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Critical revision of the myxomycete (Myxomycetes, Myxomycota) collection at the Mycological herbarium LEP. I. Yaroslavl Region

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Summary. Scientific collections are the basis for studying biological diversity. The Mycological herbarium of the A. A. Jaczewski Laboratory of mycology and phytopathology (LEP), All-Russian Institute of Plant Protection (Saint Petersburg, Pushkin), was founded at the end of the 19th century and is one of the oldest mycological herbaria in Russia. In the period from 2018 to 2024, a critical revision of the collection of myxomycete fructifications numbering about 2000 herbarium specimens was carried out. The herbarium contains a series of 73 specimens collected in spring–summer 1916 in the Yaroslavl Governorate by I. P. Javoronkowa. Information about this collection has not been published yet. As a result of the revision, 42 species and 3 varieties belonging to 21 genera of myxomycetes were identified, of which 32 species and 3 varieties are new for the Yaroslavl Region, including the first record of *Enteridium simulans* for Russia. An additional analysis of literary sources allowed us to expand this list to 46 species from 22 genera. The present work is the first step for further study of myxomycetes in this part of Russia.

Критическая ревизия коллекции миксомицетов (Мухотусеtes, Мухотусоta) микологического гербария LEP. І. Ярославская область

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Ключевые слова: ВИЗР, история микологии, редкие виды, слизевики, Amoebozoa, Myxogastrea.

Аннотация. Научные коллекции являются основой для изучения биологического разнообразия. Микологический гербарий лаборатории микологии и фитопатологии имени А. А. Ячевского Всероссийского научно-исследовательского института защиты растений (Санкт-Петербург, г. Пушкин), был основан конце XIX в. и является одним из старейших микологических гербариев в России. В период с 2018 по 2024 гг. была проведена критическая ревизия коллекции плодовых тел миксомицетов, насчитывающей около 2000 гербарных образцов. В гербарии находится серия из 73 образцов, которые были собраны весной – летом 1916 г. в Ярославской губернии И. П. Жаворонковой. Информация об этих сборах ранее не была опубликована. В результате ревизии выявлено 42 вида и 3 разновидности, относящихся к 21 роду миксомицетов, из которых 32 вида и 3 разновидности являются новыми для Ярославской области, а *Enteridium simulans* впервые отмечен для России. Дополнительно проведенный анализ литературных источников позволил расширить этот список до 46 видов из 22 родов. Представленная работа является первым шагом для дальнейшего изучения миксомицетов этой части России.

Introduction

Herbarium collections provide source material for a range of basic and applied research (Chapman, 2005). For taxonomists, these materials are a valuable source of information about the characteristics of the described species and the limits of their morphological variability (Ronikier et al., 2022).

Herbarium collections also provide important information about the distribution and ecology of plant and fungal species in historical retrospective. They store primary data on the state of ecosystems in the past and allow to assess their response to global environmental changes (Willis et al., 2017; James et al., 2018). Moreover, the study of herbarium specimens can provide valuable information about relationships between organisms. For example, the study of herbaria of higher plants helps to study changes in the range of parasitic fungi over time (Bradshaw, Tobin, 2020). Another important role of herbaria is the resource for libraries of nucleotide sequences of marker genes (DNA barcodes) (de Vere et al., 2015; Borg Dahl et al., 2018, etc.). These libraries can be used to establish possible geographic isolation, confirm the correctness of the morphological characters and their taxonomic significance, etc. It is difficult to overestimate the importance of voucher and type specimens, which ensure the safety of information about the species. Herbarium specimens are also a historical document that allows us to understand the evolution of scientists' views on the status of a particular taxon. Thus, herbarium collections are an important source of primary information for a variety of studies. Their preservation, digitization and publication are necessary to obtain data in completely different fields of knowledge.

