preserved region of ferruginized tissue (probably, placenta, marked by arrow) and well-defined longitudinal ribbing on sporangium surface; Udmurtia, Votkinsky District, Kostovaty locality; upper part of the Kazanian Stage.



site, rather small resin bodies up to 300 µm in diameter can be found (Fig. 4a). In some cases, they look like solitary bodies of a more or less round shape but can form a well-defined chain (Fig. 4b) becoming smaller towards its ending. A distinct longitudinal ribbing is well preserved on the sporangium surface, the thin longitudinal ribs can bifurcate.

**Comparison.** *P.?* *musiformis* sp. nov. differs from other *Permotheca* species by its larger size, linear, cigar-shaped outline of sporangia, bifurcating longitudinal ribs on the sporangium surface.

**Remarks.** The collection includes twelve specimens of *P.?* *musiformis* sp. nov. In most cases, the synangia were buried in a lateral position (Figs. 4a, 4c, 4e), however, rarely (one specimen out of twelve) they were buried in an adaxial position (Fig. 4d). An unstructured piece of ferruginized tissue with remnants of coaly matter (see arrow at Fig. 4f) can be seen in one specimen (Fig. 4e, 4f), at the base of the synangium. Probably, this could be the place of attachment of the synangium to a shoot or a placenta separated from a parent plant with the synangium.

Despite the visual similarity of *P.?* *musiformis* sp. nov. structures to synangia of *Permotheca*, attempts at pollen extraction from their remains have not been successful.

**Occurrence.** Kazanian Stage of the Kama region of Udmurtia.

**Material.** Kostovaty (9 specimens), Chepanikha (3 specimens).

## DISCUSSION

The discussion of *Permotheca* species below should help to define the state of the taxon and the advisability of considering it as a genus associated with Peltaspermales.

### *Species Associated with Order Peltaspermales*

The first species for which evidence of their association with Peltaspermales were obtained (Table 1) were three species from the upper Permian sediments of the Russian Platform: *P. vesicasporoides*, *P. striatifera*, and *P.?* *vittatinifera* (Gomanko and, Meyen, 1986). *Permotheca vesicasporoides* and *P. striatifera* are represented by isolated microsynangia with a smooth synangium surface, which were probably attached to thick axes in a helical order. These species are almost indistinguishable in morphology. Only a number of features of fine structure and a type of in situ pollen allow these two species to be distinguished from each other, and to be associated with other dispersed plant parts.

Sporangia of *P. vesicasporoides* contain pollen grains of *Vesicaspora*-type. Identical pollen grains are found in quantity in coals composed of *Phylladoderma*

and on the leaves themselves (Meyen and Gomankov, 1971). The *Vesicaspora* pollen grains associate with *Phylladoderma*, and demonstrate the same variability in some localities (Gomankov and Meyen, 1980). Pollen grains of *Vesicaspora*-type were also found in *Nucicarpus* seeds from *Cardiolepis* cupules (Meyen, 1977). On a cuticle of *P. vesicasporoides*, papillae similar to those from the cuticle of *Phylladoderma* leaves were found. Summing up, all these features allowed *P. vesicasporoides* to be reliably associated with the family Angaropeltidaceae of the order Peltaspermales.

*Permotheca striatifera* differs from *P. vesicasporoides* primarily in that its sporangia contain pollen grains of *Protohaploxypinus*-type (Gomankov and Meyen, 1986; Zavialova and Karasev, 2015). Identical pollen grains were found in quantity in a coprolite together with numerous fragments of *Tatarina* cuticles (Gomankov and Meyen, 1979). Gomankov and Meyen (1986) demonstrated that the tapetal membrane of a spore mass is similar to a megaspore membrane of *Salpingocarpus bicornutus* Meyen, 1986, and *Protohaploxypinus* pollen grains were found in the same seeds. Also, the association of *P. striatifera* with *Tatarina* and seed-bearing discs *Peltaspermopsis* Gomankov, 1986, which is preserved in a number of localities, was supported. All this connects *P. striatifera* with the family Peltaspermaceae.

*Permotheca?* *vittatinifera* containing *Vittatina subsaccata* f. *connectivalis* (Zauer) Varyukhina ex. Utting, 1994 pollen grains in the sporangia is also associated with the family Peltaspermaceae. This association is based on the fact that identical pollen grains were found in peltoids *Peltaspermopsis buevichiae* Gomankov et S. Meyen, 1986 in the form of mass aggregations and in seeds *Salpingocarpus variabilis* Meyen, 1986 together with definitely foreign pollen grains (*Scutasporites* Klaus, 1963 and *Cedripites* Wodehouse, 1933), and that the association with *Tatarina* and *Peltaspermopsis* in localities is preserved (Gomankov, Meyen, 1986). However, the species *P.?* *vittatinifera* is known from nine specimens from two localities (Aristovo and Isady) (Gomankov and Meyen, 1986), consequently the question of the repeated associations requires more data. The affinity of *P.?* *vittatinifera* to the genus *Permotheca* is controversial too, as this species is known from finds of isolated sporangia only.

