# FUNGI – ГРИБЫ

## First records of *Badhamia ovispora* (Physarales, Myxomycetes) in Russia

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**Abstract.** The rare myxomycete *Badhamia ovispora* was found for the first time in Russia from the Perm Territory and Moscow Region. Morphological features of specimens of this species were studied in detail using light and scanning electron microscopy. The main features are oblong-oval spores that are almost smooth in the light microscope and the triple peridium. It discusses the distinction of *B. ovispora* from closely related species such as *B. goniospora*, *B. rhytidosperma*, *B. spinispora*, *B. verrucospora*, *Physarum apiculosporum*, *P. ovisporoides* and *P. ovisporum*. Data on *Badhamia ovispora* findings in different regions of the world are given.
**Keywords:** Amoebozoa, biodiversity, morphology, rare species, Moscow Region, Perm Territory.

## Первые находки *Badhamia ovispora* (Physarales, Myxomycetes) в России

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**Резюме.** Впервые в России (в Пермском крае и Московской обл.) найден редкий миксомицет *Badhamia ovispora*. Морфологические особенности образцов этого вида были детально изучены с помощью световой и сканирующей электронной микроскопии. Основными признаками являются удлиненно-овальные, практически гладкие в световом микроскопе споры и трехслойный перидий. Обсуждается отличие *B. ovispora* от близких видов, таких как *B. goniospora*, *B. rhytidosperma*, *B. spinispora*, *B. verrucospora*, *Physarum apiculosporum*, *P. ovisporoides* и *P. ovisporum*. Приводятся данные о находках *Badhamia ovispora* в разных регионах мира.
**Ключевые слова:** Amoebozoa, биоразнообразие, морфология, редкий вид, Московская область, Пермский край.

The genus *Badhamia* Berk. was described in 1852. According to the original concept of the genus proposed by M. J. Berkeley, it includes species with single-layered peridium, grouped spores and capillitium forming a three-dimensional network of tubes (Berkeley, 1852). Unlike the genus *Physarum* Pers. described in 1794, where capillitium is represented by translucent limeless tubes connecting lime nodes (Person, 1794), in *Badhamia* these tubes are completely or almost entirely calcareous (Berkeley, 1852). The type species of the genus *Badhamia* is *B. capsulifer* (Bull.) Berk. (≡ *Sphaerocarpus capsulifer* Bull., = *Physarum hyalinum* Pers.). Berkeley additionally included in the genus *Badhamia utricularis* (Bull.) Berk. and three species described by him: *B. nitens* Berk., *B. pallida* Berk. (considered a synonym of *B. nitens*) and *B. fulvella* Berk. However, morphology the latter is not fully clear due to the brief description (Carter, Nannenga-Bremekamp, 1972).

The concept of the genus was later expanded in the works of M. J. Berkeley himself (1873) and J. T. Rostafinski (1874). The latter proposed to use as a diagnostic feature only the reticulate structure of capillitium, but not the presence of grouped spores or single-layered peridium. This concept of the genus was supported by later authors and has been maintained to this day (Lister, 1925; Martin, Alexopoulos, 1969; Ing, 1999; Poulain *et al.*, 2011). However, in case of abnormal sporocarp

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development, the capillitium tubes in *Badhamia* can be almost limeless. Moreover, even under normal development, in some species lime does not completely fill the translucent capillitium tubes (Carter, Nannenga-Bremekamp, 1972). Therefore, an important unifying feature of the genus *Badhamia* is the structure of the capillitium, namely the absence of rounded node-like thickenings of tubes in places of their branching. For this reason, a number of species have been transferred from *Badhamia* to *Physarum* and vice versa (Farr, 1961; Eliasson, Lundqvist, 1979; Raub *et al*., 1979; García-Martín *et al*., 2023).

At present, the genus *Badhamia* includes 40 species (Lado, 2005–2024), 16 of which were recorded in Russia earlier (Bortnikov *et al*., 2020). The new species for Russia, *Badhamia ovispora* Racib., was identified by studying material collected in the Perm Territory and Moscow Region. Incorrect indication of morphological characters in classical monographs led to errors in the identification of specimens assigned to this species. The aim of this paper is to clarify morphological characteristics of the rare species *Badhamia ovispora* on the basis of the first finds for Russia from the Perm Territory and Moscow Region, as well as to conduct a comparative-morphological analysis of other oval-spore representatives of the genera *Physarum* and *Badhamia*.

