

GENUS *PERICHAENA* (MYXOMYCETES, TRICHIALES, ARCYRIACEAE): NOMENCLATURE HISTORY AND RECOMMENDATIONS FOR MORPHOSPECIES IDENTIFICATION

© 2022 E. S. Gubanov^{1,*}, V. I. Gmoshinskiy^{1,2,**}, F. M. Bortnikov^{1,***},
A. V. Matveev^{1,****}, and Yu. K. Novozhilov^{3,*****}

¹ Lomonosov Moscow State University, 119234 Moscow, Russia

² Polistovsky State Nature Reserve, 182840 Bezhanitsy, Russia

³ Komarov Botanical Institute, 197376 St. Petersburg, Russia

*e-mail: gubanov_5b_1315@mail.ru

**e-mail: rubisco@list.ru

***e-mail: f.m.bortnikov@gmail.com

****e-mail: andrmatveev@gmail.com

*****e-mail: yurynovozh1lov@yandex.ru

Received May 5, 2022; revised June 5, 2022; accepted June 7, 2022

The genus *Perichaena* now includes 38 morphospecies and characterized by yellow spore mass, fairly dense peridium, and the absence of spiral bands on the capillitium tubes ornamented with spines or warts. In some cases, capillitium may be reduced or absent, which tends to obscure the taxonomic boundaries of *Perichaena*, causing it to approach the genus *Licea*. During the last 50 years, many new widespread species were described in literature, however, some of them have not been included in fundamental monographs or identification keys. In this paper we summarize data on the genus *Perichaena*, including its nomenclature history, and propose illustrated identification keys to the species of this genus. The short morphological descriptions and illustrations of 13 species recorded in Russia are presented.

Keywords: identification keys, *Licea*, morphospecies, Russia, SEM, taxonomic history

DOI: 10.31857/S0026364822060046

INTRODUCTION

The current taxonomy and classification of myxomycetes (*Myxomycetes* = *Myxogastrea*) are based mainly on phenotypic (morphological) characters of sporophores and spores (e.g. Martin, Alexopoulos, 1969; Poulain et al., 2011; Lado, Eliasson, 2017) or on both morphological characters and molecular markers (Fiore-Donna et al., 2013; Leontyev et al., 2019; Leontyev, Schnittler, 2017). About 1100 morphospecies of *Myxomycetes* are known to date (Lado 2005–2022). The classification based on full length 18S rDNA sequences (Leontyev et al., 2019) contains 9 orders, 13 families and 64 genera. At the same time, 11 genera are so far *incertae sedis* due to the insufficient data and based mainly on morphological characteristics. The genus *Perichaena* Fr. (*Trichiales*) is an example of such genus of the bright-spored myxomycetes (Leontyev et al., 2019). The key characters of this genus are poorly developed or totally absent capillitium, which is never ornamented with spiral bands, fragile, relatively dense peridium, and golden yellow or orange spore mass (Rostafiński, 1875; Poulain et al., 2011). However,

none of these traits alone allows to unambiguously separate the genus *Perichaena* from all others, so they can only be used in complex.

MATERIALS AND METHODS

The illustrations in present study are based on specimens of sporophores collected and preserved according to the standard protocol (Wrigley de Basanta, Estrada-Torres, 2017) in the Collection of *Myxomycetes* at the Department of Mycology and Algology of the Lomonosov Moscow State University (MYX), Moscow, Russia, and in the Komarov Botanical Institute (LE), Saint Petersburg, Russia.

Photographs of the appearance of sporophores were made by a Micromed 3 var. 3LED optical microscope with E3CMOS06300 digital camera with top illumination. The series of pictures were taken in different optical sections and processed by Helicon Focus ver. 6.0.18 software. The sizes of spores, capillitium, and sporocarps were calculated via ToupView and ImageJ ver. 1.52a. Some illustrations were made by Zeiss (DM)

Discovery V20 and AxioZoom V16 motorized stereo microscopes.

Microscopic measurements and observations were made under a Zeiss Axio Imager A1 light microscope with differential interference contrast (LM) using Axio Vision 4.8.0.0 software (Carl Zeiss Imaging Solutions) and a Micromed 3 var. 3LED optical microscope with E3CMOS06300 digital camera. For microscopy, sporocarps were preserved as permanent slides in polyvinyl-lactophenol or 4% KOH. The spore surface and structure of capillitium were studied using a JSM-6390 LA, Jeol JSM-6380 LA (Jeol, Tokyo, Japan), Quattro S (Thermo Fisher Scientific, Waltham, MA, USA) or Camscan-S2 scanning electron microscope (Cambridge Instruments, UK). Specimens for SEM were mounted on copper stubs with a double-sided tape and coated with gold-palladium.

RESULTS

Nomenclature history of the genus *Perichaena*

In 1783, A. Batsch described the species *Lycoperdon corticale* Batsch (Batsch, 1783, *f.* 1), providing it with a very short Latin description without illustrations or any type specimen designation. Eight years later J. Bulliard (1791), despite he was acquainted with the Batsch's publication, independently described the species *Sphaerocarpus sessilis* Bull., providing it with a Latin diagnosis, a French description and a link to his previously published illustration (Bulliard, 1789, p. 129, pl. 417).

In 1796, C. Persoon described the species *Trichia gymnosperma* Pers. (Persoon, 1796). The protologue in this case contained direct references to *Lycoperdon corticale* Batsch and *Sphaerocarpus sessilis* Bull. This means that Persoon has included their types in *Trichia gymnosperma* species. For this reason, the name *Trichia gymnosperma* can be regarded as a superfluous, illegitimate name for *Lycoperdon corticale* Batsch, which was published previously (Art. 52 of Shenzhen Code, Turland et al., 2018).

In 1797, H. Schrader in his notes on *Trichia gymnosperma* Pers. (Schrader, 1797) suggested replacing the species name with "circumscissa" as a more appropriate one. However, the name "*Trichia circumscissa* Schrad." has not been validly published because Schrader did not specify the corresponding binomial. A reference by J. Rostafiński (Rostafiński, 1875) "*Trichia circumscissa* Schrad." among synonyms of *Perichaena corticalis* also cannot be considered as a valid name publication according to the Art. 36.1 (Art. 36.1 of Shenzhen Code, Turland et al., 2018). Therefore, "*Trichia circumscissa* Schrad." should be regarded as a nomen nudum.

In 1801, C. Persoon transferred the species *Trichia gymnosperma* to the genus *Licea* (Persoon, 1801), changing the specific epithet to "*circumscissa*". This combination (*Licea circumscissa*), as in the case of *Tri-*

chia gymnosperma Pers., can be regarded as a superfluous name.

In 1805, J. Albertini and L. Schweinitz described two varieties of *Licea circumscissa* Pers.: *L. circumscissa* var. *populina* (as α , *populina*) and *L. circumscissa* var. *abietina* (as β , *abietina*) (Albertini, Schweinitz, 1805).

Finally, in 1817, E. Fries validly published the genus *Perichaena* with 4 species: *P. strobilina* (Alb. et Schwein.) Fr. (\equiv *Licea strobilina* Alb. et Schwein.), *Perichaena abietina* (based on *Licea circumscissa* var. *abietina* Alb. et Schwein.), *Perichaena populina* (Alb. et Schwein.) Fr. (based on *Licea circumscissa* var. *populina* Alb. et Schwein.), and *Perichaena quercina* (Alb. et Schwein.) Fr. (Fries, Lindgren, 1817). The genus type was not designated by Fries and therefore had to be designated later. Since *P. strobilina* probably belonged to *Pucciniomyces*, *P. quercina* could not be reliably determined as one of the currently recognized species within *Perichaena* (Lado, 2005–2022), the choice had to be done between the left *P. abietina* and *P. populina* (both are based on the varieties of *Licea circumscissa*) (Fig. 1–5).

Since *Trichia gymnosperma* Pers. and *Licea circumscissa* Schrad. were considered superfluous names for the previously published name *Lycoperdon corticale* Batsch – it was necessary to change the specific epithet of the type species of *Perichaena* in accordance with its basionym. It was done by J. Rostafiński in 1875 who published the combination *Perichaena corticalis* (Batsch) Rostaf.

Thus, *P. corticalis* (Batsch) Rostaf. is currently recognized as the genus *Perichaena* type species.

Morphological characters of *Perichaena*

Type of sporophore. All fructification types known among myxomycetes are represented in the genus including individual sporangia (sessile or stalked) or elongated, sometimes vermiculate plasmodiocarps [*P. chryosperma* (Fig. 6, E), *P. microspora*, *P. patagonica*, and *P. vermicularis* (Fig. 8, K)]. In some cases, sporangia of *P. brevifila*, *P. depressa* (Fig. 7, A), *P. madagascariensis*, and *P. nigra* form dense clusters and can be deformed from mutual compression. In additions, *P. syncarpon* forms rather large fructifications, that are interpreted as pseudoaethalia (Martin, Alexopoulos, 1969) or even as aethalia (Yamamoto, 2006).

Color of peridium and spore mass. Most species within the genus *Perichaena* have yellow spore mass, except *P. pulcherrima*, which has purple spores (Wrigley de Basanta et al., 2013). Moreover, its spore mass color can vary from brown, brick-red to almost purple (Martin, Alexopoulos, 1969). However, the capillitium of *P. pulcherrima* looks quite typical for the genus *Perichaena*: it is hollow, often relatively thin (about 4 μ m in diameter) and ornamented with well-visible spines. Based on all the features, except for the spore color, this species also can be attributed to the genus *Perichaena*.

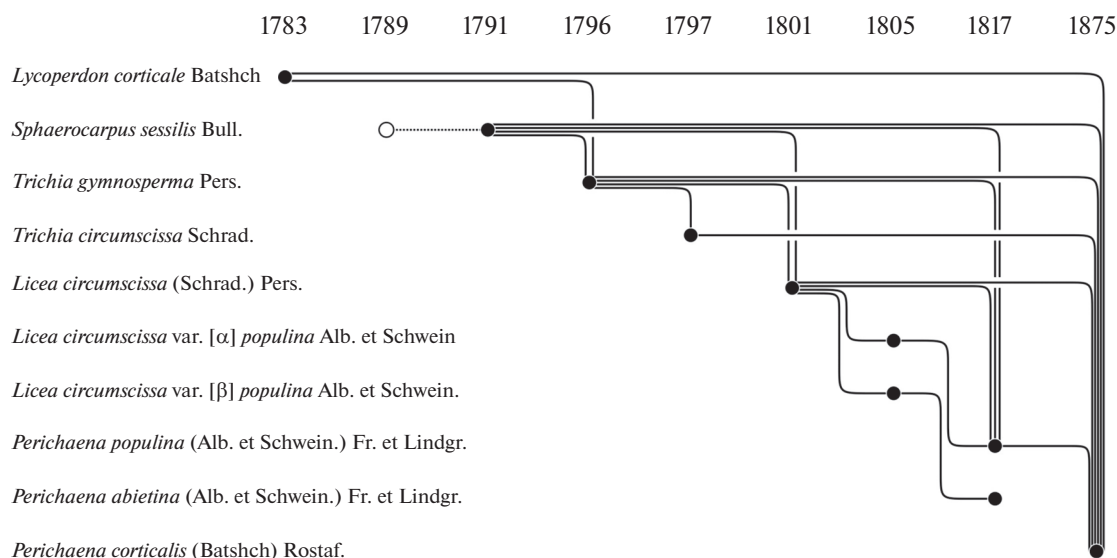


Fig. 1. Nomenclature history of *Perichaena corticalis*. Black dots – publications with taxon descriptions, white dot – publication of species description without genus diagnosis.

Size and ornamentation of spores. Spores of the genus *Perichaena* representatives are usually pronouncedly ornamented. There are no representatives with smooth spores described. Spores can be ornamented with small warts [for example, *P. corticalis* (Fig. 6, J, K), *P. depressa* (Fig. 7, D), *P. vermicularis* (Fig. 8, L), etc.], a fine mesh [*P. microspora* and *P. reticulospora* (Fig. 8, I)] or may have unique ornamentation such as *P. echinolophospora*, *P. heterospinispora* (Fig. 7, G) or *P. polygonospora* (Fig. 8, B–C).

Spores of the genus *Perichaena* are usually 8–14 μm in diam. *P. microspora* has small spores (6–7 μm in diam.), whereas the spores of *P. megaspora* can be reached up to 25 μm in diam.

Peridium morphology. The most species of the genus *Perichaena* have a double peridium, consisting of the inner usually membranous layer, which is thin, almost transparent and more or less iridescent, and the outer filled with granular refuse material and colored in orange to dark brown, sometimes black tints (Fig. 8, D). The peridium layers of some species are merged (Martin et al., 1983), e.g. in *P. pachyderma* (Mitchell et al., 2011), in other cases the outer peridium layer can be partially destroyed, e.g. in *P. madagascariensis* (Wrigley de Basanta et al., 2013), and some species have a one-layered peridium, e.g. in *P. reticulospora* (Fig. 8, H) (Keller, Reynolds, 1971).

Peridium can dehisce in different ways. In most cases, dehiscence by irregular fragments [e.g., *P. chryso sperma* (Fig. 6, E) or *P. pedata* (Fig. 7, J)]. However, there are quite a few species whose outer layer cracks by circumscissile dehiscence along a preformed line [*P. depressa* (Fig. 7, A), *P. corticalis* (Fig. 6, H), *P. quadrata* (Fig. 8, D), and *P. nigra*] or platelets separated by definite lines [*P. calongei* (Fig. 6, A), *P. syncarpon*, and

P. tessellata]. Usually, the outer layer of peridium is rather tightly connected with the inner one, however, in many species the inner peridium can detach from the outer one and becomes clearly visible in the form of a membrane covering the spore mass, like in *P. depressa* (Fig. 7, A), *P. quadrata* (Fig. 8, D).