Mycological Herbarium of the A. A. Jaczewski Laboratory of Mycology and Phytopathology of the

All-Russian Institute of Plant Protection (VIZR), St. Petersburg, Pushkin, has the international acronym LEP. It is based upon Gzhatsky district of the Smolensk Governorate (Berestetskaya et al., 2012). While working at the specimens collected by Arthur Arthurovich Jaczewski (= Yachevskiy) in 1891-1892 in Switzerland, northern Algeria and in the Saint Petersburg Botanical Garden, A. A. Jaczewski began cataloguing the fungi of Russia. He and his students collected extensive material, partially summarized in a series of publications. By 1917, the collection consisted of approximately 100 thousand specimens. After the revolution, the herbarium was actively expanded, in particular by N. A. Naumov who organized many specialized mycological expeditions. During the years of the siege of Leningrad, the herbarium was moved to the buildings of the All-Union Institute of Plant Industry and was saved owing to the heroic efforts of Prof. S. M. Tupenevich (Khokhryakov, Potlaychuk, 1972). Currently, more than 150 thousand specimens have been deposited in the herbarium. A significant part of the material was collected in the territory of the former USSR as well as in many countries of Western Europe, Asia and North America. The herbarium also contains materials from Africa, Australia, Central and South America, the Pacific and Indian Ocean islands (Berestetskaya et al., 2012). The collection is organized according to the systematic principle. The herbarium is represented by antique oak cabinets and large boxes in which sheets with the species names placed where individual specimens are written.

The section of the herbarium dedicated to myxomycetes is quite compact, occupying two full cabinets and represented by approximately 2000 storage units. Nevertheless, it is rich in myxomycete taxa due to the wide geography of expeditions as well as purchases and exchanges of large collections of exsiccata. In the period from 2018 to 2024, we carried out a complete revision of myxomycete specimens stored in the mycological herbarium. This work opens a series of publications on the results of this revision and is devoted to specimens collected in the Yaro-slavl Region, Central Russia. Until now, information about them has not been published.

Materials and methods

Photographs of sporocarps were taken with Olympus SZX16 dissecting microscope (Olympus, Tokyo, Japan) equipped with a PROKYON digital camera (Jenoptik, Jena, Germany). Series of pictures were taken in different optical sections and processed using Helicon Focus ver. 6.0.18. The dimensions of spores, capillitium, and sporocarps were calculated using ToupView 3.7 and ImageJ ver. 1.52a (free license).

Microscopic measurements and photographs were made with a light microscope with differential contrast using Olympus BX 53 light microscope equipped with a PROKYON digital camera (Jenoptik, Jena, Germany). For microscopy, sporocarps were mounted in 4 % KOH.

For each specimen, three parameters were recorded: the level of preservation on a five-point scale (according to dela Cruz et al., 2009, modified after Gmoshinskiy et al., 2020) (Table 1), storage type (b – box, e – envelope), mounting method (m – mounted with glue, n – not mounted, freely positioned in box or envelope).

 Table 1. Criteria adopted to establish the level of preservation of the myxomycete collection of A. A. Jaczewski Mycological Herbarium

| Level | Description |
|-------|--|
| 0 | No trace of sporophores and spores in the box. |
| 1 | Sporophores are heavily damaged. Only scales of peridium or some spores stay in the box. |
| | Sporophores are heavily damaged. Only stalks and hypothallus of the sporophores are preserved. Precise |
| 2 | species identification is impossible. |
| | Sporophores are damaged, but it is possible to identify species by using a set of diagnostic characters. There |
| 3 | are \geq 10 complete sporophores in collection. |
| | Sporophores in good condition, but many of them are slightly damaged (in particular, broken peridium, |
| 4 | whole colonies are pressed as a result of incorrect storage, etc.). |
| 5 | Sporophores in excellent condition. |

Results

During the critical revision of the myxomycete collection stored in the Mycological Herbarium LEP, a series of specimens from the Yaroslavl Region dating back to 1916 was discovered. According to the signatures on the envelopes, the place of collection was the Yaroslavl Governorate, and on field labels are additionally indicated: Tunoshna and Tsibirino villages. Collection and identification of the specimens was carried out by I. P. Javoronkowa (Javoronkova in author's spelling on labels). It should be noted that the field labels on specimens collected by I. P. Javoronkowa bear the monogram "И. Т." as the collector and identifier. The only exception is specimen LEP 339, where the collector is indicated as "Jaczewski" on the envelope, but the field label also shows the monogram "И. Т.". Some specimens had additional attachments with morphological descriptions, and the surname "Троицкая" (Troitskaya) on them. We led to the hypothesis that "И. Т." means I. Troitskaya and "И. Ж." is I. P. Javoronkowa and they are the same person. This hypothesis was based on the fact that the specimen LEP 26, collected in 1915 in the vicinity of Petrograd, has a field label with monogram "N. Ж." and the herbarium label stating "Javoronkova". The handwriting on the field label of LEP 26 is very similar to that of all specimens from the Yaroslavl Region, in particular to LEP 29 (Fig. 1). In addition to specimens from Yaroslavl and Petrograd Governorates, the collection also includes specimens from Saratov Governorate and suburbs of Kiev.