## Materials and Methods

Morphological studies. The specimens were collected in the field using the standard methods (Wrigley de Basanta, Estrada-Torres, 2022). Sporocarps with fragments of substrate were glued onto U-shaped card trays and placed into matchboxes to prepare herbarium specimens. The specimens, subjected to two freezing-thawing cycles at –18 °C were air dried and placed into ziplock bags.

For light microscopy (LM), sporocarps were preserved as semi-permanent slides in 4% KOH. Specimens for scanning electron microscope (SEM) were mounted onto copper stubs covered by varnish and sputter-coated with gold-palladium. The spore surface and capillitium structure were studied with a Quattro S (Thermo Fisher Scientific, Waltham, MA, USA), at the Interdepartmental Laboratory of Electron Microscopy at the Faculty of Biology of Moscow State University. The program Helicon Focus ver. 6.0.18 was used to create stacked images of sporocarps under a Micromed 3 var. 3LED microscope with E3CMOS06300 digital camera and top illumination. Microscopic measurements of spores, capillitium, and sporocarps were made under the same microscope with the freeware ToupView 3.7 and freeware ImageJ ver. 1.52a. Nomenclature follows Lado (2005–2024).

Specimens examined

*Badhamia ovispora*: **Russia, Perm Territory,** Perm District, near Perm city, [58.10195°N, 56.40555°E], on dead branch of *Tilia cordata* Mill., 21 IX 2023, *Peters*, det. *Gmoshinskiy*, *Peters*, MYX 23701 (Fig. 1A–E); **Moscow Region,** Serpukhov District, Prioksko-Terrasnyi Natural State reserve, 54.89532°N, 037.652430°E, on inner bark surface of dead, standing upright tree of *Populus* sp., 17 X 2024, *Kireeva*, det. *Kireeva*, *Gmoshinskiy*, MYX 24684 (Fig. 1F–I).

*Badhamia spinispora*: **Kazakhstan,** East Kazakhstan Oblast, Kurshimskiy Distict, near Amanat village, Zaysan intermountain depression, 48.02167°N, 84.38500°E, desert complex of feather grass-sagebrush, saltwort and lichen-saltwort communities on loamy sand soils, litter of plants, specimen isolated in a moist chamber culture, 8 I 2010, *I. V. Zemlianskaya* (*И. В. Землянская*), det. *Gmoshinskiy*, LE 275300 (Fig. 3C).

*Physarum apiculosporum*: **Russia, Tyumen Region,** on pig dung (*Sus domesticus* Erxleben, 1777), 15 VII 1988, *M. A. Linnik* (*М. А. Линник*), *V. P. Prokhorov* (*В. П. Прохоров*), specimen isolated in a moist chamber culture 15 X 2012, det. *Gmoshinskiy*, MYX 4117 (Fig. 2A, B); **Moscow Region,** Odintsovo District, Zvenigorod biological station, road to Karinskoye village, [55.70°N, 36.69°E], cow dung (*Bos taurus* L., 1758), 7 VII 2000, *M. A. Linnik, V. P. Prokhorov*, *Gmoshinskiy*, specimen isolated in a moist chamber culture 15 X 2009, det. *Gmoshinskiy*, MYX 3258 (Fig. 2C, D); **Germany,** Prov. Brandenburg, Triglitz in der Prignitz, on an old dung heap, 12 VII 1915, *O. Jaap*, Myxomycetes exsiccati # 163, LEP 90 (Fig. 2E–G).

## Results

**Badhamia ovispora** Racib., 1884, Rozpr. Spraw. Posiedzen Wydz. Mat.-Przyr. Akad. Umiejetn 12: 72. (Fig. 1)

Sporangia are sessile, on restricted brown base, scattered or in dense groups, pulvinate, slightly elongated or reniform, sometimes angular when mature, white, 0.5–0.7 mm in diam.; 0.5–0.55 mm tall. Hypothallus is membranous, limeless, reddish-brown, inconspicuous. Peridium is triple: the outer layer is thin, membranous, translucent, making sporangia glossy, almost colorless at the top and light pinkish-brown at the base; the middle layer is firmly attached to the outer layer, thick, white, consisting of irregularly distributed lime deposits, irregularly dehiscent and showing the inner layer that is membranous and gray from lime deposits. Stalks and columella are absent. Capillitium consists of large irregular white thickenings, connected by thin, usually calcareous tubes; sometimes large nodes may join into pseudocolumella.