Refuse crystalline material on the peridium

Among taxa of the bright-spored clade *Lucisporomycetidae* (Leontyev et al., 2019) the species of *Perichaena* and *Dianema* can form refuse deposits of calcium and silicon oxalates on the peridium surface. Such material can be quite often found in different quantity in *P. corticalis*, *P. dictyonema*, *P. liceoides*, and *P. vermicularis*. However, they are usually completely absent in sporophores developing in moist chamber cultures (Gilbert, 1990). Crystalline material can be deposited sometimes not only on the peridium surface, but also in the sporangium stalk, as in *P. stipitata* (Estrada-Torres et al., 2009). It should be noted that white crystals sometimes form on the sporophore surface of some *Licea* species, e.g. in *Licea pseudoconica* (Keller, Brooks, 1977) forming a relatively large “cap” of multifaceted (but not stellate) crystals on the peridium surface.

Stalk. Nine species of the genus form well-developed stalks of sporophores. In some cases, they can be very short and appear as a simple continuation of hypothallus with a narrowed sporangium base [*P. calongei* (Fig. 6, A, B), *P. polygonospora* (Fig. 8, A), and *P. reticulospora* (Fig. 8, H)]. However, there are species with very well-defined stalks: *P. heterospinispora* (Fig. 7, E, F), *P. longipes*, *P. papulosa*, *P. pedata* (Fig. 7, J), *P. pulcherrima*, and *P. stipitata*. The stalk is usually formed as a hypothallus extension and can often contain refuse material.

Table 1. Comparative features of species the genera *Perichaena* and *Licea*

Character	<i>Perichaena</i>	<i>Licea</i>
Capillitium	usually present	absent or reduced to papillae on the surface of peridium
Spore mass color	usually yellow (exceptions: <i>Perichaena pulcherrima</i> and <i>P. grisea</i>)	usually brown, black or reddish; rarely yellowish
Spore ornamentation	usually well-developed	usually poorly developed or absent (spores smooth)
Peridium	usually double; sometimes outer layer can be reduced or merged with the inner one	usually single; cartilaginous, dense
Dehiscence	usually irregular or rarely by a circle slit, forming a lid, or by lines of dehiscence, forming plates	along the lines of dehiscence, forming plates, or by a small lid, rarely irregular

Capillitium. Most species of the genus *Perichaena* are characterized by the presence of capillitium in the form of hollow tubes. They usually form a network with a small number of free ends. At the same time, it is relatively thin comparing with other representatives from the order *Trichiales*. For most species the diameter of tubes varies from 2 to 4 µm; however, the species *P. acetabulifera*, *P. patagonica*, and *P. longipes* are characterized by slightly larger capillitium tubes (up to 6 µm). Capillitium can be almost smooth (*P. frustrifilaris*) or ornamented with large spines [*P. calongei* (Fig. 6, C), *P. chryso sperma* (Fig. 6, F)], warts [*P. brevifila*, *P. pedata* (Fig. 7, K)], crater-like depressions (*P. acetabulifera*), reticulum often visible only with SEM (*P. dictyonema*); and in some cases, capillitium can be in the form of perforated bands (*P. poronema*). It is important to note that capillitium of the *Perichaena* species is never ornamented with spiral thickenings (Poulain et al., 2011). The exception is the capillitium of *P. minor* (G. Lister) Hagelst., and it was, therefore, transferred to *Hemitrichia* (Martin, Alexopoulos, 1969).

Nine species of the genus have a strongly reduced (e.g. *P. brevifila* and *P. grisea*) capillitium. In *P. echinolophospora* (Novozhilov, Stephenson, 2015), *P. heterospinispora*, *P. polygonospora* (Novozhilov et al., 2008), *P. taimyriensis* (Novozhilov, Schnittler, 2000), *P. liceoides* (Rostafiński, 1875; Kuhnt, 2019), *P. pachyderma* (Mitchell et al., 2011), and *P. nigra* (Lado et al., 2014) the capillitium even is completely absent. All species without capillitium have small sporocarps (0.1–0.5 mm in diam.) and usually form fruit bodies on the dung of herbivorous animals, often in arid conditions (Eliasson, 2017).

Comparative morphological characteristics of the genera *Perichaena* and *Licea*

The genus *Perichaena* is morphologically very similar to some species of the genus *Licea* (Eliasson, 1977). Some features are sufficient to unambiguously separate these two genera. From the taxonomic point of view, the most “convenient” is the presence of capillitium in *Perichaena* and its absence in *Licea*, but this feature is

not constant in either genus. As it was mentioned above, there are at least nine species in the genus *Perichaena*, which almost completely lack capillitium, while in some species of the genus *Licea* there are outgrowths on the peridium plate edges, which some authors interpret as a highly reduced capillitium (Gilbert, 1996). Moreover, the molecular phylogeny obtained for a very limited set of data on the marker gene sequences shows that the genus *Licea* is not a monophyletic group (Leontyev et al., 2019). It was shown that *L. variabilis* is more closely related not to other *Licea* species but to the genus *Dianema* (Fiore-Donno et al., 2013).

Thereby, in order to assign a species to a particular genus one has to study a set of characters. We present a whole set of features proposed for the assignment of species without capillitium to the genus *Perichaena* from the study of Yu.K. Novozhilov (Novozhilov et al., 2008) in a table form for convenience (Table 1).

Identification keys for the genus *Perichaena*

Traditionally, the genus *Perichaena* has been considered a relatively small taxon. Thus, in the monograph by J. Rostafiński (1875) there are only 6 species (of which only 2 are currently valid: *Perichaena corticallis* and *P. depressa*). G.W. Martin and C.J. Alexopoulos (1969) recognized 9 species (8 of them are currently regarded as valid).

Recently, thanks to the widespread use of the moist chamber culture method and the intensive studies in tropics and arid regions, a large number of new species have been described, which are different in morphology and ecology (Novozhilov et al., 2008; Wrigley de Basanta et al., 2013; Novozhilov, Stephenson, 2015; Walker et al., 2015; Lizárraga et al., 2019).

The genus *Perichaena* currently encompasses 38 species which are listed in the nomenclatural information system of Eumycetozoa (Lado, 2005–2022). Thirty of them (almost 80%) were described since the fundamental monograph of G.W. Martin and C.J. Alexopoulos (1969) has been published, and only

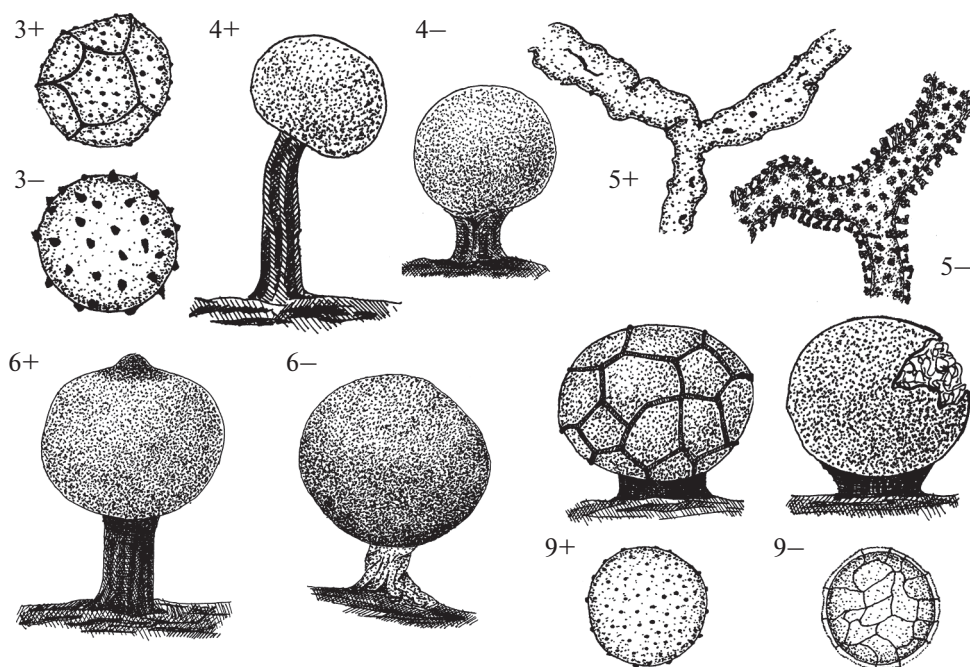


Fig. 2. Illustration of morphological characteristics for group 1 of dichotomous identification key. Numbers correspond to the numbers of the definitive theses.

18 species were included in the monograph of Poulain et al. (2011).

So far, there are no identification keys that take into account all currently known species of the genus *Perichaena*; moreover, the insufficiently detailed description of some species makes it difficult to identify them. In this paper we attempt to present the identification keys for all known species of the genus *Perichaena* and to clarify the differences between the species for further taxonomic analysis of the genus as a whole.

The dichotomous key is based on the following most distinguishable characters: fruiting body type, presence and structure of a stalk, peridium thickness, dehiscence type, size and ornamentation of spores and capillitium and some others. To make it easier to follow, many steps are provided with illustrations. It should be especially noted that we tried to convey exactly the character that is spoken of in the thesis or antithesis. Therefore, working with the key, in no case can you rely solely on illustrations, but you should pay more attention to the descriptive part of the identification steps.

Dichotomous key

- 1. Sporophores – stalked sporangia Group 1
- Sporophores – sessile sporangia or plasmodiocarps, rarely aethalia or pseudoaethalia..... Group 2

Group 1 (Fig. 2)

- 1. Peridium violet-red; spores violet-brown in mass, from brick-red to orange-red in transmitted light XXIX *P. pulcherrima*
- Peridium black, brown, ochraceous, orange or yellow; spores golden-yellow or orange in mass, light-yellow in transmitted light 2
- 2. Capillitium absent 3
- Capillitium present 4
- 3. Spores (9.0) 10.0–11.5 (12.5) μm diam. (including ornamentation), ornamented with large warts, with a coarse network of rounded ridges 1.0–1.5 μm high, and thus causing the spore to appear angular XXVI *P. polygonospora*
- Spores (10.5) 12–13 (14.5) μm diam., subglobose, ornamented with individual large spines 0.9–1.2 μm in height XIII *P. heterospinispora*
- 4. Stalk long, exceeding half of the total height 5
- Stalk shorter, rarely exceeding half of the total height 6
- 5. Capillitium 3–4 μm diam., smooth in transmitted light, ornamented with minute warts XXV *P. pedata*
- Capillitium thicker, 3.2–6.2 μm diam., densely ornamented with large spines or papillae, branched, with coral-like projections; due to ornamentation often looks furry XV *P. longipes*
- 6. Sporangia bear one prominent dark wart or papilla as a thickness of peridium on the top of the sporotheca XXIII *P. papulosa*
- Dark wart or papilla on the peridium is absent 7
- 7. Peridium single, thin, membranous 8
- Peridium double, outer layer thick, cartilaginous; inner layer thin, membranous 9
- 8. Spores 12–15 μm diam.; stalk usually white XXXII *P. stipitata*

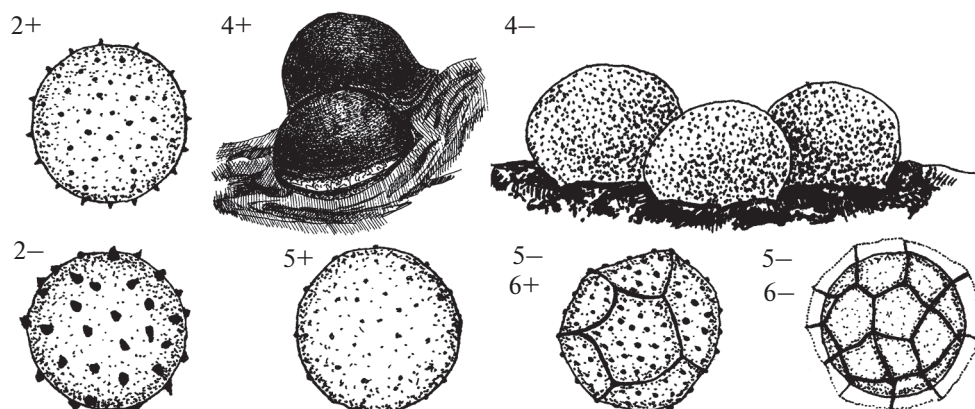


Fig. 3. Illustration of morphological characteristics for key 1 from group 2 of dichotomous identification key. Numbers correspond to the numbers of the definitive theses.

- Spores 9–10 μm diam.; stalk brown or black XXV *P. pedata*
- 9. Outer layer of peridium consists of dark, edged, polygonal peridial plates, which make sporangium look like a soccer ball; dehiscence along plates, spores warted IV *P. calongei*
- Outer layer of peridium is entire, dehiscence irregular not along plates; spores reticulate XXXI *P. reticulospora*

Group 2

- 1. Capillitium absent Subgroup 1
- Capillitium present, sometimes faintly discernible or in the form of weakly branching filaments Subgroup 2

Subgroup 1 (Fig. 3)

- 1. Peridium single, thin, membranous 2
- Peridium single or double, but outer layer always thick, cartilaginous 3
- 2. Spores ornamented with thin, spines or warts; hypothallus poorly developed, imperceptible XIV *P. liceoides*
- Spores ornamented with large, scattered, pyramid-like spines; hypothallus well noticeable, light yellow, membranous XIII *P. heterospinispora*¹
- 3. Spores more than 13 μm diam. 4
- Spores less than 12 μm diam. 5
- 4. Sporangia black, dehiscing by round slit forming a lid XXI *P. nigra*
- Sporangia orange, yellow or brown, opening irregularly... XXXIV *P. taimyriensis*
- 5. Spores warted; peridium very thick (2–5 μm) XXII *P. pachyderma*
- Spores reticulate; peridium thinner 6
- 6. Spores polygonal, ornamented with scattered composite large warts, which may form clusters XXVI *P. polygonospora*
- Spores globose or subglobose ornamented with regular honeycomb-like arrangements of crests, forming a reticulum; peridium can be double..... IX *P. echinolophospora*

Subgroup 2 (Fig. 4–5)

- 1. Peridium single, membranous 2
- Peridium double (layers may be closely appressed and peridium may seem to be single), thick, cartilaginous 9
- 2. Spores 6–7.5 μm diam. XX *P. microspora*
- Spores 10–15 μm diam. 3
- 3. Sporocarps bluish-grey, sometimes with a yellow tints XI *P. grisea*
- Sporocarps brown, black, orange or yellow 4
- 4. Aethalia or pseudoaethalia XIX *P. membranacea*
- Sporangia or plasmodiocarps 5
- 5. Capillitium poorly developed, in the form of short, rarely branching elaters or absent..... 6
- Capillitium well-developed, forming a dense net 7
- 6. Sporangia evenly colored, usually from yellow to grey XXVIII *P. pseudoliceoides*
- Sporangia obviously two-colored: brown or black at the top and yellow at the base XXXVI *P. thindii*
- 7. Sporangia; peridium brown-orange, iridescent; capillitium 5–7 μm diam., more or less the same in different parts XXXVIII *P. verrucifera*
- Sporangia or short plasmodiocarps, yellowish in color; capillitium 2–6 μm diam., with thickenings and thinnings, seem to have irregular edges 8
- 8. Sporangia, subglobose; peridium thin, membranous, without granular material; obligate coprophilic species XVI *P. luteola*
- Plasmodiocarps, short, often curved or irregular sporangia; peridium incrassate with inclusions of granular material; forming on tree bark I *P. acetabulifera*²
- 9. Sporangia white, without refuse granular material; capillitium often perforated XXVII *P. poronema*
- Sporocarps almost black, brown, orange or yellowish, sometime with refuse granular material; capillitium non-perforate 10
- 10. Peridium divided into polygonal or areolated plates..... 11
- Peridium not divided into platelets 12

¹ Aberrant form. Usually stalked sporangia.