A collector biographical note

Until the end of the 19th century, the development of education in the Russian Empire was characterised by gender asymmetry. Compared to other European countries, Russia faced a particularly challenging situation regarding women's higher education and career opportunities, which became particularly critical in the fields of agricultural science and practice. In September 1904, first private Higher Agricultural Courses for Women named after Ivan A. Stebut were opened in St. Petersburg. A few years later, they became a full-fledged high school with a four-year degree program. Many prominent scientists were listed as teachers, for example, classes in phytopatology were taught by A. A. Jaczewski (Elina, 2018).

One of the students was Iraida Petrovna Javoronkowa (married Troitskaya), born in Yaroslavl on February 5, 1893. While still studying, her first work (presented by A. A. Jaczewski) was published in a prestigious journal of Mycological Society of France (Javoronkowa, 1914). The article was about the parasite *Ramularia myxophaga* Javoron. on spores of *Didymium difforme* (Pers.) Gray, which she accidentally discovered during experiments with the germination of myxomycete spores (Javoronkowa, 1915). For a long time, one of her interests was collecting the fruiting bodies of myxomycetes in the field, even after completing the Courses in 1916. However, the main scientific field of I. P. Javoronkowa was phytopathology; in the 1930s, several articles and a workshop manual on plant bacterioses were published (Javoronkowa, 1931). Thereafter, her scientific career was interrupted; in the 1940s, she worked in a seed control laboratory in Kansk, Siberia, and then in 1949 at the Kansk forest school (Lipschitz, 1950).



Fig. 1. Herbarium and field labels of specimens: a - LEP 26; b - LEP 29.

An annotated species list

The database of the herbarium LEP has 73 specimens of myxomycetes collected in the Yaroslavl Governorate, only 6 of which could not be identified due to the low preservation of the material, and one specimen was missing from the herbarium.

Although all specimens were collected more than a century ago and the entire collection was transported several times from institution to institution, even species with heavily calcified and fragile fruiting bodies were in excellent (8 specimens / 11 % of the total), good (13 / 18 %) and satisfactory (28 / 38 %) condition. The number of specimens with a low degree of preservation was small (23 / 32 %). We assume this is due to the fact that the specimens were stored in matchboxes additionally placed in paper bags. Most of the fruiting bodies were glued to the bottom of the box, which ensured the safety of the specimens even during transportation.

As a result of the revision, 42 species and 3 varieties of myxomycetes belonging to 21 genera were identified. Of these, 32 species and 3 varieties were new for the Yaroslavl Region, including *Enteridium simulans* Rostaf. recorded for the first time for the territory of Russia.

An annotated species list of myxomycetes from the Yaroslavl Region stored in the Mycological herbarium LEP is presented below in alphabetical order. After the species name, the authors of the taxon and, if necessary, synonyms are listed. Taxa names and authors correspond to the online nomenclatural information system of Eumycetozoa (Lado, 2005–2024). New species for the Yaroslavl Region are marked with asterisk "*". The next line shows collector's original determination, the place and date of collection, and the type of substrate. Number (LEP) and parameters (see section Materials and Methods) of the specimen are given in brackets below.

* Arcyria cinerea (Bull.) Pers.

as *Arcyria cinerea* Pers., Tunoshna, 24 VII 1916 (LEP 1717 [4-b-m]); as *Arcyria cinerea* Pers., Tunoshna, birch stump, 16 VI 1916 (LEP 1722 [3-b-m]).

Arcyria denudata (L.) Wettst.

= *A. punicea* Pers.

as Arcyria punicea Pers., Tunoshna, spruce stump, 04 VII 1916 (LEP 1775 [4-b-m]).