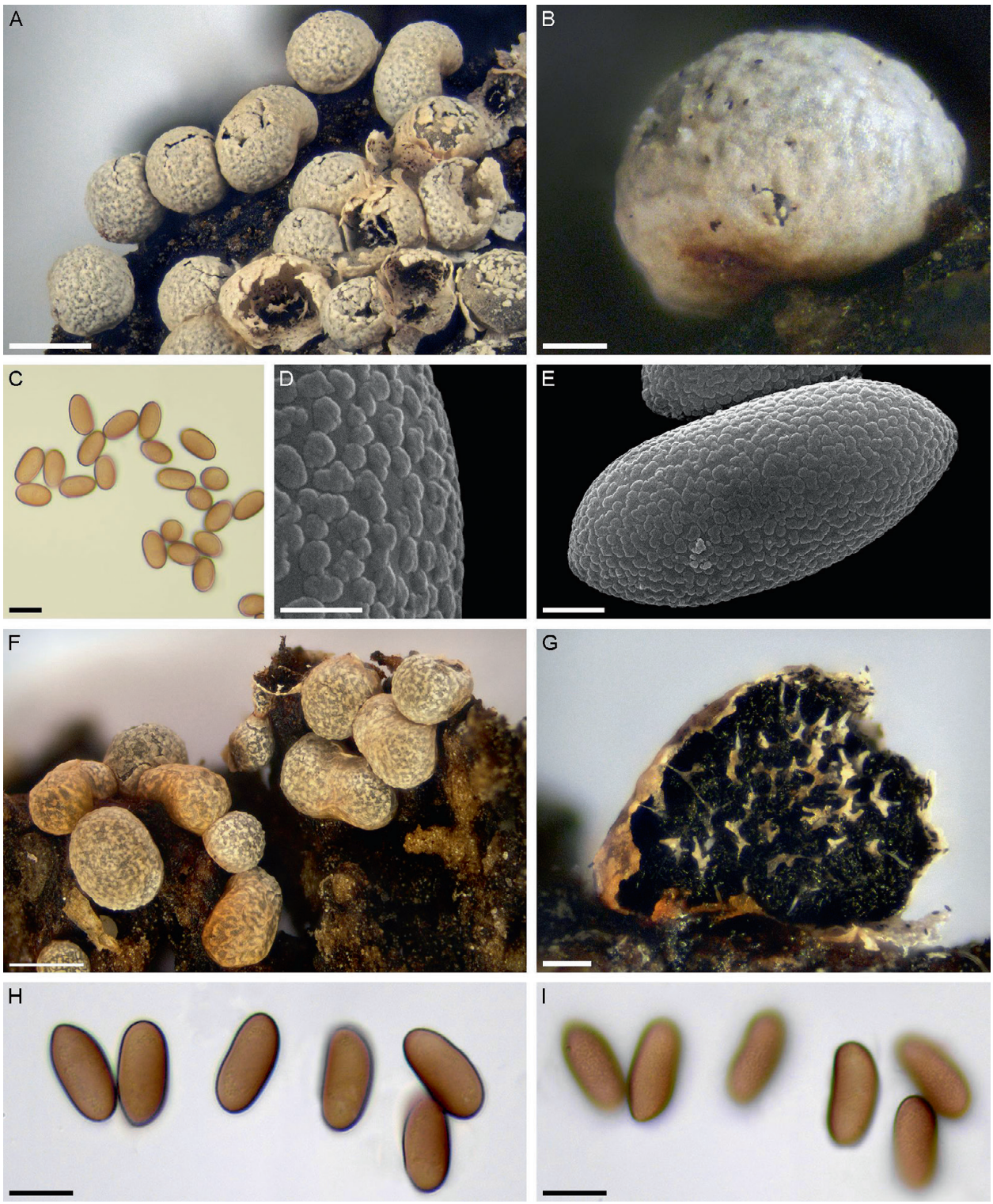


Fig. 1. *Badhamia ovispora* (A–E — from MYX 23701; F–I — from MYX 24684).
A, B — mature sporangia; C — spores in transmitted light (TL); D — spore surface in SEM; E — spore in SEM;
F — mature sporangia; G — damaged sporangium with capillitium; H, I — spores in TL.
Scale bars: A, F — 500 μm; B, G — 100 μm; C, H, I — 10 μm; D — 1 μm; E — 2 μm.
Authors of photographs: A, B, F–I — N. I. Kireeva; C–E — D. A. Peters, V. I. Gmoshinskiy.