### *Species Presumably Associated with the Order Peltaspermales*

Later assumptions of affinity to peltaspermales were made for *P. helbyi*, *P. disparis*, *P. colovratika*, and *P. bifurcata* (Table 1).

*Permotheca helbyi* is the only *Permotheca* species that was described from the Triassic of Australia rather than the Permian of the Russian Platform (Retallack, 2002). The pollen organ of *P. helbyi* species is repre-

**Table 1.** Types of in situ pollen from sporangia of *Permotheca* and association of *Permotheca* species with macroremains of plants and supergeneric taxa. The order of species is from those which can be found in more ancient deposits to those which can be found in more recent deposits

<i>Permotheca</i> species	In situ pollen	Leaves	Seeds	Other organs	Group	Reference
<i>P. bifurcata</i>		<i>Permocallipteris</i>			Callipterids	Naugolnykh, Kerp, 1996
<i>P. deodara</i>	—	<i>Mauerites</i>		—	Preginkgophytes	Naugolnykh, 2007
<i>P. fimbriata</i>	—			—		
<i>P. disparis</i>	<i>Vesicaspora/Falcisporites</i>	<i>Permocallipteris retensoria</i>		Peltoids <i>Peltaspermum retensorium</i>	Callipterids	Naugolnykh, Kerp, 1996 Naugolnykh, 1998
<i>P. colovratika</i>	<i>Vesicaspora/Falcisporites</i>	<i>Psygmothyllosum</i> var. <i>Cuneatum</i>			Psygmothylloids	Naugolnykh, 2013
<i>P. ? musaformis</i> sp. nov.	—			—		
<i>P. sardykensis</i>	cf. <i>Piceapollenites</i>			—		
<i>P. vesicasporoides</i>	<i>Vesicaspora magnalis</i>	<i>Phylladoderma</i> ( <i>Aequistomia</i> )	<i>Nucicarpus</i>	Seed cupules <i>Cardiolepis</i>	Angatopeltaceans	Meyen, Gomankov, 1971 Meyen, 1977 Gomankov, Meyen, 1980
<i>P. striatifera</i>	<i>Protohaploxylinus</i>	<i>Tatarina</i>	<i>Salpingocarpus bicornutus</i>		Peltasperms	Gomankov, Meyen, 1979 Gomankov, Meyen, 1986
<i>P. ? vittatinifera</i>	<i>Vittatina subsaccata</i> f. <i>Connectivalis</i>	<i>Tatarina</i>	<i>Salpingocarpus variabilis</i>	Peltoids <i>Peltaspermopsis buevichiae</i>	Peltasperms	Gomankov, Meyen, 1986
<i>P. helbyi</i>	<i>Falcisporites</i>	<i>Lepidopteris callipteroides</i>		Peltoids <i>Peltaspermum townrovi</i>	Peltasperms	Retallack, 2002



sented by a racemose microsporoclad with long microsporophylls and aggregations of microsporangia oriented to the abaxial side; however, it is not entirely clear whether these aggregations are dangling or are definitely displaced to the abaxial sporophyll side. Sporangia of *P. helbyi* contain pollen of *Falcisporites*-type (Retallack, 2002). In these features, *P. helbyi* resembles pollen organs of peltasperms of a genus *Townrovia* (Retallack, 1981; Bomfleur et al., 2011) or pollen organs of corystosperms of the genus *Pteruchus* Thomas, 1933 (Thomas, 1933; Yao et al., 1995), which occur in the Triassic of Gondwana. Probably, *P. helbyi* should be affiliated to one of these genera, however, this decision might be made after a study of the type-material only. Retallack (2002) associated *P. helbyi* with Peltaspermales on the basis of that this species was found with leaves *Lepidopteris callipteroides* Retallack, 2002 and peltoids *Peltaspermum townrovii* Retallack, 2002 in the type locality, while no other gymnosperms are present in this locality.