² Compare with *P. vermicularis*, which forms long plasmodiocarps and sometimes has a single peridium.

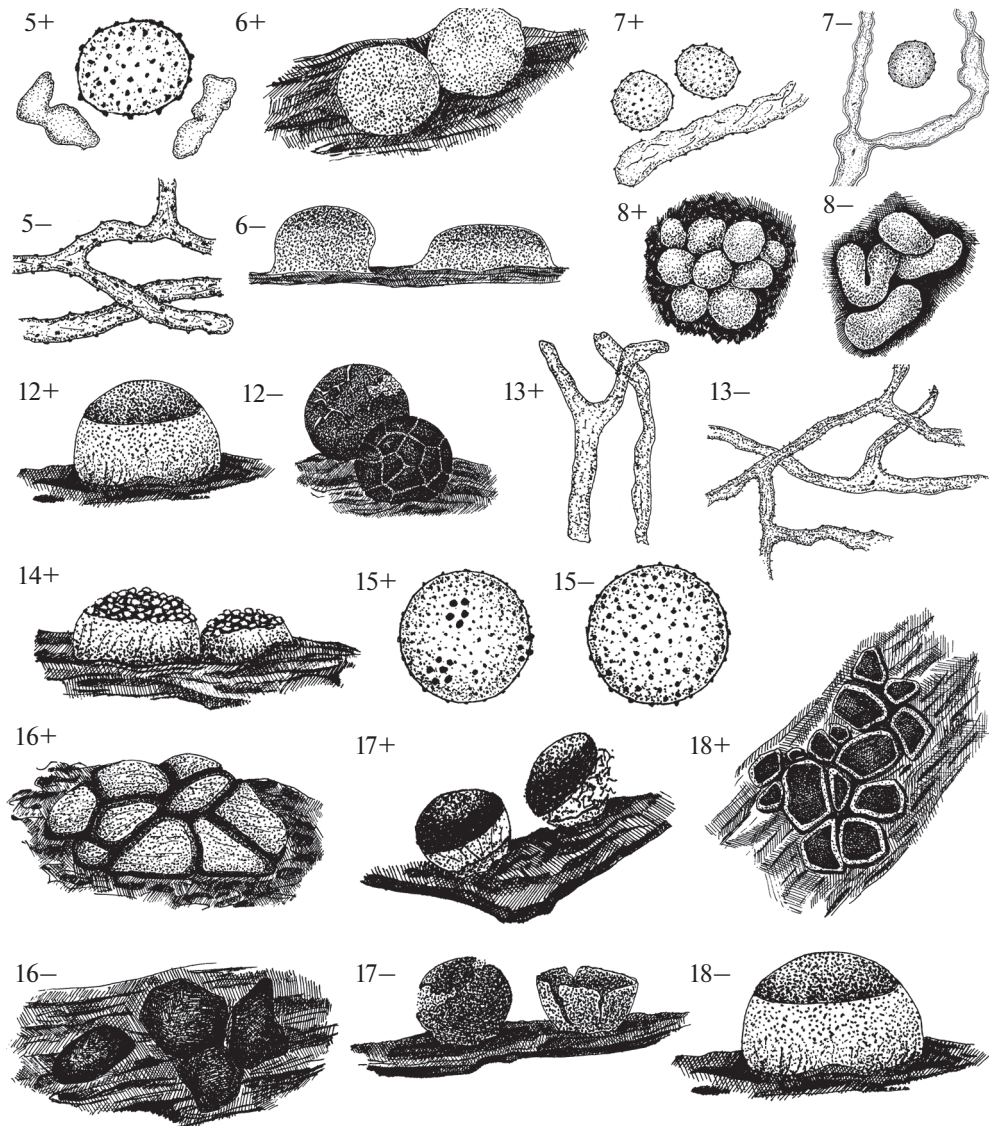


Fig. 4. Illustration of morphological characteristics for key 2 from group 2 of dichotomous identification key. Numbers correspond to the numbers of the definitive theses.

- 11. Peridium marked with dark lines; dehiscence along plates; sporophores – elongated sporangia and ring-sharped plasmodiocarps IV *P. calongei*
- Peridium not marked dark lines, dehiscence not along plates; sporophores – sessile sporangia..... II *P. areolata*
- 12. Dehiscence round, resulting in a lid and a saucer-shaped cup..... 13
- Dehiscence in other ways: into plates by dehiscence lines or irregularly 20
- 13. Capillitium poorly developed, consists of very short, rarely branching threads about 45 μm long III *P. brevifila*
- Capillitium normally developed 4
- 14. Peridium dark cap-like in upper part of sporangia and membranous, transparent at the bottom sporangia VIII *P. dictyonema*
- Peridium is uniformly thickened and does not form a cap 15
- 15. Spores ornamented by densely distributed small warts and scattered large warts VII *P. heterobaculata*
- Spores evenly ornamented by uniform warts 16
- 16. Sporangia from yellow to deep yellow-brown or bronze, with a dark line of thicker refuse material near the base³, which is noticeable even before dehiscence XVII *P. madagascariensis*
- Sporangia from brown to black or reddish, without dark line at the base 17
- 17. The outer peridium layer dehisces by a marginal fissure, forming a lid and a shallow cup connected by a membranous inner peridium layer 18
- The peridium dehiscence irregular, the sporangium upper part separated from a cup by a wide slit covered by a membranous peridium no forming a lid..... VI *P. corticalis*⁴

³ Do not confuse with a part of peridium, which attaches to substrate after dehiscence in the form of a cup.

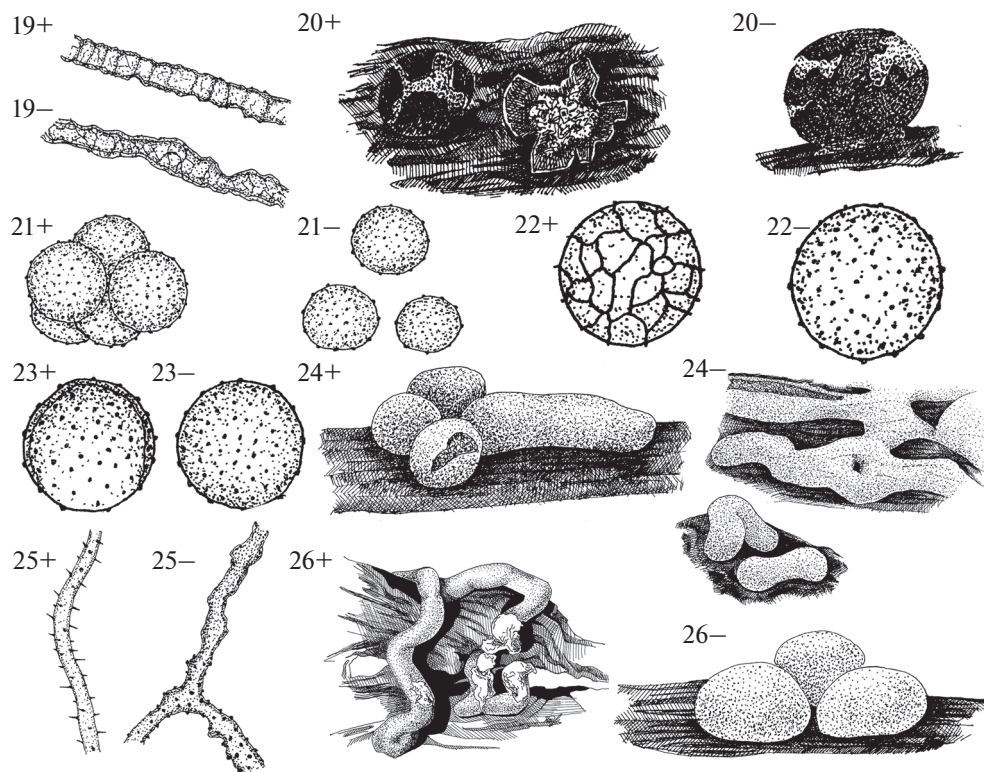


Fig. 5. Illustration of morphological characteristics for key 2 from group 2 of dichotomous identification key. Numbers correspond to the numbers of the definitive theses.

- 18. Sporangia 1–1.5 mm diam., strongly flattened, from chestnut to milky chocolate in color VII *P. depressa*
 – Sporangia 0.1–1 mm diam., usually convex (only sometimes flattened), from dark-brown to almost black..... 19
- 19. Sporangia 0.5–1 mm diam.; capillitium reticulate; usually forming on leaf litter VIII *P. dictyonema*⁵
 – Sporangia less than 0.5 mm diam.; capillitium almost smooth, warted or ornamented with small, irregular-shaped outgrowths, not forming a reticulum; usually forming on bark or wood.....XXX *P. quadrata*
- 20. Dehiscence into plates by specific peridium lines 21
 – Dehiscence irregular 22
- 21. Spores clustered into groups of 4–16; sporophores – sporangia or pseudoaethalia XXXIII *P. syncarpon*
 – Spores free; sporophores – only sporangia..... XXXV *P. tessellata*
- 22. Spores reticulate XXXI *P. reticulospora*
 – Spores warted or spinulose 23
- 23. Spores usually more than 14 µm diam., with a lighter area (germination pore) on the one side; capillitium 3–8 µm diam.; nivicolous species 24
 – Spores usually less than 14 µm diam., without a lighter area; capillitium 2–4 µm diam.; non-nivicolous species 25
- 24. Sporophores – sporangia or short plasmodiocarps, spores ornamented with warts which are always wider than higher XVIII *P. megaspora*
 – Sporophores – branched or reticulate plasmodiocarps, rarely sporangia; spores ornamented with always higher than wider spines XXIV *P. patagonica*
- 25. Capillitium ornamented with large (more 1 µm high) spines..... V *P. chrysosperma*
 – Capillitium ornamented with short spines, warts or irregular reticulum..... 26
- 26. Sporophores – usually twisted or annular plasmodiocarps XXXVII *P. vermicularis*
 – Sporophores – globose or slightly elongated sporangia.....27
- 27. Spores 11–13 µm diam., capillitium ornamented with short spines or warts, sometimes poorly developed, consisting of straight or rarely branching threads..... VI *P. corticalis*
 – Spores 13–16 µm diam., capillitium well-developed, consisting of long, branching threads, ornamented with irregular reticulum with meshes of different size..... X *P. frustrifilaris*

Polytomic identification keys

Sometimes the use of dichotomous identification keys could be not useful. So we have created a web application with a multiple-access taxonomic key, which can be found at address: <https://perichaena.myxomycetes.org>. The source code available at: <https://github.com/MSU-Myxomycetes/PerichaenaKey>.

⁴ Compare with non-stalked forms of *P. pedata*, which differ in ornamentation of capillitium.

⁵ Compare with *P. frustrifilaris*, which is different in spiny spores and peridium color.

Morphological diagnoses for *Perichaena* species

I. *Perichaena acetabulifera* Lizárraga, G. Moreno et Flores-Romero. — Sporangia sessile or short plasmodiocarps. Peridium single, membranous, olive-yellow, sometimes with granular material. Dehiscence irregular. Capillitium well-developed, 2–6 µm diam., edges look broken. Spores 11–14 µm diam., ornamented with rare, irregularly placed warts. Similar species: Differs from other species (for example, *P. vermicularis* with short plasmodiocarps) by thick capillitial threads with broken edges and potato-eye ornamentation. From *P. luteola* – by the sporocarp type (may be sporangia), the presence of granular material in the peridium, and the substrate type (wood, not dung). Descriptions: Lizárraga et al. (2019). Illustrations: Lizárraga et al. (2019, Pl. 1). Type locality: Mexico.

II. *P. areolata* Rammeloo. — Sporangia sessile or on a restricted base. Peridium double, from light-brown to yellow, divided into polygonal or areolate plates. Capillitium well-developed, 2.5–4 µm diam., ornamented with spines 2–3 µm high. Spores 10.2–12.1 µm diam. Similar species: Differs from other species by the peridium, divided into areolate plates. From species with sessile subglobose sporangia (like *P. corticalis*, *P. liceoides*, *P. dictyonema*) – by a well-developed capillitium ornamented with long spines. Descriptions: Rammeloo (1981). See also Keller, Eliasson (1992) and Lado et al. (2009). Illustrations: Lado et al. (2009, f. 4). Type locality: Rwanda.