Spores are black in mass, light-violet-brown in transmitted light (TL), free, ovate, reniform to allantoid, with uniformly thick wall, 13.2–18.0(19.0) × (6.8)7.1–8.0(8.3) μm in diam., minutely papillate in TL. Under SEM, the spores are ornamented by uniformly distributed flat areolated warts.

Our specimens completely matches the protologue (Raciborski, 1884). However, in contrast to the description made during the revision of the type material of *Badhamia ovispora* (Keller *et al*., 1975), the hypothallus in our specimens has no lime inclusions and is represented by a pinkish-brown, almost inconspicuous film. In addition, the peridium in our specimens has three rather than two layers. The presence of a firmly attached pinkish-brown outer layer in our samples makes sporangia glossy and reddish-brown at the base. The size of spores in the samples was different: 13.2–15.0 × 7.2–8.0 μm in diam. (mean = 14.1 μm, SD = 0.9, n =100; mean = 7.6 μm, SD = 0.4, n = 100) in MYX 23701 from the Perm Territory, and (15.1)16.2–18.0 (19.0) × (6.8)7.1–8.0(8.3) μm in diam. (mean = 17.14 μm, SD = 0.9, n = 100 μm; mean = 7.59 μm, SD = 0.4 μm, n = 100) in MYX 24684 from the Moscow Region.

## Discussion

*Badhamia ovispora* is a very rare species. The type specimen was collected by M. Raciborski in August 1882 on the trunk of *Populus* × *canescens* (Aiton) Sm. in Poland, in the vicinity of Krakow (Raciborski, 1884). However, the paper does not provide an illustration of the spores, which caused misunderstanding of the morphology of *Badhamia ovispora*. It was not until 1975 that the type specimen stored in the herbarium of the Botanical Institute of the Polish Academy of Sciences in Krakow was revised (Keller *et al*., 1975). In the course of this work, the morphology of sporocarps was described and the spores were imaged using scanning electron microscopy (SEM), which revealed that the spores of this species were not smooth, but covered with small areolated warts and lacked crest-like thickenings.

Most of the finds reported as *Badhamia ovispora* were shown to belong to another undescribed species (Keller *et al*., 1975). The main features of this new species were: rib-like thickening on the spore surface (Figs. 2B, C, F, 3B), double peridium formed by a thin glossy film (Fig. 2A, D) adhered to the inner, shell-like, highly limed layer, and confinement to herbivorous animal droppings, compost heaps or other decaying herbaceous plants (Keller *et al*., 1975). The species was later described as *Physarum apiculosporum* Härk. (Härkönen, 1978) and by another group of researchers later as *Badhamia semiannulata* Raub et H. W. Keller (Raub *et al*., 1979). Therefore, the second name is a heterotypic synonym of the first one (Lado, 2005–2024). An attempt was also made to consider *Physarum apiculosporum* in the genus *Badhamia* (Eliasson, Lundqvist, 1979), with no support by present-day researchers (Lado, 2005–2024).

Many finds of *Badhamia ovispora* in numerous check lists should rather be attributed to *Physarum apiculosporum*. Moreover, the most common monographs provide the misleading description and image of this species (Lister, 1925: Pl. 12; Hagelstein, 1944; Martin, 1949; Martin, Alexopoulos, 1969: Pl. 212), which leads to identification errors.

Additional difficulties with the interpretation of this species were also introduced by its misunderstanding in the exsiccata series. Keller *et al.* note that "a specimen collected in Germany by Otto Jaap and distributed as # 163 in his exsiccata series under the name *Badhamia ovispora* is indeed the smooth-spored *Badhamia*" (Keller *et al*., 1975). We studied this sample preserved in Mycological Herbarium of the All-Russian Institute of Plant Protection (under number LEP 90) and confirmed its conspecificity with *Physarum apiculosporum* (Fig. 2 E–G).

According to published data, *Physarum apiculosporum* is mostly found on the droppings of herbivorous animals in arid regions (Eliasson, Lundqvist, 1979; Cox, 1981; Keller, Schoknecht, 1989a), but there is information about its occurrence on the bark of trees and shrubs, including *Pithecellobiurn dulce* (Roxb.) Benth. (Eliasson, 1991).