*Arcyria incarnata (Pers. ex J. F. Gmel.) Pers.

as *Arcyria incarnata* Pers., Tunoshna, birch stump, 17 VII 1916 (LEP 1747 [3-b-m]); as *Arcyria incarnata* Pers., Yaroslavl Governorate, decaying wood, 01 IX 1916 (LEP 1770 [3-e-n]).

*Arcyria obvelata (Oeder) Onsberg.

= *A. nutans* (Bull.) Grev.

as Arcyria nutans Greville, Tunoshna, spruce stump, 01 VII 1916 (LEP 1776 [4-b-m]).

Ceratiomyxa fruticulosa (O. F. Müll.) T. Macbr.

as *Ceratiomyxa mucida* Schroeter, Tunoshna, wood, 01 VII 1916 (LEP 20 [2-b-m]); as *Ceratiomyxa mucida* Schroeter, Tunoshna, birch stump, 01 VII 1916 (LEP 24 [4-b-m]); as *Ceratiomyxa mucida* Schroeter, Tunoshna, pine stump, 03 VI 1916 (LEP 27 [5-b-m]); as *Ceratiomyxa mucida* Schroeter, Tunoshna, pine stump, 30 V 1916 (LEP 29 [3-b-m]); as *Ceratiomyxa mucida* Schroeter, Yaroslavl Governorate, decaying wood of birch, 01 VII 1916 (LEP 38 [2-b-m]).

**Ceratiomyxa fruticulosa* var. *porioides* (Alb. et Schwein.) G. Lister.

= *C. porioides* (Alb. et Schwein.) J. Schröt.

as *Ceratiomyxa porioides* Schroeter, Tunoshna, birch stump, 20 VI 1916 (LEP 54 [5-b-m]).

**Craterium aureum* (Schumach.) Rostaf. (Fig. 2a).

as *Physarum sulphureum* Alb et Schw, Tunoshna, aspen stump, 17 VII 1916 (LEP 478 [3-b-m]).

The substrate is several fibers of decaying wood affected by white rot. Sporangia are stalked, erect, scattered over the substrate, spherical or slightly elongated, sporothecae 0.4-0.5 mm in diameter, 0.5-0.6 mm in height, total sporangium height 0.7-0.9 mm, bluish or brownish-yellow. The peridium is single-layered, thin, bluish-greenish, covered in the upper part with yellow scales of lime. Cracking occurs at the top, leaving an irregular calyculus at the base of the sporangium. The hypothallus small, discoid. The stalk is up to 1/3 of the total sporophore height (0.3–0.4 mm high), straight, wrinkled, cream-colored, yellowish, slightly darker at the base. The capillitium consists of large, irregularly shaped, light yellow lime nodules connected by fairly short, thin, glassy tubes; lime nodules sometimes form a pseudocolumella in the center of the sporangium. The spores are black or dark brown in mass, lighter in transmitted light, 8–9 µm in diameter, delicately warted.

The morphology of the studied specimen was fully consistent with the currently accepted species concept (Martin, Alexopoulos, 1969; Moreno, Oltra, 2010). This specimen was collected on decaying wood, which is unusual for *C. aureum* that usually occurs on leaf litter (Martin, Alexopoulos, 1969; Ing, 1999). However, according to our observations, if leaf litter partially covers decaying wood, then colonies of sporangia can sometimes spread to adjacent open areas of wood.

Craterium leucocephalum (Pers. ex J. F. Gmel.) Ditmar. (Fig. 2b, c).

as *Craterium leucocephalum* Ditmar, Tunoshna, birch root, 24 VII 1916 (LEP 254 [4-b-n]).

The examined specimen is in good preservation and is represented by a typical variety. *Craterium leucocephalum* var. *scyphoides* (Cooke et Balf.) G. Lister is distinguished by a more rounded shape of sporangia. On the contrary, *C. leucocephalum* var. *cylindricum* (Massee) G. Lister has very elongated sporangia (Moreno, Oltra, 2010).