III. *P. brevifila* T.E. Brooks et H.W. Keller. — Sporangia sessile, slightly compressed. Peridium double, but layers are closely appressed; outer layer thicker including of granular matter; inner layer membranous. Dehiscence by a round lid. Capillitium poorly developed, consists of short (less than 45 µm), rarely branched threads 2–3 µm diam., ornamented with warts. Spores 14–15 µm diam., minutely warted. Similar species: Differs from *P. depressa*, *P. dictyonema*, and *P. quadrata* by a poorly developed capillitium. From *P. corticalis* with a poorly developed capillitium – by the greyish color of peridium and a poorly developed hypothallus. Descriptions: Keller, Brooks (1971); Yamamoto (2006). Illustrations: Keller, Brooks (1971, f. 1–2); Yamamoto (2006, f. 21). Type locality: USA (Georgia).

IV. *P. calongei* Lado, D. Wrigley et Estrada (Fig. 6, A–D). — Sporangia short-stalked or almost sessile, stalk dark. Peridium double; outer layer cartilaginous, divided into several polygonal plates, which make sporocyst look like a football. Capillitium forms a loose net, 2–4 µm diam., ornamented in different ways: warted, spiny, with expansions, pits or reticulum. Spores 10–13.5 µm diam., strongly warted. Similar species: Differs from *P. heterospinispora* and *P. polygonospora* by the presence of a capillitium. From other short-stalked species (like *P. pedata*) – by dark lines of dehiscence forming along the peridium and an irregularly ornamented capillitium. From *P. chrysosperma* (if case of almost non-stalked, plasmodiocarp-like sporocarps) – by the presence of dark dehiscence lines on the peridium. Descriptions: Lado et al. (2009); Araújo et al. (2015); Cavalcanti et al. (2016). Illustrations: Lado et al. (2009, f. 1–22); Araújo et al. (2015, f. 3 a–f); Cavalcanti et al. (2016, f. 1 b–e). Type locality: Argentina.

V. *P. chrysosperma* (Curr.) Lister (Fig. 6, E–G). — Plasmodiocarps round or elongate, rarely sessile sporangia. Peridium double; from ochraceous or orange to dark-brown or red-brown. Dehiscence irregular. Capillitium well-developed, 2–4 µm diam., well-ornamented with spines 2–4 µm high. Spores 8–10(12) µm diam., warted. A very polymorphous species. Usually forms ring-like sporocarps, rarely

elongate plasmodiocarps and almost never – subglobose sporangia. Similar species: Differs from *P. patagonica* by small spores and non-nivicolous ecology. From *P. vermicularis* (plasmodiocarp form) and *P. corticalis* or *P. frustifilaris* (sporangium form) – by large spines on the capillitial surface. Descriptions: Lister (1925); Martin, Alexopoulos (1969); Farr (1976); Nannenga-Bremekamp (1991); Novozhilov (1993); Lado, Pando (1997); Ing (1999); Stephenson (2021). Illustrations: Lister (1925, Pl. 184); Martin, Alexopoulos (1969, f. 67); Emoto (1977, Pl. 27); Nannenga-Bremekamp (1991, P. 95); Neubert et al. (1993, P. 205–206); Hagiwara, Yamamoto (1995, f. 37); Lado, Pando (1997, f. 75); Yamamoto (1998, P. 199); Ing (1999, f. 101); Härkönen, Sivonen (2011, f. 129); Poulain et al. (2011, f. 97); Cheng et al. (2013, f. 2–8); Massingill, Stephenson (2013, f. 2D); Cavalcanti et al. (2016, f. 1 F–I); Tran et al. (2017, f. 42); Stephenson (2021, f. 57). Type locality: England, Great Britain.

VI. *P. corticalis* (Batsch) Rostaf. (Fig. 6, H–J). — Sporangia sessile, rarely short plasmodiocarps. Peridium double; from red-brown to dark-brown, sometimes covered with lime. Dehiscence irregular, rarely round, forming a cup. Hypothallus filmy, usually common for a group of sporangia. Capillitium present, may form a dense net or consist of short, rarely branched threads, small-warted. Spores (9)11–13(14) µm diam., warted. Similar species: Differs from *P. chrysosperma* and *P. vermicularis* by subglobose sporangia and usually a poorly developed capillitium. From *P. quadrata*, *P. dictyonema* and *P. nigra* – by non-angular sporangia and usually irregular (not round) dehiscence. From *P. liceoides* – by the presence of a capillitium. From *P. frustifilaris* – by smaller (up to 13 µm diam.) spores. Descriptions: Martin, Alexopoulos (1969); Farr (1976); Nannenga-Bremekamp (1991); Novozhilov (1993) (in Russ.); Lado, Pando (1997); Ing (1999); Cavalcanti et al. (2016); Stephenson (2021). Illustrations: Lister (1925, Pl. 186); Bjornekaer, Klinge (1963, T. 4, f. 1–2); Martin, Alexopoulos (1969, f. 68); Emoto (1977, Pl. 26); Lado, Moreno (1978, f. 9); Gilbert (1990, f. 28–30); Nannenga-Bremekamp (1991, f. 95); Neubert et al. (1993, P. 206–207); Hagiwara, Yamamoto (1995, f. 36); Lado, Pando (1997, f. 76 A–C); Yamamoto (1998, P. 201); Ing, (1999, f. 102); Novozhilov, Schnittler (2008, f. 33–34); Härkönen, Sivonen (2011, f. 130; 131); Poulain et al. (2011, Pl. 93); Cavalcanti et al. (2016, f. 2 B–E); Calaça et al. (2020, f. 6). Type locality: Germany.

VII. *P. depressa* Lib. (Fig. 7, A–D). — Sporangia sessile, strongly compressed, sometimes angular due to a common lateral compression. Peridium double; both layers well-noticeable. Dehiscence round, forming a wide lateral lid, covered with the inner peridial layer. Capillitium well-developed, (1.5)2–2.5(3) µm diam., ornamented with small spines. Spores 9–12 µm diam., small-warted. Similar species: Differs from other species by large, compressed, roundly dehiscing sporangia. From *P. madagascariensis* – by a non-bronze color of peridium and the absence of a dark line of refuse material near the base of sporangia. From *P. nigra* – by the presence of a capillitium. From *P. dictyonema* and *P. quadrata* – by flattened (not convex) larger sporangia of milk-chocolate (not dark brown to black) color. Descriptions: Martin, Alexopoulos [1969, P. 112–113. Description includes morphology of *P. quadrata* (Keller, Eliasson, 1992)]; Farr (1976); Nannenga-Bremekamp (1991); Keller, Eliasson (1992); Novozhilov (1993); Lado, Pando (1997); Ing (1999); Cavalcanti et al. (2016); Stephenson (2021). Illustrations: Lister (1925, Pl. 189); Martin, Alexopoulos (1969, f. 69); Rammeloo (1974, f. 6–8); Emoto (1977,

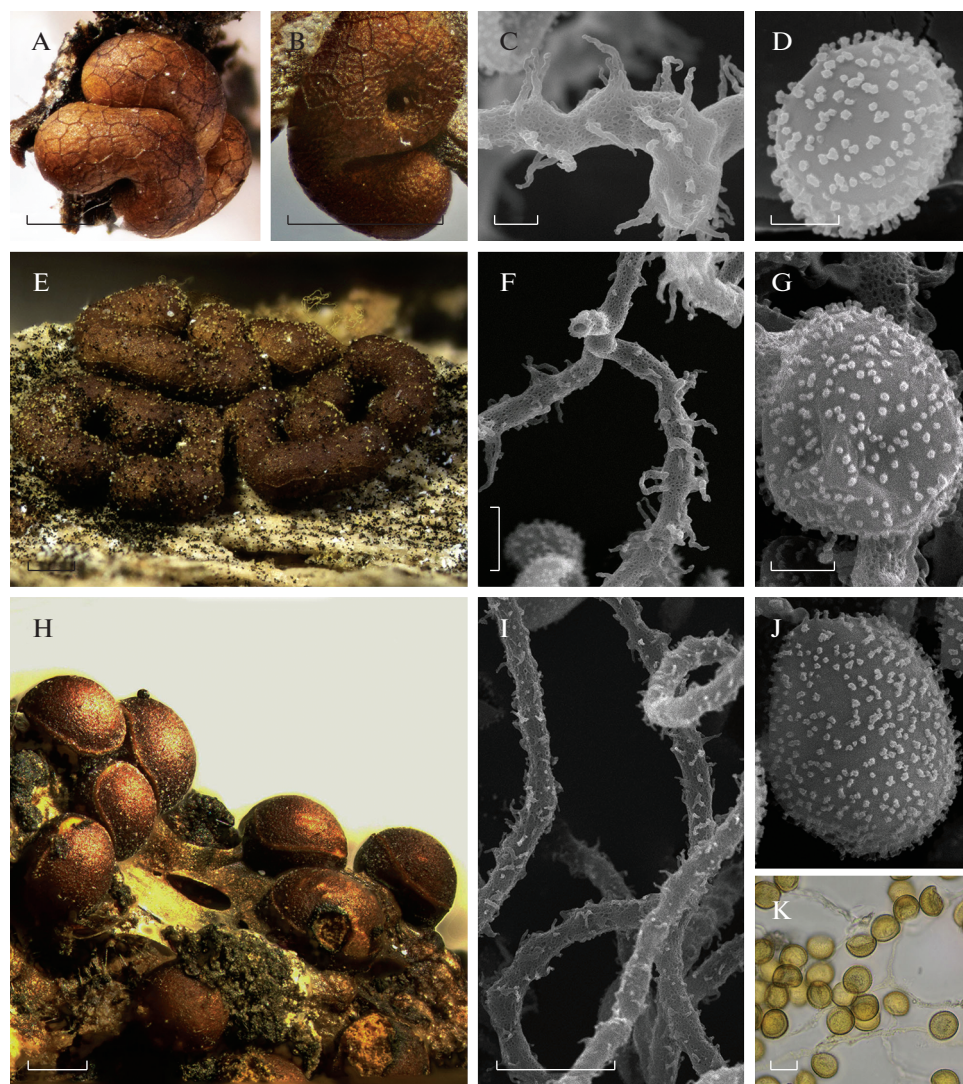


Fig. 6. A–D – *Perichaena calongei*: A, B – sporocarps; C – capillitium (SEM); D – spore (SEM). E–G – *P. chrysoasperma*: E – sporocarps; F – capillitium (SEM); G – spore (SEM); H–J: *P. corticalis*: H – sporocarps; I – capillitium (SEM); J – spore (SEM); K – spores and capillitium (LM). Scale bars: A, B, E, H – 300 μ m, I, K – 10 μ m; F – 5 μ m; C, D – 3 μ m, G, J – 2 μ m.

Pl. 23–24); Liu (1982, Pl. I, f. 4–5; Pl. X, f. 2); Keller, Eliasson (1992, f. 1–13); Neubert (1993, P. 208, 209); Hagiwara, Yamamoto (1995, f. 38); Lado, Pando (1997, f. 77); Nan-nenga-Bremekamp (1991, f. 94); Yamamoto (1998, 202); Ing (1999, f. 103); Stephenson (2003, f. 4); Poulain et al. (2011, Pl. 96); Stephenson (2011, f. 1); Cavalcanti et al. (2016, f. 2 F–H); Tran et al. (2017, f. 43); Stephenson (2021, f. 58–59). Type locality: Belgium.

VIII. *P. dictyonema* Rammeloo. – Sporangia sessile, half-round or slightly compressed, convex at the top. Peridium double; inner layer membranous, outer – cartilaginous, often covered with granular material. Dehiscence by a round lid, forming a cap. Capillitium well-developed, 2–2.5 μ m diam., ornamented with warts or thin reticulum (can be detected only using SEM). Spores 10–12 μ m diam., evenly warted. Similar species: Differs from *P. depressa* by convex form and a darker color of sporangia. From *P. quadrata* – by larger sporangia, reticulate ornamentation of capillitium and presence of regularly forming cap made of granular material. *P. dictyonema* is morphologically very similar to *P. quadrata*

and they might represent the same species (Lizárraga et al., 2016a). Descriptions: Rammeloo (1981); Stephenson (2021). Illustrations: Tran (2017, f. 44); Poulain et al. (2011, f. 94). Type locality: Rwanda.

IX. *P. echinolophospora* Novozh. et S.L. Stephenson. – Sporangia sessile. Peridium single or double; inner layer membranous, outer (if present) cartilaginous, bright-red-yellow. Dehiscence irregular. Capillitium absent. Spores 12–13 μ m diam., ornamented with honeycomb-like outgrowths, forming large-meshed reticulum. Border of outgrowth is serrated. Similar species: Differs from many other species by the absence of a capillitium and the reticulate ornamentation of spores. From *P. reticulospora* – by the absence of a capillitium. From *P. polygonospora* – by the ornamentation of spores: meshes are honeycomb-like, the form of spores is round (not polygonal). Descriptions: Novozhilov, Stephenson (2015). Illustrations: Novozhilov, Stephenson (2015, f. 1–8). Type locality: Vietnam.