Unlike *Physarum apiculosporum*, *Badhamia ovispora* is not a coprophilous species. All findings of *Badhamia ovispora* that match the morphology of the type specimen (*sensu* Keller *et al*., 1975) were made on dead bark or wood. It is most likely that *B. ovispora* should be assigned to the corticuloid or xylotrophic complex (Eliasson, Lundqvist, 1979). Therefore, the inclusion of *Badhamia ovispora* in general lists of coprophilous myxomycetes (Eliasson, Keller, 1999; Calaça *et al*., 2020) is erroneous.

Thus, specimens of *Badhamia ovispora*, with herbivorous animal droppings or plant remains indicated as substrate require additional morphological investigation. Until appropriate studies are conducted, such specimens should be regarded as doubtful.

Iconography of *Badhamia ovispora*: Raciborski, 1884: Pl. 4, Fig. 2a, b; Krzemieniewska,

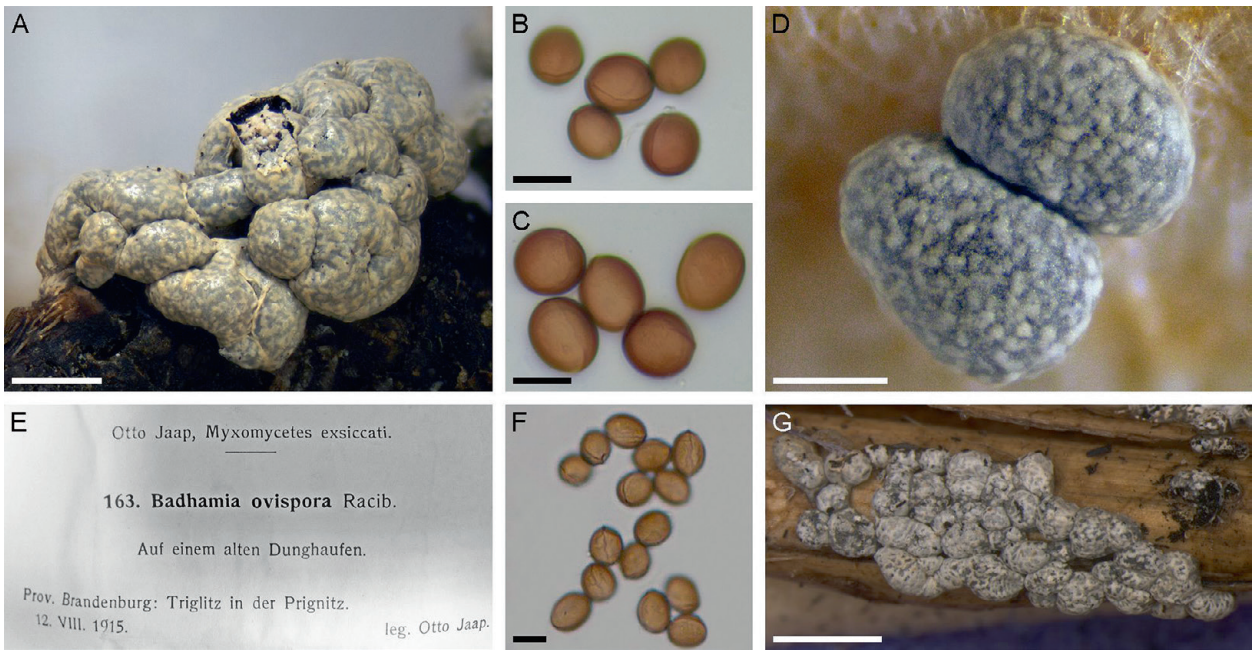


Fig. 2. *Physarum apiculosporum* (A, B — from MYX 4117; C, D — from MYX 3258; E–G — from Otto Jaap Myxomycetes exsiccati #163 (LEP 90)).
A, D, G — sporophores; B, C, F — spores in TL; E — lable of sample LEP 90.
Scale bars: A, G — 500 μm; B, C — 10 μm; D — 200 μm; F — 20 μm.
Authors of photographs: A–D — N. I. Kireeva; E–G — V. I. Gmoshinskiy, N. I. Kireeva.

1960: Tab. II. Fig. 7; Keller *et al.*, 1975: Figs. 1–10; Poulain *et al.*, 2011: Pl. 196.