Herbarium specimen LEP 270 is an empty envelope, labeled as *C. leucocephalum*, with a collection date of 24 VII 1916, while specimen LEP 254 is in a box with the same collection date on the field label and contains fruiting bodies of *C. leucocephalum*. It can be assumed that these are two parts of the same specimen, so we indicate only LEP 254 as a storage unit. Specimen LEP 1570, in addition to the fruiting bodies of *Hemitrichia clavata* (see below), contains several destroyed sporangia with preserved peridial fragments covered with light lime and yellow crystalline disks. Due to its poor preservation, we have listed it as *Craterium* cf. *leucocephalum*.

Craterium minutum (Leers) Fr.

= Craterium pedunculatum Trentep.

as *Craterium pedunculatum* Trentepohl, Yaroslavl Governorate, bark, 17 VIII 1916 (LEP 288 [3-b-m]).

*Cribraria argillacea (Pers. ex J.F. Gmel.) Pers.

as *Cribraria argillacea* Pers., Tunoshna, pine stump, 17 VII 1916 (LEP 1062 [3-b-m]).

*Cribraria aurantiaca Schrad.

as *Cribraria aurantiaca* Schroeter, Yaroslavl Governorate, pine stump, 21 VII 1916 (LEP 1076 [3-b-m).

*Cribraria cancellata (Batsch) Nann.-Bremek.

 \equiv *Dictydium cancellatum* (Batsch) E. Sheld.; \equiv *Dictydium cancellatum* (Batsch) T. Macbr. (Combination previously proposed by Sheldon, 1895).

as *Dictydium cancellatum* Macbride, Yaroslavl Governorate, spruce trunk, 01 VII 1916 (LEP 1630 [1-b-m]); as *Dictydium cancellatum* Macbride, Yaroslavl Governorate, birch trunk, 24 VI 1916 (LEP 1633 [3-b-m]); as *Dictydium cancellatum* Macbride, Yaroslavl Governorate, decaying wood, 04 VII 1916 (LEP 1640 [1-e-m]).

*Cribraria microcarpa (Schrad.) Pers.

as *Cribraria microcarpa* Pers., Yaroslavl Governorate, poplar trunk, 21 VI 1916 (LEP 1084 [3-b-m]).

*Diderma umbilicatum Pers. (Fig. 2d-f).

as *Chondrioderma radiatum* Rostafinski, Yaroslavl Governorate, decaying wood and bark, 17 VIII 1916 (LEP 572 [3-b-m]).

The specimen is represented by a fragment of a leaf, on the surface of which there are about 20 sporangia, half of which are destroyed (Fig. 2d). Sporophores are sporangia on short stalks, aggregated into groups, slightly overlapping each other but not losing their individuality, 0.7–0.9 mm tall, light brownish-gray, cushion-shaped, 1.0–1.2 mm in diameter, 0.5–0.7 mm thick, with a small depression at the base. The peridium is single-layered, heavily calcified, shell-shaped, gray-pinkish-brown, with stripes of light pink (flesh) color. The dehiscence is irregular and occurs along the light lines. The hypothal-

lus is almost inconspicuous. The stalk is short (0.3– 0.4 mm in height), thick (0.2–0.4 mm in diameter), narrowed at the base and widening at the top, heavily calcified, almost smooth, slightly rough, fleshcolored (Fig. 2f). The columella is dome-shaped, heavily calcified, slightly rough, ochraceous, darker at the base (Fig. 2d). The capillitium is represented by thin glassy, tortuous, weakly branching and occasionally anastomosing filaments, with a small number of nodular thickenings (Fig. 2e). The spores are dark brown in mass; violet-brown in transmitted light, spherical, slightly oval, with a faintly visible light spot, (9.0–)9.5–10.5(–11.2) µm in diameter (Mean = 10.03; SD = 0.49; n = 40), warty (Fig. 2e).

The most typical features of this species are: a single-layered peridium formed by white granules of lime, cushion-shaped sporangia with a small depression at the base, a light, heavily calcified and almost smooth stalk, and a large, light, heavily calcified columella (Ing, 1999). A species quite similar in external morphology, *D. montanum* (Meyl.) Meyl., is distinguished by the presence of a two-layered peridium. For many years, *D. umbilicatum* was considered a light color variant of *D. radiatum* (L.) Morgan (\equiv *Chondrioderma radiatum* (L.) Rostaf.) (Ing, 1999), so it is not listed in most 20th-century identification manuals.

Didymium melanospermum (Pers.) T. Macbr.