X. *P. frustrifilaris* Q. Wang, Yu Li et J.K. Bai. – Sporangia sessile. Peridium double; outer layer thick, cartilaginous;

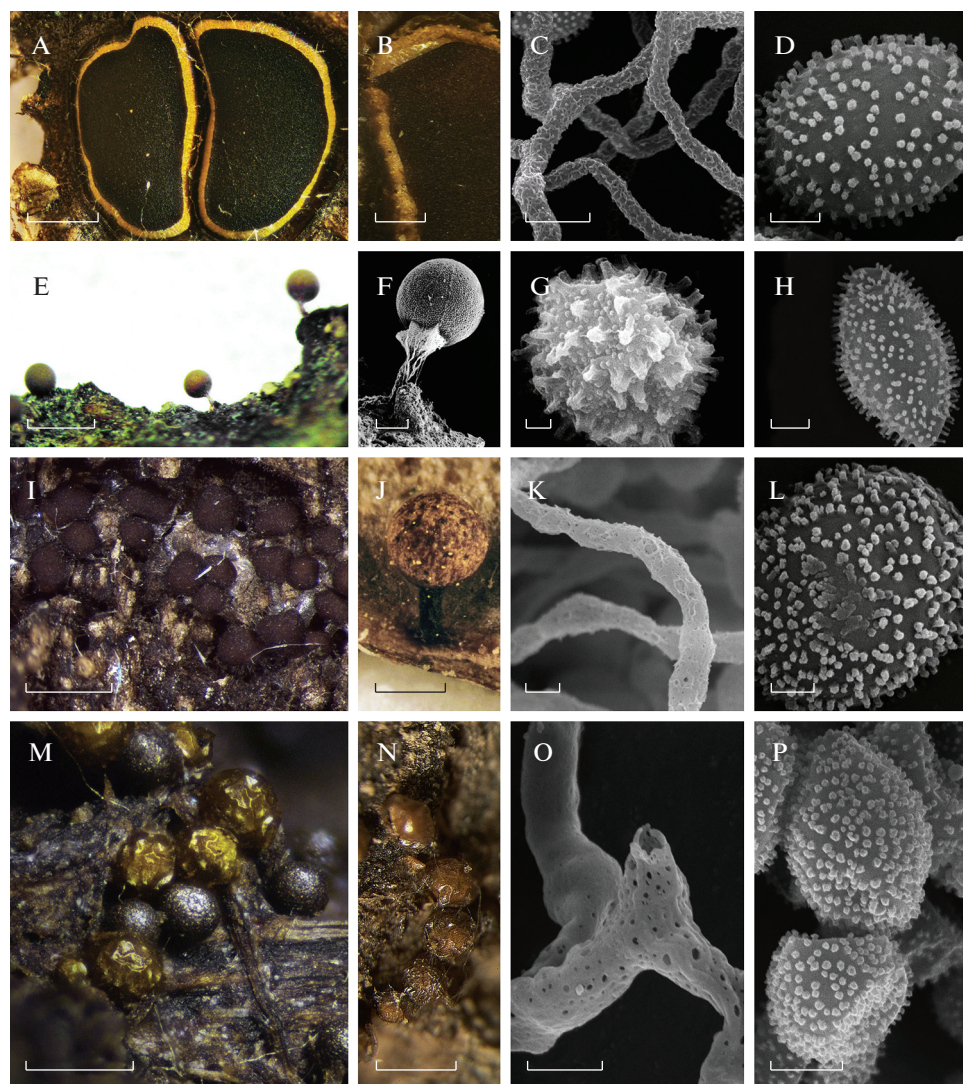


Fig. 7. A–D – *Perichaena depressa*: A, B – sporocarps; C – capillitium (SEM); D – spore (SEM). E–G – *P. heterospinispora*: E, F – sporocarps; G – spore (SEM). H–I – *P. liceoides*: H – spore (SEM); I – sporocarps. J–L – *P. pedata*: J – sporocarp; K – capillitium (SEM); L – spore (SEM). M–P – *P. luteola*: M, N – sporocarps; O – capillitium (SEM); P – spores (SEM). Scale bars: I – 1000 μm ; M, N, E – 500 μm ; A, J – 300 μm ; B – 150 μm ; F – 100 μm ; C – 5 μm ; H, K, O, P – 3 μm ; D – 2 μm ; G, L – 1 μm .

dark red-brown, spotty or reticulate. Dehiscence irregular, forming a cup. Capillitium reticulate, consists of long branched threads 2–3 μm diam., slightly reticulate. Spores 13–15 μm diam., ornamented with large conical spines. **Similar species:** Differs from *P. corticalis* – by larger spores ornamented with spines. From *P. vermicularis* (sporangia form) – by the reddish color of peridium and the reticulate ornamentation of a capillitium. **Notes:** Found only in the type locality (Walker et al., 2015). **Descriptions:** Wang et al. (2000). **Illustrations:** Wang et al. (2000, Pl. 1, f. 1–4). **Type locality:** China.

XI. *P. grisea* Q. Wang, Yu Li et J.K. Bai. – Sporangia sessile or plasmodiocarps, greyish-blue. Peridium single, membranous. Dehiscence irregular. Capillitium poorly developed, consists of long, thin (1.6–2.1 μm diam.), branched, and almost non-colored threads, ornamented with irregular thickenings. Spores brown in mass, 10–11 μm diam., almost smooth. **Similar species:** Differs from all other species by the greyish-blue peridium and the thin, non-colored capilli-

tium. **Notes:** Found only in the type locality (Walker et al., 2015). **Descriptions:** Wang et al. (2000). **Illustrations:** Wang et al. (2000, Pl. 1, f. 5–8). **Type locality:** China.

XII. *P. heterobaculata* Rammeloo. – Sporangia sessile. Peridium double; outer layer cartilaginous, incrustated by granular material; inner layer membranous. Dehiscence by a round lid, forming a cup. Capillitium well-developed, consists of threads 2.5–3 μm diam., ornamented with minute, irregularly placed warts or short spines. Spores ornamented with warts of two types: minute light warts and groups of larger, darker warts. **Similar species:** Differs from other species by the irregular ornamentation of spores: groups of darker warts. **Descriptions:** Rammeloo (1981). **Illustrations:** Absent. **Type locality:** Rwanda.

XIII. *P. heterospinispora* Novozh., Zeml., Schnittler et S.L. Stephenson (Fig. 7, E–G). – Sporangia sessile or stalked. Stalk short, formed from hypothallus, warted; less than a half of the total sporangium height, from brown to black. Peridium single, thin, from light-yellow-brown to olive-

brown, reddish-brown in lower part. Dehiscence irregular, forming a cup. Capillitium absent. Spores, including ornamentation, (10.5)12.0–13.0(14.5) μm diam., ornamented by well-noticeable pyramidal spines. Similar species: Differs from other species by the absence of a capillitium and a short membranous stalk. From species with no capillitium (*P. polygonospora* when stalked and *P. liceoides* when sessile) – by large spines on spores. Descriptions: Novozhilov et al. (2008). Illustrations: Novozhilov et al. (2008, f. 1–8). Type locality: Russia (Volgograd Oblast).

XIV. *P. liceoides* Rostaf. (Fig. 7, H–I). – Sporangia sessile. Peridium single, thin, membranous; sometimes includes granular material, rarely seems double. Dehiscence irregular, rarely by a round lid. Capillitium absent. Spores (10)11–13(15) μm diam., ornamented with warts or spines 0.8–1 μm high. Similar species: Differs from other species (*P. corticalis* or *P. vermicularis* with sporangia) by the absence of a capillitium. From *P. thindii* – by evenly colored (not two-colored) sporangia. From *P. heterospinispora* (very short-stalked, almost sessile form/case) – by smaller spines or even warts as the spore ornamentation. From *P. corticalis*, that can almost lack a capillitium – by a single peridium and spiny spores. From *Licea tenera* – by the peridium structure and the spore ornamentation. The outer peridium surface of *Perichaena liceoides* is rough and encrusted with granular deposits, spores have two types of ornamentation: spines with small lateral appendices up to 8 per spine with very small verrucae scattered between the spines (Novozhilov et al., 2003). Notes: see description of type material in Gilbert, 1990. Descriptions: Lister (1911); Gilbert (1990); Ing (1999); Schmittler, Novozhilov (2000); Novozhilov et al. (2006); Yamamoto (2006); Kuhnt (2019). Illustrations: Gilbert (1990, f. 1–8); Lado, Pando (1997, f. 76 D); Ing (1999, f. 104); Novozhilov et al., (2003, f. 2 i–k); Novozhilov et al. (2006, f. 41–46); Yamamoto (2006, Pl. 22); Kosheleva et al. (2008, f. 28–30); Kuhnt (2019, f. 5 b–d; f. 6 a–e). Type locality: Germany (see Kuhnt, 2019).

XV. *P. longipes* L.M. Walker, Leontyev et S.L. Stephenson. – Sporangia stalked. Stalk straight, from brown to black, more than $\frac{3}{4}$ of sporangium height. Peridium single, dense. Capillitium thick, (2.6)3.2–5.8(6.2) μm diam., branched and anastomosed, forming a net with almost no free endings; densely ornamented with warts or coralloid protrusions. Spores (7.5)7.8–9.1(10.7) μm diam., almost smooth (ornamented with areolate warts noticeable via SEM). Similar species: Differs from other stalked species by a capillitium (for example, *P. stipitata*, *P. calongei*) with a very long stalk. From *P. pedata* and *P. papulosa* – by a very thick, “shaggy” capillitium. Descriptions: Walker et al. (2015). Illustrations: Walker et al. (2015, f. 1). Type locality: Panama.

XVI. *P. luteola* (Kowalski) Gilert (Fig. 7, M–P). – Sporangia sessile. Peridium single, thin, bright. Dehiscence irregular. Capillitium consists of depressed tubules, that can be thicker or thinner, 2–3 μm diam.; free ends rare. Spores 12–15 μm diam., spiny. Similar species: Differs from *P. corticalis* and alike species by a single peridium and yellow (not orange or brown) sporangia. From *P. acetabulifera* – by more compact fructifications, often a narrower capillitium, and a coprophilous lifestyle. Descriptions: Kowalski (1969); Lado, Pando (1997); Ing (1999). Illustrations: Lado, Pando (1997, f. 78); Ing (1999, f. 105); Novozhilov et al. (2006, f. 46–50); Novozhilov, Schnittler (2008, f. 35–37); Poulain et al. (2011, Pl. 99); Tran et al. (2017, f. 45). Type locality: USA (California).

XVII. *P. madagascariensis* D. Wrigley, Lado, Estrada et S.L. Stephenson. – Sporangia sessile, gregarious, sometimes appressed, polygonal; from yellow to deep-yellow-brown with a bronze tint; with a dark line at the base of sporangium or between nearby sporangia, formed from granular material. Peridium double. Dehiscence by a round lid, forming a cap and a flat cup. Capillitium tubulate, consists of tubules of different diam., ornamented very irregular with various elements: from small nodules to grouped warts. Spores 10–12.5(13) μm diam., minutely warted. Similar species: Differs from *P. depressa* and *P. quadrata* by a bronze color and a dark line, girdling sporangia. From *P. liceoides* – by a well-developed capillitium. From *P. luteola* – by a double peridium, irregular capillitium ornamentation, and a non-coprophilous lifestyle. Description: Wrigley de Basanta et al. (2013). Illustrations: Wrigley de Basanta et al. (2013, f. 37–51), Lado et al. (2014, f. 9). Type locality: Madagascar.

XVIII. *P. megaspora* A. Ronikier, Lado et D. Wrigley. – Sporangia sessile, rarely plasmodiocarps. Peridium double; layers closely appressed (as a result, peridium seems single), thick, covered with granular material. Dehiscence irregular. Capillitium well-developed, dense, forming a net-like structure; threads depressed, 3–6(8) μm diam., from smooth to warted. Spores with thicker wall on one side, from smooth to large-warted, (15)15.5–22(25) μm diam. Similar species: Differs from other species by very large spores and a depressed capillitium. From *P. patagonica* – by sporangia or short plasmodiocarps and warts that are wider than higher. Descriptions: Ronikier et al. (2013). Illustrations: Ronikier et al. (2013, f. 3–17). Type locality: Argentina.

XIX. *P. membranacea* Yu Li, Q. Wang et H.Z. Li. – Aethalia or pseudoaethalia sessile, dark-brown with a pink metallic tint. Peridium single, common to a group of sporangia in the upper part. Capillitium well-developed, non-branched, spiny. Spores 10.4–10.9(12.5) μm diam., evenly and densely warted. Similar species: Differs from other *Perichaena* species by aethalia or pseudoaethalia formation. From *P. syncarpon* – by a thin (not cartilaginous) peridium and free (not clustered) spores. Notes: Found only in the type locality (Walker et al., 2015). Descriptions: Li et al. (1990). Illustrations: Li et al. (1990, Pl. 1, f. 1–4). Figures of *P. membranacea* and *P. poronema* are confused. In this paper we provide them in a correct order. Type locality: China.

XX. *P. microspora* Penz. et Lister. – Plasmodiocarps, rarely sessile sporangia. Peridium single, yellow, membranous, may contain granular material near the fructification base. Dehiscence irregular, in the upper part. Capillitium well-developed, consists of long, sometimes branched threads, 1–3 μm diam. with a lot of spines and sometimes enlarged, round fragments. Spores 6–7.5 μm , ornamented with small spines, visible only by using immersion oil. Similar species: Differs from all other species by very small spores, not reaching 8 μm diam. Descriptions: Martin, Alexopoulos (1969); Farr (1976); Yamamoto (2006). Illustrations: Lister (1925, Pl. 185 a, b); Martin, Alexopoulos (1969, f. 70); Novozhilov et al. (2001, f. 12–14); Yamamoto (2006, f. 23); Cavalcanti et al. (2016, f. 3). Type locality: Indonesia.

XXI. *P. nigra* D. Wrigley, Lado et Estrada. – Sporangia sessile, often grouped, from globose to discoid. Peridium double; outer layer very thick (about 10 μm), cartilaginous, deep-black; inner layer membranous. Dehiscence by a round lid at the base, forming a large cap. Capillitium absent. Spores (13.5)14–16(16.5) μm diam., ornamented with separate warts or lines (noticeable only using SEM). Similar species: Differs from *P. corticalis*, *P. depressa*, *P. dictyonema*, and *P. quadrata* in the absence of a capillitium and the per-

idium color. From *P. liceoides* – by a double, thick peridium. From *P. taimyriensis* – by black (not yellow) color and round (not irregular) dehiscence. Descriptions: Lado et al. (2014). Illustrations: Lado et al. (2014, f. 10). Type locality: Argentina.