Iconography of *Physarum apiculosporum*: Lister, 1925: Pl. 12; Martin, Alexopoulos, 1969: Pl. 212; Keller *et al.*, 1975: Figs. 11, 12; Härkönen, 1978: Figs. 1–6; Ing, 1999: Fig. 210; Neubert *et al.*, 1995: 168; Novozhilov, Schnittler, 2008: Figs. 11–13, but not Figs. 1–10; Novozhilov *et al.*, 2009: Fig. 4, but not Figs. 5–7; Härkönen, Sivonen, 2011: Figs. 212, 213, but not Fig. 214; Moreno *et al.*, 2011: Figs. 1–12; Poulain *et al.*, 2011: Pl. 195 (limeless plasmodiocarp).

Accepted records of *Badhamia ovispora*

**Canada:** British Columbia, East Kootenay, 49.65750°N, 115.89583°W, on inner bark of *Populus tremuloides* Michx., 14 X 2023, *T. Ehlers* (Ehlers, 2023). **France:** Le Monetier-les-Bains, Kasse village, 1500 m a. s. l., on bark of *Fraxinus* sp., 5 VIII 2008, *Y. Mourgues*, MM 37558 (Poulain *et al.*, 2011). **Poland:** Kapelance, near Krakow, 21 VIII 1882, *M. Raciborski*, KRAM (Raciborski, 1884). **Russia:** see above. **Spain:** Province of Ávila, near La Carrera, 40.34722°N, 5.55444°W, 5 II 2015, *F. B. Bermejo* (Bermejo, 2015). **USA:** Colorado, along the south fork of Middle Boulder creek at the Fourth-of-July Campground, 12.9 km NW of Nederland, 3124 m a. s. l., Boulder Country, on inner bark surface that had separated from the cambium of a decaying gymnosperm log (probably *Picea engelmanii* Perry) partially submerged in water, 21 VIII 1964, *H. Aldrich*, HA 13 (Cooke, 1968; Keller *et al.*, 1975); portions of this sample were deposited in different herbaria (see Keller *et al.*, 1975); Colorado, *E. C. Smith*, NYBG 10632, NYBG 10635 (Keller *et al.*, 1975); Colorado, Pike National Forest, 9.8 km southeast of Bailey on Buffalo Creek Road, [39.338056°N, 105.341667°W], on bark of *Populus* sp., with a brief description of morphology, 21 VIII 1985, *D. H. Mitchell,* DBG-F-015599 (Sam Mitchel Herbarium of Fungi, 2024a).

Therefore, the specimens from the Perm Territory and Moscow Region is the ninth and tenth morphologically confirmed records of *Badhamia ovispora* in the world.

Doubtful records of *Badhamia ovispora*

All the other indications of *B. ovispora* made before 1975 are doubtful (Keller *et al.*, 1975). Findings of *B. ovispora* from Brazil (Oliveira *et al.*, 2024) and Sweden (Myrdal, 2022) are questionable, as the authors report detection of sporocarps on rabbit droppings (*Lepus* sp.). The detection of *B. ovispora* in Iran is also questionable as the paper provides neither illustrations nor spore description or substrate characterization (Joshaghani *et al.*, 2013). Samples of *B. ovispora* from Spain (Pando, 2021) and the USA (Sam Mitchel Herbarium of Fungi, 2024b) were found on gymnosperms, but the findings are not supplemented with spore microphotographs and require additional morphological investigation.