The next two species described from Cis-Urals, *Permotheca disparis* and *P. colovratika*, are morphologically very similar. Naugolnykh (2013) gave the number of sporangia per synangium as a distinctive feature: *P. colovratika* has four sporangia and *P. disparis* has on average six or seven sporangia. The first mention of the affinity of synangia of the *P. disparis* type was by Naugolnykh and Kerp (1996), who reconstructed a plant with leaves *Permocallipteris retensoria* (Zalessky) Naugolnykh, 2014, ovule-bearing fructifications *Peltaspermum* Harris, 1937, dispersed seeds *Cordaicarpus* sp. and pollen organs of *Permotheca*-type. Synangia *Permotheca* were included in this complex based on co-occurrence in a number of localities. The cuticular structure of the sporangium wall was also studied. It was noted in the description that the wall cuticle is thin, with outlines of elongated, longitudinally oriented cells with papillae preserved on it (Naugolnykh, Kerp, 1996). Unfortunately, it is not clear from the article, which specimens were used for the study of the cuticle. Naugolnykh (1998) proposed to designate the studied synangia of *Permotheca*-type as the species *P. disparis*, and later some of these specimens were designated as two new species: *P. bifurcata* and *P. colovratika* (Naugolnykh, 2007, 2013). In the context of new understanding of the species, Naugolnykh (2007) considers that it is appropriate to designate as *P. disparis* only those isolated synangia which meet the diagnosis and for which data on microstructural (cuticular) structure of sporangia and architecture of the bearing axis are unknown. However, earlier Krassilov et al. (1999) studied the cuticular features of a sporangium of *P. disparis* which meets the diagnosis from the paper by Naugolnykh (2007). It was noted in the description that the walls of the sporangia that they studied are three-layered, the upper layer is represented by narrow fusiform cells 40 µm wide arranged

in the gently arched axial files (Krassilov et al., 1999). The species *P. colovratika* was defined in particular on the basis of studied cuticular structure of the sporangium wall. According to the description (Naugolnykh, 2013), the sporangium epidermis of *P. colovratika* is represented by elongated, trapezoid in outline cells 60–90 × 20–30 µm, which are positioned in regular rows arranged in a spiral order relative to the long axis of the sporangium, in some cases with papillae of small size. Ribbing on the sporangium surface is presented due to cuticle stiffening ribs of rigidity between which several rows of epidermal cells are positioned. Sporangium walls are vascularized in both *P. disparis* and *P. colovratika*.

From sporangia of *P. disparis* pollen grains of *Vesicaspora*-type were extracted, however, it should be noted that both monosaccate and disaccate pollen grains were present in the sporangia and designation of the studied pollen grains as genus *Vesicaspora* was justified by their ultrastructure (Krassilov et al., 1999). The diagnosis of *P. colovratika* includes pollen of *Falcisporites*-type (Naugolnykh, 2013), although the author of the species noted in the description that pollen of this type may be designated not only as the genus *Falcisporites*, but also as *Alisporites* and *Vesicaspora*. It is not unusual that different authors designate the same pollen as *Vesicaspora* and *Falcisporites*. For instance, Gomankov and Meyen (1986) designated pollen grains from sporangia of *P. vesicasporoides* as *Vesicaspora*, while Balme (1995) designated it as *Falcisporites* despite the fact that *Vesicaspora* is a monosaccate pollen whose saccus is divided into two bladders connected by bridges, whereas *Falcisporites* is a protobisaccate pollen. *Vesicaspora* pollen grains in some cases may look bisaccate if the bridges were displaced towards the proximal side and were not visible because of the flattening of the pollen grain during the burial processes (Gomankov and Meyen, 1980). Osborn and Taylor (1993) demonstrated that sacci of pollen grains from *Pteruchus*-like sporangia may be connected by thin bridges. According to Balme (1995), these pollen grains should be designated as *Falcisporites* or *Alisporites*. Such uncertainty in designations is explained by the fact that a gradual transition from mono- to bisaccate pollen grains exists. Probably, the both pollen types are consequences of natural variability or variability caused by a flattening of pollen grains during the burial processes; besides, limits of variability of fossil pollen taxa are still unknown and, probably, it is not unreasonable to call the pollen type under discussion as *Vesicaspora*/*Falcisporites*-type. Ultrastructure study may help to distinguish these pollen morphotypes with greater confidence. In summary, it may be deduced that there are no distinct morphological boundaries between *P. disparis* and *P. colovratika*. This may indicate that these species may be considered as synonyms.

*Permothea bifurcata* was described based on a single specimen from the Kungurian deposits of the Cis-Urals (Naugolnykh, 2007). The state of preservation prevented making slides of cuticles or extracting pollen grains; however, this species can be easily distinguished from other *Permothea* species morphologically by its bifurcating axis. No other *Permothea* species with known structure of the sporangiophores has such architecture of bearing axes. It is also suggested that a bunch of sporangia was attached to a short placenta, which is also unknown in any other *Permothea* species (apart from, probably, *P. ? musaformis* sp. nov., if it can be shown that this species truly belongs to *Permothea* and was actually attached to an axis by a placenta). Two suggestions were made on the association of *P. bifurcata* with other dispersed plant organs. Naugolnykh and Kerp (1996) associated the complex of specimens of *Permothea*-like organs, including the specimen of *P. bifurcata*, with leaves of peltasperms of *Permocallipteris*-types (*P. retensoria*), seed-bearing discs of *Peltaspermum*-type and seeds of *Cordaicarpus*-type relying on their co-occurrences in several localities. Later Naugolnykh (2007) defined the *P. bifurcata* species based on the same material and suggested that this species may be associated with leaves of the *Mauerites*-type as far as analogous microsporocladus associate with *Sphenobaiera* Florin. Unfortunately, it is currently impossible to make any more reliable suggestion on the systematic affinity of *P. bifurcata*.