XXII. *P. pachyderma* D.W. Mitch., G. Moreno et Lizárraga. – Sporangia sessile. Peridium single, but very thick (2–5 µm). Dehiscence irregular. Capillitium usually absent, very rarely presented as smooth filaments 2 µm diam., attached to the inner peridial side. Spores 10–11(12) µm diam., warted. Coprophilous. Similar species: Differs from *P. corticalis* and alike species by the absence of a capillitium. From *P. liceoides* – by single, but very thick peridium. From *P. nigra* – by spores less than 12 µm diam. From coprophilic *Licea* species – by yellow spore mass. Descriptions: Mitchell et al. (2011); Lizárraga et al. (2016a). Illustrations: Mitchell et al. (2011, f. 1–25); Lizárraga et al. (2016a, f. 28–33). Type locality: Mexico.

XXIII. *P. papulosa* C.H. Liu et J.H. Chang. – Sporangia stalked. Stalk short (to a half of sporangia height), from dark-brown to black. Peridium single, semihyaline, forming a big, well-noticeable dark papilla (or several papillae) at the top. Dehiscence irregular. Capillitium well-developed, 3–4 µm diam., minutely warted. Spores 9–10 µm diam., spiny. Similar species: Differs from *P. pedata* by smaller sporangia, warted (not spinulose) capillitium, and dark papilla at the top of sporangium. Descriptions: Liu et al. (2007). Illustrations: Liu et al. (2007, f. 1). Type locality: Taiwan.

XXIV. *P. patagonica* A. Ronikier et Lado. – Plasmodiocarps branched or reticulate, rarely sporangia. Peridium single, covered with darker granular material. Dehiscence irregular. Capillitium well-developed, dense, branched, forming a net; consists of tubules 3–6 µm diam., more or less ornamented with warts or spines, connected by lines. Spores (13)14–19(20) µm diam., spinulose. Nivicolous. Similar species: Differs from *P. vermicularis* by bigger (0.65–1.15 mm wide) plasmodiocarps, wider capillitium threads, and very large spores. From *P. chrysoesperma* – by a warted (not spinulose), wide capillitium and big spores. From *P. megaspora* – by plasmodiocarps (not sporangia) and smaller and spiny (not warted) spores. Descriptions: Ronikier et al. (2020). Illustrations: Ronikier et al. (2020, f. 9 A–D; f. 10 A–D). Type locality: Argentina.

XXV. *P. pedata* (Lister et G. Lister) G. Lister ex E. Jahn (Fig. 7, J–L). – Sporangia stalked, rarely almost sessile. Stalk dark-brown, usually less than a half of sporangium height. Peridium single, membranous, with granular material. Dehiscence irregular. Capillitium well-developed, threads branched, 3–5 µm diam., minutely spinulose. Spores 9–10 µm diam., warted or short spinulose. Similar species: Differs from *P. calongei* by the absence of dehiscence lines on the peridium. From *P. stipitata* – by a dark (not white) stalk. From stalked *P. reticulospora* – by non-reticulate spores. From *Hemitrichia minor* – by a capillitium, which is not ornamented with spiral bands. Descriptions: Ing (1999); Nannenga-Bremekamp (1991); Liu et al. (2007). Illustrations: Mitchell (1978, f. 36a, 36b); Neubert, Bauman (1986); Nannenga-Bremekamp (1991, P. 97); Neubert et al. (1993, P. 209); Yamamoto (1998, P. 203); Ing (1999, f. 106); Müller (2005, f. 5); Yamamoto (2006, P. 203); Liu et al. (2007, f. 2 A–F); Poulain et al. (2011, Pl. 92); Cavalcanti et al. (2016, f. 3); Johannesen, Vetlesen (2020, f. 45 H–I). Type locality: England.

XXVI. *P. polygonospora* Novozh., Zeml., Schnittler et S.L. Stephenson (Fig. 8, A–C). – Sporangia sessile or short-stalked. Stalk, if present, never reaches a half of sporangium

height, from brown to black. Peridium single, cartilaginous, brown-orange. Dehiscence irregular or areolate. Capillitium absent. Spores (9)10–11.5(12.5) µm diam., polygonal. Similar species: Differs from other species by the absence of a capillitium and polygonal spores. From *P. echinolophospora* and *P. reticulospora* – by the spore form: spores of *P. polygonospora* are polygonal with ribs (not reticulate or honeycomb-like). Also differs from *P. echinolophospora* by smaller spores (less than 12 µm diam.) and from *P. reticulospora* – by the absence of a capillitium. Descriptions: Novozhilov et al. (2008); Lizárraga et al. (2016b). Illustrations: Novozhilov et al. (2008, f. 9–17); Lizárraga et al. (2016b, f. 14–19). Type locality: Russia (Volgograd Oblast).

XXVII. *P. poronema* Yu Li et H.Z. Li. – Sporangia sessile. Peridium double; outer layer thick, white (but not calcareous!); inner layer dark-brown. Dehiscence by a round lid, forming a cup. Capillitium well-developed, sometimes branched, 1.25–1.8(2.5) µm diam., ornamented with warts or irregular reticulum, sometimes perforate. Spores (8)8.8–9.5(10) µm diam., warted. Similar species: Differs from *P. thindii* and *P. depressa* by the color of sporangia and the capillitium form. From *P. dictyonema* – by the absence of granular material on the peridium surface, an occasionally reticulate capillitium, and smaller spores. Descriptions: Li et al. (1990). Illustrations: Li et al. (1990, Pl. 2). Figures of *P. membranacea* and *P. poronema* are confused. In this paper we provide them in a correct order. Type locality: China.

XXVIII. *P. pseudoliceoides* Kuhnt et Mar. Meyer. – Sporangia always sessile, on restricted base, spherical, 185–320 µm in diam. Peridium single, membranous, dark-yellow to yellow-brown, nearly transparent in transmitted light. Capillitium contains short elaters and net-like, fully reticulate elements. Spores dark yellowish in mass, (9)10–12.5(13.5) µm in diam., almost smooth or faintly warted by oil immersion. Similar species: Differs from *P. liceoides* by presence of capillitium and smooth or warted (not spinulose) spores. Differs from *P. luteola* by smaller spores. Also, author have noticed, that this species may be similar to *Licea punctiformes*, but differs by presence of capillitium. Other differences have not been described. Descriptions: Kuhnt (2021). Illustrations: Poulain et al. (2011, f. 100) (sp. *liceoides*); Kuhnt (2021, abb. 42 a–f; 43 a–d, 44 a–e, 45a, 46 a–f). Type locality: France.

XXIX. *P. pulcherrima* Petch. – Sporangia stalked, rarely sessile. Stalk wrinkled, reddish-brown, sometimes common for a group of sporangia. Peridium double; outer layer thick, containing granular material, from violet-brown to violet-red. Capillitium poorly developed, consists of red-brown soft threads 3–4 µm diam., ornamented with single warts or spines 1–2 µm high. Spores violet-brown in mass, 15–17 µm diam., spinulose. Similar species: Differs from other species by a violet peridium and large spores. Descriptions: Martin, Alexopoulos (1969). Illustrations: Lister (1925, Pl. 188); Emoto (1977, Pl. 123); Poulain et al. (2011, Pl. 91); Wrigley de Basanta et al. (2013, f. 18–19; 52–55). Type locality: Ceylon.

XXX. *P. quadrata* T. Macbr. (Fig. 8, D–G). – Sporangia sessile, crowded, slightly-depressed, from pillow-form to subglobose. Peridium double; outer layer thick, non-hyaline, brown; inner layer membranous, hyaline. Dehiscence by a round lid, forming a cup, but the lid often stays covered with the inner peridial layer. Capillitium well-developed, branched and anastomosed, 1.5–2.5 µm diam., ornamented by warts and ribs, rarely forming very irregular reticulum. Spores 9–11(12) µm diam., warted. Similar species: Differs from *P. depressa* by smaller and less depressed sporangia, al-

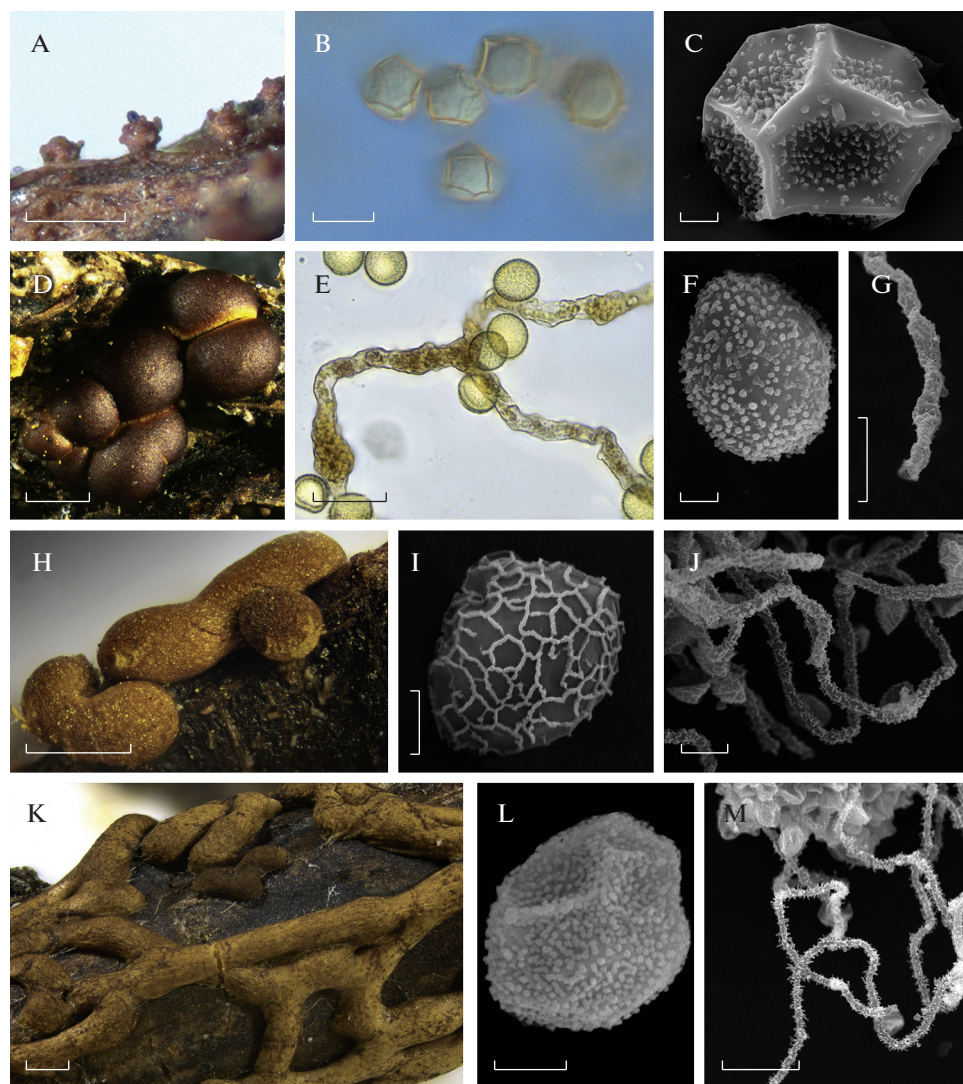


Fig. 8. A–C – *Perichaena polygonospora*: A – sporocarps; B – spores (LM); C – spore (SEM); D–G – *P. quadrata*: D – sporocarps; E – spores and capillitium (LM); F – capillitium (SEM); G – spore (SEM). H–J – *P. reticulospora*: H – sporocarps; I – spore (SEM); J – capillitium (SEM). K–M – *P. vermicularis*: K – sporocarps; L – spores (SEM); M – capillitium (SEM). Scale bars: H – 400 μ m; D, K – 300 μ m; A – 200 μ m; M, E – 20 μ m; B, G, J – 10 μ m; F, I, L, M, L – 3 μ m; C – 2 μ m.

so usually a darker peridium. From *P. dictyonema* – by smaller sporangia (less than 0.5 mm diam.), the absence of a cap on the peridium formed from granular material, and a non-reticulate capillitial surface. **Descriptions:** Macbride (1899); Keller, Eliasson (1992); Lizárraga et al. (2016a); López-Villalba, Moreno (2020). **Illustrations:** Keller, Eliasson (1992, f. 14–31); Yamamoto (1998, P. 204); Poulain et al. (2011, Pl. 95); Lado et al. (2013, f. 47–53); Wrigley de Basanta et al. (2013, f. 56–60); Lizárraga et al. (2016a, 34–42); Lado et al. (2019, f. 7 A–C); López-Villalba, Moreno (2020, f. 4). **Type locality:** USA (Pennsylvania). See also Keller, Eliasson (1992).

XXXI. *P. reticulospora* H.W. Keller et D.R. Reynolds (Fig. 8, H–J). – Sporangia sessile or stalked. Stalk, if present, short (less than a half of sporangium high), dark. Peridium double; outer layer with granular material; inner layer membranous, hardly-noticeable. Dehiscence irregular. Capillitium rarely-branched, 2.5–3 μ m diam., almost smooth, with few short spines. Spores 11–12.5 μ m, orna-

mented with a well-noticeable, regular reticulum, forming (6)8–11(13) cells per spore side. **Similar species:** Differs from sessile species by reticulate spores. From stalked sporangia with reticulate spores (*P. polygonospora*, *P. echinolphospora*) – by the presence of a capillitium. **Descriptions:** Keller, Reynolds (1971). **Illustrations:** Keller, Reynolds (1971, f. 1–5); Novozhilov, Stephenson (2015, f. 9–11). **Type locality:** Philippines.

XXXII. *P. stipitata* Lado, Estrada et D. Wrigley. – Sporangia stalked. Stalk long (usually more than a half of sporangium high), white. Peridium single, membranous. Dehiscence irregular. Capillitium poorly developed, tubulose, threads 1.4–3.6 μ m diam., branched. Spores 12–15 μ m diam., warty. **Similar species:** Differs from other stalked species by a white, calcareous stalk. From *P. pedata* (limeless form) by larger spores. **Descriptions:** Estrada-Torres et al. (2009); Lizárraga et al. (2015). **Illustrations:** Estrada-Torres et al. (2009, f. 45–56); Lizárraga et al. (2015, f. 31–36). **Type locality:** Mexico.