 \equiv *D. farinaceum* Schrad. [nom. illeg.]

as *Didymium farinaceum* Schr., Tunoshna, dry leaves, 10 VIII 1916 (LEP 720 [2-b-m]).

*Didymium nigripes (Link) Fr.

as *Didymium nigripes* (Link) Fries, Tunoshna, mosses, 03 VIII 1916 (LEP 741 [5-b-m]).

*Didymium serpula Fr.

= *D. complanatum* (Batsch) Rostaf. [nom. illeg., non *D. complanatum* Schrad.]

as *Didymium complanatum* Rost., Tunoshna, birch bark, 16 VIII 1916 (LEP 677 [3-b-m]).

*Enteridium simulans Rostaf. (Fig. 3).

 \equiv *Reticularia simulans* (Rostaf.) D.W. Mitch.

 \equiv *R. olivacea* var. *simulans* (Rostaf.) Nann.-Bremek.

as *Enteridium olivaceum* Ehrenberg, Yaroslavl Governorate, decaying wood, 17 VIII 1916 (LEP 1155 [4-b-m]).

This is the first record of *E. simulans* in Russia (Bortnikov et al., 2020). The specimen consists of several aetalia, one of which has a damaged peridi-

um and scattered spores. Aethalia scattered over the substrate, flattened, on a narrowed base, elongatedcylindrical, about 2 mm in diameter, up to 5 mm long, dark olive. The cortex is dark olive, brown, covered with numerous light lines creating a reticulate pattern, cartilaginous (Fig. 3a), olive-yellow in transmitted light. Dehiscence is irregular. The hypothallus is reddish-brown, inconspicuous. The pseudocapillitium is brown, spongy, dense, represented by a network of perforated plates, firmly attached to the inner surface of the peridium and the base of the fruiting body. The spores are olive-brown in mass; light olive-brown in transmitted light, spherical, with a uniformly thickened wall, free, the diameter of the spores together with ornamentation is $(10.8-)11.3-12.7(-13.4) \mu m$ (Mean = 11.97, SD = 0.75, n = 20), decorated with large spines (Fig. 3b).



Fig. 2. *Craterium aureum*, *C. leucocephalum*, and *Diderma umbilicatum*: a - Craterium aureum (LEP 478) – sporangia; b, c – *Craterium leucocephalum* (LEP 254) – sporangia; d–f – *Diderma umbilicatum* (LEP 572): d, f – sporangia, e – capillitium and spores in transmitted light (TL). Scale bars: $a - 200 \mu m$; b, c, f – 500 μm ; d – 1000 μm ; e – 10 μm .

Many authors consider this species to be a variety of *E. olivaceum*. A distinctive feature of *E. simulans* are free spores, which are uniformly ornamented with fairly large spines, while in *E. olivaceum* the spores are collected in dense clusters, resulting in the ornamentation being well expressed only on the part of the spore not facing the inner side of the cluster. *Reticularia splendens* Morgan also has a spongy structure. This species can be easily distinguished due to the finely reticulate ornamentation of the spores, the usually larger size of the fruiting body and the light brown color of the spore mass and cortex (Martin, Alexopoulos, 1969). It is believed that *E. simulans* may be quite widespread in Europe, but it is mistaken for *E. olivaceum* (Nannenga-Bremekamp, 1973; Ing, 1999).



Fig. 3. Enteridium simulans (LEP 1155): a – partially destroyed aethalium, b – spores (TL). Scale bars: a – 1 mm; $b - 10 \mu m$.

**Fuligo gyrosa* (Rostaf.) E. Jahn

 \equiv *Physarum gyrosum* Rostaf.

as *Fuligo septica* Gmelin, Tunoshna, 01 VIII 1916 (LEP 177 [4-b-m]).

This species differs from *F. septica* by dense, rosette-like sporangia forming compact groups, elastic capillitium with large, elongated nodules, as well as brownish, pinkish and purple tones in the coloring of the peridium (Martin, Alexopoulos, 1969).

Fuligo septica (L.) F. H. Wigg.

as *Fuligo septica* Gm., Tunoshna, wood, 20 VII 1916 (LEP 132 [3-b-m]).

*Fuligo septica var. candida (Pers.) R. E. Fr.