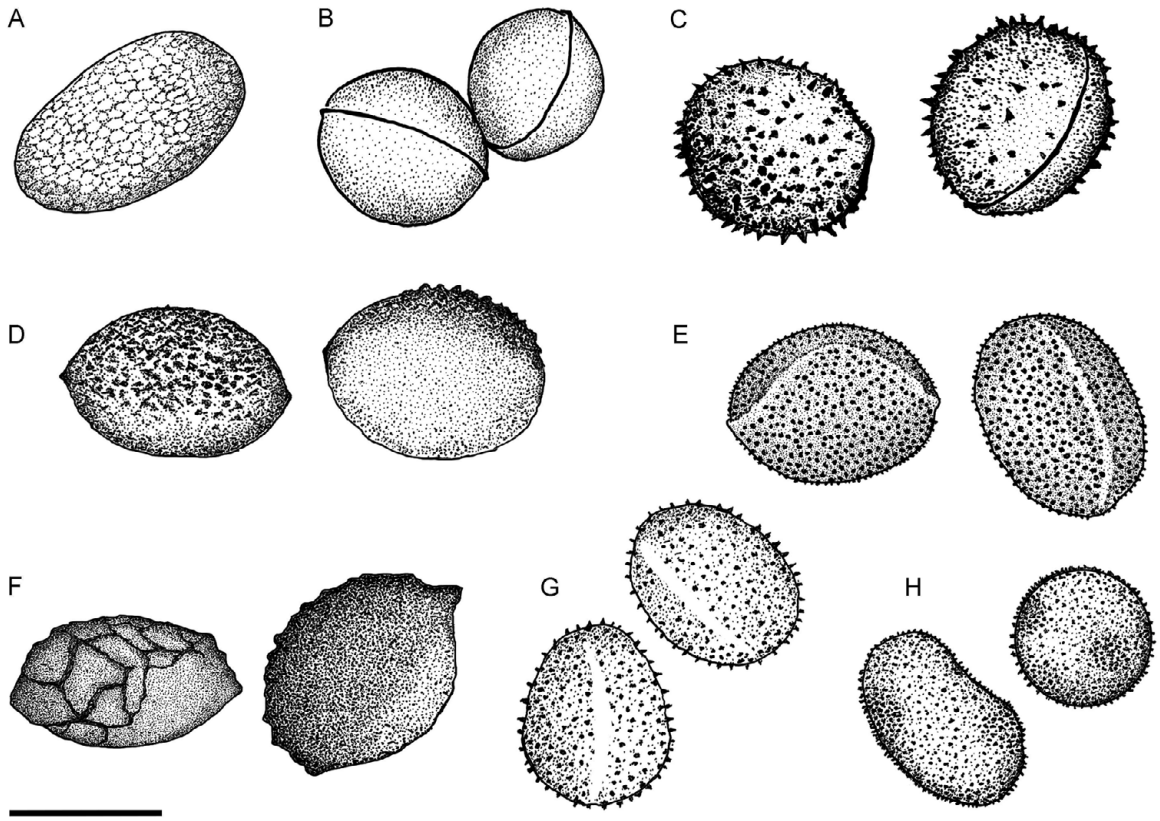


Fig. 3. Comparative morphology of spores of oval-spored species of *Physarum* and *Badhamia*.
A — *Badhamia ovispora* (from MYX 23701); B — *Physarum apiculosporum* (from MYX 4117); C — *Badhamia spinispora* (from LE 275300); D — *Badhamia verrucospora* (from Moreno *et al*., 2011: Fig. 31); E — *Badhamia goniospora* (from Kuhnt, 2024: Abb. 167); F — *Badhamia rhytidosperma* (from Zemlyanskaya *et al*., 2020: Fig. 3b); G — *Physarum* cf. *ovisporum* (from Poulain *et al*., 2011: Pl. 298); H — *Physarum ovisporioides* (from Yamamoto *et al*., 2002: Fig. 7).
Scale bar: 10 μm. Author of illustrations: N. I. Kireeva.

Several new oval-spored species of the genera *Physarum* and *Badhamia* have been described to date. *Physarum spinisporum* Eliasson et N. Lundq. is characterized by oval spores covered with rib and large spines (Eliasson, Lundqvist, 1979). Later, it was transferred to the genus *Badhamia* and is now considered as *B. spinispora* (Eliasson et N. Lundq.) H. W. Keller et Schokn. (Keller, Schoknecht, 1989a).

In the study of the species diversity of myxomycetes of the Colorado Plateau, another specimen was found that was similar to *Physarum apiculosporum* but only had well-defined spiny ornamentation on one side of the spore (Novozhilov *et al*., 2003). This specimen was later described as a new species, *Badhamia verrucospora* G. Moreno, D. W. Mitch. et Novozh. (Moreno *et al*., 2011). This species has not been recorded in Russia (Bortnikov *et al*., 2020).

Another species with oval spores is *B. goniospora* Meyl. (= *Badhamia dearnessii* Hagelst.). This species is also characterized by globose sporangia on a narrowed base covered by simple membranous peridium with white lime. The spore size of *B. goniospora* is 13–15 × 11–13 μm in diam. (Poulain *et al*., 2011), which is very similar to that of *B. ovispora*. However, the spore surface is covered with well-marked, evenly distributed warts. In addition, a good distinguishing feature is the presence of a light line, visible on most spores (Kuhnt, 2024) and that gives them a slightly angular shape (Kowalski, 1975).