XXXIII. *P. syncarpon* T.E. Brooks. — Pseudoaethalia or aethalia, rarely sporangia. Peridium double; outer layer cartilaginous, from red-brown to almost black; inner layer membranous, closely adjoins to the outer one. Dehiscence into polygonal plates via preformed ribs on the peridium. Capillitium forming a poorly developed net, threads branched and anastomosed, warted or spiny, sometimes reticulate, 2–3 µm diam. (sometimes much wider because of nodes). Spores (8)10–12(14) µm diam., clustered (2–20 spores in group), spinulose. Similar species: Differs from all other species by large aethalia or pseudoaethalia and clustered spores. Descriptions: Martin, Alexopoulos (1969); Moreno et al. (2006); Yamamoto (2006). Illustrations: Martin, Alexopoulos (1969, f. 72); Lizárraga et al. (2005, f. 13–14); Yamamoto, (2006, Pl. 24). Type locality: USA.

XXXIV. *P. taimyriensis* Novozh. et Schnittler. — Sporangia sessile, often grouped. Peridium double; outer layer thick due to granular material, shining; inner layer thin, membranous. Dehiscence irregular. Capillitium absent. Spores (13)13.5–14.5(15) µm diam., almost smooth or a bit warted. Similar species: Differs from *P. liceoides* by a thick peridium and larger spores. From *P. pachyderma* — by larger spores (more than 13 µm). From *P. nigra* — by the orange or brown (not black) color of peridium and irregular dehiscence (not forming a lid). Descriptions: Novozhilov, Schnittler (2000). Illustrations: Novozhilov, Schnittler (2000, f. 1). Type locality: Russia (Taimyr).

XXXV. *P. tessellata* G. Lister. — Sporangia sessile. Peridium double; outer layer thick, black–violet; inner layer thin, semihyaline, shining. Dehiscence via preformed ribs on the peridium, forming petals. Capillitium forms a poorly developed net, threads 1.5 µm diam., ornamented with minute, well-noticeable warts. Spores 9–10 µm diam., evenly warted. Similar species: Differs from other species by the color of peridium and the type of dehiscence. From *P. syncarpon* — by smaller sporangia (nor aethalia) and free (not clustered) spores. Descriptions: Lister (1931); Martin, Alexopoulos (1969). Illustrations: Lister (1931, f. 2 a–c); Emoto (1977, Pl. 28); Yamamoto (1998, P. 205). Type locality: Japan.

XXXVI. *P. thindii* Nanir. — Sporangia sessile, rarely stalked or plasmodiocarps. Peridium single, thin, membranous, thickened in the upper part; evidently bicolor — from brown to black at the top and bright yellow below. Dehiscence by round lid or irregular. Capillitium poorly developed, long, rarely anastomosed, 2.5 µm diam., spinulose. Spores 12–13.8 µm diam., spinulose. Similar species: Differs from *P. corticalis* and *P. liceoides* by the obviously two-colored sporangia. From *P. verrucifera*, *P. luteola* and others — by a poorly developed capillitium. Descriptions: Nanir (1981). Illustrations: absent. Type locality: India.

XXXVII. *P. vermicularis* (Schwein.) Rostaf. (Fig. 8, K–M). — Plasmodiocarps, rarely sporangia. Peridium double; outer layer cartilaginous, from light ochraceous to brown; inner layer membranous. Capillitium well-developed, threads branched, 2–3.5 µm diam., ornamented with short spines (less than 1 µm high) or almost smooth. Spores 10–14 µm diam., warted or short-spinulose. Similar species: Differs from *P. chrysosperma* by short spines on the capillitium. From *P. acetabulifera* (short or curved plasmodiocarps) — by a thinner and non-hirsute capillitium and a double peridium. From *P. liceoides* and *P. corticalis* (sporangia form) — by the presence of a well-developed, short spinulose capillitium. Descriptions: Martin, Alexopoulos (1969); Farr (1976); Novozhilov (1993); Lado, Pando (1997); Nannenga-Bremekamp (1991); Ing (1999). Illustrations: Lister (1925, Pl. 187 a–c); Martin, Alexopoulos (1969, f. 73);

Emoto (1977, f. 26); Lado, Moreno (1978, f. 10); Mitchell (1978, f. 37 a–b); Liu (1982, Pl. 2, f. 1–2; Pl. 10, f. 4); Neuberger et al. (1993, P. 211–212); Hagiwara, Yamamoto (1995, f. 39); Lado, Pando (1997, f. 79); Yamamoto (1998, P. 206–207); Ing (1999, f. 107); Yamamoto et al. (2005, f. 15); Castillo et al. (2009, f. 27–32); Poulain et al. (2011, f. 98); Lado et al. (2014, f. 3F); Cavalcanti et al. (2016, f. 3 J–M); Nannenga-Bremekamp (1991, P. 96). Type locality: USA (North Carolina).

XXXVIII. *P. verrucifera* Y. Yamam. et Shuang L. Chen. — Sporangia sessile, grouped. Peridium thin, membranous, brown-orange until dehiscence. Dehiscence irregular. Capillitium well-developed, threads long, with swollen ends, 5–7 µm diam., ornamented with spines, warts or fragmented reticulum. Spores 10–12 µm diam., spinulose. Similar species: Differs from other species by a single peridium and very thick capillitium. Descriptions: Yamamoto et al. (2002). Illustrations: Yamamoto et al. (2002, f. 3). Type locality: Japan.

We are grateful to N.I. Kireeva for drawings of *Perichaena* sporophores; to A.P. Seryogin and I.V. Sokolova for their invaluable help during historical surveys; to the employees of the Laboratory of Electronic Microphotography, MSU. The work of V.I. Gmoshinskiy on identification keys and diagnosis was supported by the Russian Ministry of Science and Higher Education (Grant Number 075-15-2021-1396). The work of V.I. Gmoshinskiy on photographs and drawings of *Myxomycetes* was founded by the Polistovskiy Nature Reserve (project FOIV – 1-22-66-3) The research of Yu.K. Novozhilov is funded by the Komarov Botanical Institute RAS (AAAA-A19-119020890079-6).

REFERENCES

- Albertini J.B., Schweinitz L.D. *Conspectus fungorum in Lusatae Superioris agro Niskiensi crescentium e methodo Persooniana*. Lipsiae, 1805.
- Araújo J.C., Lado C., Xavier-Santos S. *Perichaena calongei* (Trichiales): a new record of Myxomycetes from Brazil. *Current Research in Environmental and Applied Mycology*. 2015. V. 5. P. 352–356. <https://doi.org/10.5943/cream/5/4/5>
- Batsch A.J.G.C. *Elenchus Fungorum. Gattungen und Arten der Schwämme. Halae Magdeburgicae*, 1783.
- Bjørnekær K., Klinge A.B. *Die Dänischen schleimpilze. Myxomycetes Daniae*. Friesia. 1963. V. 7(2). P. 149–280.
- Bulliard J.B. *Herbier de la France*. Paris, 1789.
- Bulliard J.B.F.P. *Histoire des champignons de la France, ou traité élémentaire, renfermant dans un ordre méthodique les descriptions et les figures des champignons qui croissent naturellement en France*. V. 1. Paris, 1791.
- Calaça F.J.S., Araújo J.C., Moreira I.C. et al. First reports of fimicolous myxomycetes (*Protozoa: Amoebozoa*) from Brazilian Cerrado and Pantanal biomes. *Karstenia*. 2020. V. 58. P. 374–384. <https://doi.org/10.29203/ka.2020.503>
- Castillo A., Moreno G., Illana C. *Myxomycetes from Cabañeros national Park (Spain)*. *Bol. Soc. Micol. Madrid*. 2009. V. 33. P. 149–170.

- Cavalcanti L. de H., Bezerra A.C.C., Barbosa D.I. et al.* Occurrence and distribution of *Perichaena* (Trichiaceae, Myxomycetes) in the Brazilian Northeastern Region. *Acta Bot. Brasilica*. 2016. V. 30. P. 102–111. <https://doi.org/10.1590/0102-33062015abb0238>
- Cheng C.B.T., Yu K.N.T., Campos M.L. et al.* Occurrence and diversity of *Myxomycetes* (plasmodial slime molds) along the northern slope of Mt. Makulot, Cuenca, Batangas, Philippines. *Asian J. Biodiversity*. 2013. V. 4. P. 65–83. <https://doi.org/10.7828/ajob.v4i1.297>
- Eliasson U.* Recent advances in the taxonomy of *Myxomycetes*. *Botaniska Notiser*. 1977. V. 130. P. 483–492.
- Eliasson U.* Review and remarks on current generic delimitations in the myxomycetes, with special emphasis on *Licea*, *Listerella* and *Perichaena*. *Nova Hedwigia*. 2017. V. 104. P. 343–350. https://doi.org/10.1127/nova_hedwigia/2015/0283
- Emoto Y.* The *Myxomycetes* of Japan. Tokyo, 1977.
- Estrada-Torres A., Wrigley de Basanta D., Conde E. et al.* *Myxomycetes* associated with dryland ecosystems of the Tehuacán-Cuicatlán Valley Biosphere Reserve, Mexico. *Fungal Diversity*. 2009. V. 36. P. 17–56.
- Farr M.L.* *Myxomycetes*. *Flora neotropica*. 16. N.Y., 1976.
- Fiore-Donno A.M., Clissmann F., Meyer M. et al.* Two-gene phylogeny of bright-spored *Myxomycetes* (slime moulds, superorder *Lucisporidia*). *PLOS One*. 2013. V. 8. e62586. <https://doi.org/10.1371/journal.pone.0062586>
- Fries E.M., Lindgren J.* *Symbolae Gasteromycorum ad illustrandam Floram Suecicam*. Officina Berlingiana. Lundae, 1817.
- Gilbert E.* On the identity of *Perichaena liceoides* (*Myxomycetes*). *Mycol. Res.* 1990. V. 94 (5). P. 698–704. [https://doi.org/10.1016/S0953-7562\(09\)80671-0](https://doi.org/10.1016/S0953-7562(09)80671-0)
- Gilbert E.* Morphological and ultrastructural features in selected species of *Licea* (*Myxomycetes*). *Nordic J. Bot.* 1996. V. 16. P. 515–546. <https://doi.org/10.1111/j.1756-1051.1996.tb00267.x>
- Hagiwara H., Yamamoto Y.* *Myxomycetes* of Japan. Tokyo, 1995.
- Härkönen M., Sivonen E.* The myxomycetes of Finland. *Norrlinia*. 2011. V. 22. P. 1–224.
- Ing B.* The myxomycetes of Britain and Ireland. London, 1999.
- Johansen E.W., Vetlesen P.* New and rare myxomycetes (*Mycetozoa*, *Myxogastrea*) in Norway, including a complete checklist of Norwegian myxomycetes species. *Agarica*. 2020. V. 40. P. 1–138.
- Keller H.W., Brooks T.E.* A new species of *Perichaena* on decaying leaves. *Mycologia*. 1971. V. 63 (3). P. 657–663.
- Keller H.W., Brooks T.E.* Corticolous *Myxomycetes* VII: contribution toward a monograph of *Licea*, five new species. *Mycologia*. 1977. V. 69. P. 667–684. <https://doi.org/10.2307/3758857>
- Keller H.W., Reynolds D.R.* A new *Perichaena* species with reticulate spores. *Mycologia*. 1971. V. 63 (2). P. 405–410. <https://doi.org/10.1080/00275514.1971.12019118>
- Keller H.W., Eliasson U.H.* Taxonomic evaluation of *Perichaena depressa* and *P. quadrata* based on controlled cultivation, with additional observations on the genus. *Mycol. Res.* 1992. V. 96 (2). P. 1085–1097.
- Kosheleva A.P., Novozhilov Y.K., Schnittler M.* Myxomycete diversity of the state reserve “Stolby” (south-eastern Siberia, Russia). *Fungal Diversity*. 2008. V. 31. P. 45–62.
- Kowalski A.T.* A new coprophilous species of *Calonema* (*Myxomycetes*). *Madroño*. 1969. V. 20 (4). P. 229–231.
- Kuhnt A.* Bemerkenswerte Myxomycetenfunde: Neue Arten, Neukombinationen und Nachweise seltener Arten, Teil 2. *Ber. Bayerischen Botanisch. Gesellschaft*. 2019. V. 89. P. 139–222.
- Kuhnt A.* Bemerkenswerte Myxomycetenfunde: Neue Arten, Neukombinationen und Nachweise seltener Arten, Teil 3. *Ber. Bayerischen Botanisch. Gesellschaft*. 2021. V. 91. P. 119–194.
- Lado C., Moreno G.* Contribucion al estudio de los *Myxomycetes* en España. *Peninsular. II. Anal. Inst. Bot. Cavanilles*. 1978. V. 34. P. 401–415.
- Lado C., Pando F.* *Myxomycetes, I. Ceratiomyxales, Echinosteliales, Liceales, Trichiales*. *Flora Mycol. Iberica*. 1997. V. 2. P. 1–323.
- Lado C., Wrigley de Basanta D., Estrada-Torres A. et al.* Description of a new species of *Perichaena* (*Myxomycetes*) from arid areas of Argentina. *Anales Jard. Bot. Madrid*. 2009. V. 66 (1). P. 63–70. <https://doi.org/10.3989/ajbm.2229>
- Lado C., Wrigley de Basanta D., Estrada-Torres A. et al.* The biodiversity of myxomycetes in central Chile. *Fungal Diversity*. 2013. V. 59. P. 3–32. <https://doi.org/10.1007/s13225-012-0159-8>
- Lado C., Wrigley de Basanta D., Estrada-Torres A. et al.* Myxomycete diversity of the Patagonian Steppe and bordering areas in Argentina. *Anales Jard. Bot. Madrid*. 2014. V. 71. e006. <https://doi.org/10.3989/ajbm.2394>
- Lado C., Eliasson U.* Taxonomy and systematics: current knowledge and approaches on the taxonomic treatment of *Myxomycetes*. In: *S.L. Stephenson, C. Rojas* (eds). *Myxomycetes: biology, systematics, biogeography, and ecology*. London, 2017, pp. 205–252.
- Lado C., Wrigley De Basanta D., Estrada-Torres A. et al.* Diversity of *Myxomycetes* in arid zones of Peru part II: the cactus belt and transition zones. *Anales del Jardín Botánico de Madrid*. 2019. V. 76 (2). e083 <https://doi.org/10.3989/ajbm.2520>
- Lado C.* 2005–2022. An on line nomenclatural information system of *Eumycetozoa*. <http://www.nomen.eumycetozoa.com>. Accessed 15.02.2022.
- Leontyev D.V., Schnittler M.* The phylogeny of *Myxomycetes*. In: *S.L. Stephenson, C. Rojas* (eds). *Myxomycetes: biology, systematics, biogeography, and ecology*. London, 2017. P. 83–106, Academic Press, London. <https://doi.org/10.1016/B978-0-12-805089-7.00003-2>
- Leontyev D.V., Schnittler M., Stephenson S.L. et al.* Towards a phylogenetic classification of the *Myxomycetes*. *Phytotaxa*. 2019. V. 399 (3). P. 209–238. <https://doi.org/10.11646/phytotaxa.399.3.5>
- Li Y., Li H.-Z., Wang Q. et al.* *Myxomycetes* from China VII: New species and new records of *Trichiaceae*. *Mycosystema*. 1990. V. 3. P. 93–98.
- Lister A.* A monograph of the *Mycetozoa* being a descriptive catalogue of the species in the herbarium of the British Museum. Ed. 2nd, revised by G. Lister. London, 1911.