#### *Species of Unknown Systematical Affinity*

Associations of species *P. sardyensis*, *P. deodara*, *P. fimbriata*, and *P. ? musaformis* sp. nov. (Table 1) with other dispersed organs of fossil plants are currently unknown.

The species *P. sardyensis* is significantly different from other *Permothea* species in that it is represented by sporangia sitting on a branched sporangiophore, whereas other *Permothea* species are represented by synangia. *Permothea sardyensis* also differs in such a feature as *in situ* pollen which is represented by *Piceapollenites*-type (preliminary data). Such pollen type was not previously described for *Permothea*, however, our study of *in situ* pollen from our material demonstrated that pollen grains of *Piceapollenites*-type can also be found in sporangia of *P. disparis*. Therefore, a link between *P. sardyensis* and other *Permothea* species is not entirely clear.

*Permothea deodara* is known from three specimens from the Kungurian deposits of the Middle Cis-Urals. *Permothea deodara* is represented by microsporocladus, which are made of a pedicle broadening towards the base and broadened fertile part bearing rosette-like synangia composed of eight or nine sporangia with a surface covered with thin longitudinal ribbing. Therewith, as the author of species noticed (Naugolnykh,

2007), isolated synangia of *P. deodara* are very similar to synangia of *P. disparis* and may be assigned to this species if the cuticular structure of the sporangium wall was not studied. The epidermis of *P. deodara* is made of anisogonal cells, elongated in the longitudinal direction,  $30\text{--}50 \times 20\text{--}30 \mu\text{m}$  (Naugolnykh, 2007) which form spirally up-tending rows; in some cases, trichome structures and resin channels can be found.

*Permothea fimbriata* is represented by a thin bearing axis broadening towards the base, on which rosette-like sporangia composed of 14–16 oblong sporangia are placed on thin sporangiophores. Attachment scars are placed on the adaxial surface of the sporangia. Cuticular structure of sporangium wall and type of *in situ* pollen are unknown. *Permothea fimbriata* stands apart from other species of the genus because of prominent synangiophores.

The species *P. ? musaformis* sp. nov. is assigned to the genus *Permothea* tentatively until it can be demonstrated whether the structures of *P. ? musaformis* sp. nov. are microsynangia. It is united with the genus *Permothea* by general morphological structure: sporangia are fused at their bases, covered with well-defined ribs (as, for instance, in *P. disparis*), also resin bodies are present. Nonetheless, *P. ? musaformis* sp. nov. differs significantly from other *Permothea* species in other details of morphology.

#### CONCLUSIONS

The genus *Permothea* is a heterogeneous genus and is comprised of species which are, probably, not related to each other. Proposing an emended diagnosis for the genus *Permothea*, we aimed to bring into focus the heterogeneous composition of the genus and its undefined position within Gymnospermae. The type species of the genus, *P. sardyensis*, with branching sporangiophores is most different from other species of the genus, which are characterized by fused bases of sporangia. Most of the species also significantly differ from each other. Thus, the only species of *Permothea* from the Triassic of Gondwana, *P. helbyi*, may belong to the genera *Townrovia* or *Pteruchus*. The early Permian species *P. bifurcata* is the only species with a placenta and bifurcating axis, *P. fimbriata* differs in the prominent synangiophores. Most of the species were described from insufficient material, that does not allow the intraspecific variability to be estimated even approximately. *Permothea ? vittatinifera* and *P. ? musaformis* sp. nov. are two species which were ascribed to the genus tentatively. *Permothea disparis* is probably a collective species, and *P. colovratia* may be considered as a junior synonym of *P. disparis* (as, probably, is *P. deodara*). There is also no agreement in palynological data: pollen grains of *Vesicaspora/Falcisporites*, *Piceapollenites*, *Protohaploxylinus*, and *Vittatina* types were described from different species. All these pollen



types are also significantly different in morphology. Systematic affinity was established reliably for only a few *Permothea* species, and it must not be ruled out that some species may belong to other groups of gymnosperms rather than peltasperms and angaropeltaceans, considering the variability in morphological structure.

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