*Badhamia rhytidosperma* H. W. Keller et Schokn. is characterized by oval spores with reticulate ornamentation covering only half of the spore surface (Keller, Schoknecht, 1989b; Zemlyanskaya *et al*., 2020). Finds of this species were made on the bark of shrubs.

In the genus *Physarum,* two more species with irregular and sometimes nearly oval spores were described, *P. ovisporum* G. Lister and *P. ovisporioides* Y. Yamam. et Shuan L. Chen. Both of these species have typical physaroid capillitium represented by enlarged limed nodes connected by thin translucent limeless tubes and spores ornamented with small warts. *Physarum ovisporum* has slightly elongated or irregularly shaped spores with a light-colored cracking zone and

a single-layered peridium (Lister, 1921; Johannesen, Vetlessen, 2020; Yamamoto, 2021). *Physarum ovisporioides* has oval or strongly elongated spores ornamented with small warts that sometimes cluster in 2–3 groups per visible part of the spore and two-layered peridium (Yamamoto *et al*., 2002).

For many species from *Badhamia* and *Physarum* the genus assignment is a subject of discussions. This complicates practical work and can lead to errors in identification. At present, at least eight species with oval or almost oval spores have been described in these genera. For this reason, below we present the general identification key for species with oval spores of these genera.

**Key for identifying of the oval-spored *Badhamia* and *Physarum* species**

1. Spores are with well-defined ornamentation distributed over the entire surface in TL ..... 2
— Spores are smooth or with warted or wrinkled-reticulate only along one side in TL ..... 5
2. Light band or dark rib on the spore surface is no visible in TL. Spores are minutely warted with 2–3 groups of aggregated warts on hemisphere ..... ..... *Physarum ovisporioides* (Fig. 3H)
— Light band or dark rib on the spore surface is visible in TL. The warts and spines on the spore surface are not clustered ..... 3
3. Spores bearing large, irregularly distributed spines. Angular spores with dark ribs ..... ..... *Badhamia spinispora* (Fig. 3C)
— Spores with uniformly dispersed small warts. Spores with light-colored line ..... 4
4. Capillitium consisting of calcareous with some limeless tubes (badhamioid) ..... ..... *Badhamia goniospora* (Fig. 3E)
— Capillitium consisting of round lime nodes connected translucent limeless tubes (physaroid) ..... ..... *Physarum ovisporum* (Fig. 3G)
5. In TL and under immersion spores are warted or wrinkled-reticulated on one side and smooth on the other ..... 6
— In TL and under immersion spores are almost smooth or encircled with low crest on one side ..... 7
6. Spores are wrinkled-reticulate over about half of the spore surface, otherwise smooth ..... ..... *Badhamia rhytidosperma* (Fig. 3F)
— Spores warted over about half of the spore surface, otherwise smooth ..... *Badhamia verrucospora* (Fig. 3D)
7. Spores conspicuously marked by ring of low ridge along one side, in optical section apiculate at one or both ends, otherwise smooth. On straw, decaying leaves, and dung of herbivorous animals ..... ..... *Physarum apiculosporum* (Fig. 3B)
— Spores covered with small areolated warts and not apiculate. On dead bark and wood ..... ..... *Badhamia ovispora* (Fig. 3A)

## Conclusions

The initial misinterpretation of *Badhamia ovispora* sporocarp morphology demonstrates the importance of complete descriptions and high-quality illustrative material leveraging modern technologies, especially for rare species and type specimens. When reporting finds of rare species, it is essential that the material is properly described in publications and deposited in collections accessible to a wide range of researchers so that it can be revised later. On the one hand, this approach complicates biodiversity research, but on the other hand, it makes the resulting species lists much more informative.

The current concept of the genus *Badhamia* is based on the structure of capillitium, which can change depending on environmental factors. As it has already been shown in a number of studies, the genera *Badhamia* and *Physarum* in their current understanding are not monophyletic (García-Martín *et al*., 2023). Thus, in the coming years we can expect the development of a new morphological concept for these genera.

*Badhamia ovispora* is quite close to *Physarum apiculosporum* by morphology. They have in common not only the oval shape of spores, but also the filmy outer layer of the peridium, which gives the sporangia a glossy shine. Further studies, including those using molecular phylogeny, should confirm or reject the taxonomic significance of these features for the separation of these species into a discrete group.

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