- Lister A. A monograph of the *Mycetozoa*. A descriptive catalogue of the species in the herbarium of the British Museum. Ed. 3rd, revised by G. Lister. London, 1925.
- Lister G. New species of *Mycetozoa* from Japan. *J. Botany*. 1931. V. 69. P. 297–298.
- Liu C.-H. Myxomycetes of Taiwan III. *Taiwania*. 1982. V. 27. P. 64–85.
- Liu C.-H., Chang J.-H., Yang F.-H. Myxomycetes genera *Perichaena* and *Trichia* in Taiwan. *Bot. Studies*. 2007. V. 48. P. 91–96.
- Lizárraga M., Moreno G., Illana C. et al. Myxomycetes from Chihuahua, Mexico III. *Mycotaxon*. 2005. V. 93. P. 75–78.
- Lizárraga M., Moreno G., Esqueda M. et al. Myxomycetes of Sonora (Mexico) 6. Central plains of the Sonoran Desert. *Mycotaxon*. 2015. V. 130. P. 145–164. <https://doi.org/10.5248/130.145>
- Lizárraga M., Moreno G., Esqueda M. et al. Myxomycetes of Chihuahua (México) 4. Central plains of the Chihuahuan desert. *Mycotaxon*. 2016a. V. 130. P. 1073–1101. <https://doi.org/10.5248/130.1073>
- Lizárraga M., Moreno G., Esqueda M. New records of myxomycetes from México. *Mycotaxon*. 2016b. V. 131. P. 511–520. <https://doi.org/10.5248/131.511>
- Lizárraga M., Moreno G., Flores-Romero I. *Perichaena acetabulifera* sp. nov. from Juarez City, Mexico. *Mycotaxon*. 2019. V. 134. P. 307–312. <https://doi.org/10.5248/134.307>
- López-Villalba A., Moreno G. New myxomycetes records from the Canary Islands. *Karstenia*. 2020. V. 58 (2). P. 145–156.
- Macbride T.H. The North American Slime-Moulds. N.Y., 1899.
- Martin G. W., Alexopoulos C. J. The myxomycetes. Iowa city, 1969.
- Martin G.W., Alexopoulos C.J., Farr M.L. The Genera of *Myxomycetes*. Iowa City, 1983.
- Massingill J.M., Stephenson S.L. Myxomycetes appearing in moist chamber cultures on samples of bark and wood collected from coarse woody debris. *Mycosphere*. 2013. V. 4. P. 627–633. <https://doi.org/10.5943/mycosphere/4/3/14>
- Mitchell D.W. A key to the corticolous myxomycetes. Part. 1. *Bull. BMS*. 1978. V. 12 (1). P. 18–42. [https://doi.org/10.1016/S0007-1528\(78\)80007-8](https://doi.org/10.1016/S0007-1528(78)80007-8)
- Mitchell D.W., Moreno G., Lizárraga M. A new species of coprophilous *Perichaena* from New Mexico. *Bol. Soc. Micol. Madrid*. 2011. V. 37. P. 103–108. <https://doi.org/10.29203/ka.2000.360>
- Moreno G., Lizárraga M., Esqueda M. et al. Myxomycetes de Sonora, México. II: Reserva Forestal Nacional y Refugio de Fauna Silvestre Ajos-Bavispe. *Revista mexicana de micología*. 2006. V. 22. P. 13–23.
- Müller H. Bemerkenswerte myxomyceten funde in Thüringen. *Zeitschr. Mykol*. 2005. V. 71 (2). P. 211–220.
- Nanir S.P. A new species of *Perichaena*. *Current Science*. 1981. V. 50 (17). P. 784–785.
- Nannenga-Bremekamp N.E. A Guide to temperate *Myxomycetes*. Bristol, 1991.
- Neubert H., Baumann K. Myxomyceten aus der Bundesrepublik Deutschland, III. Liste der bislang bekannten Arten. *Carolina*. 1986. V. 44. P. 61–66.
- Neubert H., Nowotny W., Baumann K. Die Myxomyceten Deutschlands und des angrenzenden Alpenraumes unter besonderer Berücksichtigung Österreichs. Band 1. *Ceratiomyxales, Echinosteliales, Liceales, Trichiales*. Berlin, 1993.
- Novozhilov Y.K. *Myxomycetes*. Definitorium fungorum Rossicum. Iss. 1. Nauka, St. Petersburg, 1993 (in Russ.).
- Novozhilov Yu.K., Schnittler M. A new coprophilous species of *Perichaena* (*Myxomycetes*) from the Russian Arctic (the Taimyr Peninsula and the Chukchi Peninsula). *Karstenia*. 2000. V. 40 (1–2). P. 117–122. <https://doi.org/10.29203/ka.2000.360>
- Novozhilov Yu.K., Schnittler M., Rollins A.W. et al. Myxomycetes from different forest types in Puerto Rico. *Mycotaxon*. 2001. V. 77. P. 285–299.
- Novozhilov Yu.K., Mitchell D.W., Schnittler M. Myxomycetes biodiversity of the Colorado Plateau. *Mycol. Progress*. 2003. V. 2 (4). P. 243–258.
- Novozhilov Yu.K., Zemlianskaia I.V., Schnittler M. et al. Myxomycete diversity and ecology in the arid regions of the Lower Volga River Basin (Russia). *Fungal Diversity*. 2006. V. 23. P. 193–241.
- Novozhilov Yu.K., Schnittler M. Myxomycete diversity and ecology in arid regions of the Great Lake Basin of western Mongolia. *Fungal Diversity*. 2008. V. 30. P. 97–119.
- Novozhilov Yu.K., Zemlyanskaya I.V., Schnittler M. et al. Two new species of *Perichaena* (*Myxomycetes*) from arid areas of Russia and Kazakhstan. *Mycologia*. 2008. V. 100. P. 816–822. <https://doi.org/10.3852/08-047>
- Novozhilov Yu.K., Stephenson S.L. A new species of *Perichaena* (*Myxomycetes*) with reticulate spores from southern Vietnam. *Mycologia*. 2015. V. 107 (1). P. 137–141. <https://doi.org/10.3852/14-012>
- Persoon C.H. *Observationes mycologicae. Seu discriptiones tam novorum, quam notabilium fungorum*. V. 1. Leipzig, 1796.
- Persoon C.H. *Synopsis methodica fungorum*. Göttingen, 1801.
- Poulain M., Meyer M., Bozonnet J. *Les Myxomycètes*. Tome 1. Sévrier, 2011.
- Poulain M., Meyer M., Bozonnet J. *Les Myxomycètes*. Tome 2. Sévrier, 2011.
- Rammeloo J. Structure of the epispore in the *Trichiaceae* (*Trichiales, Myxomycetes*), as seen with scanning electron microscope. *Bull. Soc. Roy. Bot. Belg*. 1974. V. 107. P. 353–359.
- Rammeloo J. Five new myxomycete species (*Trichiales*) from Rwanda. *Bull. Jard. Bot. Nat. Belgique*. 1981. V. 51 (1/2). P. 229–230.
- Ronikier A., Lado C., Wrigley de Basanta D. *Perichaena megaspora*, a new nivicolous species of myxomycete from the Andes. *Mycologia*. 2013. V. 105 (4). P. 938–944. <https://doi.org/10.3852/12-191>
- Ronikier A., García-Cunchillos I., Janik P. et al. Nivicolous *Trichiales* from the austral Andes: unexpected diversity including two new species. *Mycologia*. 2020. V. 112 (4). P. 753–780. <https://doi.org/10.1080/00275514.2020.1759978>

- Rostafiński J.T. Śluzowce (*Mycetozoa*). Paryż, 1875.
- Schrader H.A. Nova genera plantarum. Lipsiae, 1797.
- Schnittler M., Novozhilov Yu.K. Myxomycetes of the winter-cold desert in western Kazakhstan. Mycotaxon. 2000. V. 74 (2). P. 267–285.
- Stephenson S.L. Myxomycetes associated with decaying fronds of nikau palm (*Rhopalosylis sapida*) in New Zealand. New Zeal. J. Bot. 2003. V. 41. P. 311–317.
- Stephenson S.L. From morphological to molecular: studies of myxomycetes since the publication of the Martin and Alexopoulos (1969) monograph. Fungal Diversity. 2011. V. 50. P. 21–34.
<https://doi.org/10.1007/s13225-011-0113-1>
- Stephenson S.L. Secretive slime moulds. Myxomycetes of Australia. Melbourne, 2021.
- Tran H.T.M., Stephenson S.L., Novozhilov Yu.K. Myxomycetes of Vietnam. Hồ Chí Minh, 2017.
- Turland N.J., Wiersema J.H., Barrie F.R. et al. (eds). International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Regnum Vegetabile 159. Glashütten, 2018.
<https://doi.org/10.12705/Code.2018>
- Walker L.M., Leontyev D.V., Stephenson S.L. *Perichaena longipes*, a new myxomycete from the Neotropics. Mycologia. 2015. V. 107 (5). P. 1012–1022.
<https://doi.org/10.3852/14-330>
- Wang Q., Li Y., Bai J.K. Trichiales. Myxomycetes from China I, *Perichaena*. Mycosystema. 2000. V. 19 (2). 161–164.
- Wrigley de Basanta D., Lado C., Estrada-Torres A. et al. Biodiversity studies of myxomycetes in Madagascar. Fungal Diversity. 2013. V. 59. P. 55–83.
<https://doi.org/10.1007/s13225-012-0183-8>
- Wrigley de Basanta D., Estrada-Torres A. Techniques for recording and isolating myxomycetes. *Myxomycetes: Biology, Systematics, Biogeography, and Ecology*. London, 2017, pp. 333–363.
- Yamamoto Y. The myxomycete biota of Japan. Tokyo, 1998.
- Yamamoto Y., Chen S., Degawa Y. et al. Myxomycetes from Yunnan Province, China. Bull. Natn. Sci. Mus. Tokyo, Ser. B. 2002. V. 28 (3). P. 61–76.
- Yamamoto Y., Hagiwara H., Degawa Y. et al. Myxomycetes collected at the Tokiwamatsu Imperial Villa, Tokyo. Rept. Inst. Nat. Stu. 2005. V. 36. P. 31–65.
- Yamamoto Y. Supplement of “The Myxomycete Biota of Japan”. Fukui, 2006.
- Новожилов Ю.К. (Novozhilov) Определитель грибов России. Отдел Слизевика; вып. 1. Класс Миксомицеты / Отв. ред. И.В. Каратыгин. СПб.: Наука, 1993. 288 с.

Род *Perichaena* (*Myxomycetes*, *Trichiales*, *Arcyriaceae*): таксономическая история и рекомендации по идентификации морфовидов

Е. С. Губанов^{a, #}, В. И. Гмошинский^{a, b, ##}, Ф. М. Бортников^{a, ###},
А. В. Матвеев^{a, ####}, Ю. К. Новожилов^{c, #####}

^aМосковский государственный университет имени М.В. Ломоносова, 119234 Москва, Россия

^bПолистовский государственный заповедник, 182840 Бежаницы, Россия

^cБотанический институт им. В.Л. Комарова РАН, 197376 Санкт-Петербург, Россия

[#]e-mail: gubanov_5b_1315@mail.ru

^{##}e-mail: rubisco@list.ru

^{###}e-mail: f.m.bortnikov@gmail.com

^{####}e-mail: andrmatveev@gmail.com

^{#####}e-mail: yurynovozh1lov@yandex.ru

Род *Perichaena* включает 38 морфовидов и характеризуется желтым цветом споровой массы, достаточно плотным перидием и отсутствием спиральных утолщений на тонких нитях капилиция, которые имеют только шиповатую и бородавчатую орнаментацию. В некоторых случаях капилиций может редуцироваться или полностью отсутствовать, что несколько размывает границы рода *Perichaena* и сближает его с родом *Licea*. В последние 50 лет было описано множество видов, однако не все они были включены в фундаментальные монографии или представлены в определительных ключах. В данной работе обобщены данные о роде *Perichaena*, включая номенклатурную историю и особенности морфологии спороношений. Также приводятся иллюстрированные определительные ключи для всех видов рода. Даны краткие морфологические описания и иллюстрации 13 из 14 видов, которые были выявлены в России.

Ключевые слова: идентификационные ключи, морфовиды, Россия, таксономическая история, СЭМ, *Licea*