*Fuligo septica var. rufa (Pers.) Lázaro Ibiza

as *Fuligo septica* Gm., Yaroslavl Governorate, pine and birch wood, 10 VI 1916 (LEP 229 [3-b-m]).

Specimen LEP 229 contained several fragments of substrate with large aetalia. In one case the lime was colored reddish and in the other white. We determined such specimens as *F. septica* var. *rufa* and *F. septica* var. *candida* respectively.

*Hemitrichia clavata (Pers.) Rostaf.

as *Hemitrichia clavata* Rost., Tunoshna, decaying wood, 01 VIII 1916 (LEP 1570 [1-b-m]).

Besides *H. clavata*, this specimen contained heavily destroyed fruiting bodies that can be attributed to *Craterium* cf. *leucocephalum*.

**Hemitrichia decipiens* (Pers.) García-Cunch., J.C. Zamora et Lado

 \equiv *Trichia decipiens* (Pers.) T. Macbr.

as *Trichia botrytis* Pers., Tunoshna, aspen stump, 23 V 1916 (LEP 1333 [3-b-m]); as *Trichia decipiens* Macbride, Tsibirino, birch stump, 16 VI 1916 (LEP 509 [3-b-m]).

This species is characterized by wrinkled stalks that widen at the top and extend into the base of the sporangium. The stalks are filled with spore-like cells. The spores are decorated with a delicate reticulation, clearly visible only at high magnification. A species similar in morphology, *T. crateriformis* G. W. Martin, is distinguished by warty spores (Moreno, Castillo, 2013).

Leocarpus fragilis (Dicks.) Rostaf.

as *Leocarpus fragilis* Rostaf., Tunoshna, 18 VII 1916 (LEP 601 [4-b-m]).

In addition to the fruiting bodies of *L. fragilis*, the specimen contains several heavily destroyed sporangia of *Physarum auriscalpium* Cooke.

Lycogala flavofuscum (Ehrenb.) Rostaf.

as *Lycogala flavo-fuscum* Rost., Yaroslavl Governorate, birch trunk, 19 VI 1916 (LEP 1317 [3-e-m]).

**Metatrichia vesparia* (Batsch) Nann.-Bremek. ex G.W. Martin et Alexop.

 \equiv *Hemitrichia vesparia* (Batsch) T. Macbr.

as *Hemitrichia vesparium*, Tunoshna, rhizomorphs on a birch stump, 02 VI 1916 (LEP 1588 [2-b-n]); as *Hemitrichia vesparium* Macbride, Yaroslavl Governorate, decaying wood, 03 VIII 1916 (LEP 1594 [3-b-m]). The specimen additionally contains fragments of fruiting bodies of *Stemonitis* sp.; as *Hemitrichia vesparium* Macbride, Yaroslavl Governorate, poplar trunk, 15 V 1916 (LEP 1595 [2-b-m]); as *Hemitrichia vesparium* (Pers.) Macbride, Yaroslavl Governorate, poplar trunk, 17 VIII 1916 (LEP 1596 [5-b-m]); as *Hemitrichia vesparium* Pers., Yaroslavl Governorate, birch wood, 02 VI 1916 (LEP 1597 [2-b-m]).

**Nannengaella leucopus* (Link) J. M. García-Martín, J.C. Zamora et Lado

 \equiv *Physarum leucopus* Link

as *Physarum leucopus* Link, Tunoshna, birch stump, collection date in unknown (LEP 394 [3-b-m]).

**Oligonema favogineum* (Batsch) García-Cunch., J. C. Zamora et Lado (Fig. 4a, b)

 \equiv *Trichia favoginea* (Batsch) Pers.

as *Trichia favoginea* Pers., Tunoshna, birch stump, 19 VIII 1916 (LEP 1425 [5-b-m]). This species is distinguished by cylindrical sporangia (Fig. 4a) and coarsely reticulate spores (Fig. 4b).

**Oligonema persimile* (P. Karst.) García-Cunch., J.C. Zamora et Lado (Fig. 4c, d)

 \equiv *Trichia persimilis* P. Karst.

as *Trichia affinis* De Bary, Tunoshna, aspen stump, 01 VI 1916 (LEP 1326 [3-b-m]).

Oligonema persimile, like O. affine (de Bary) García-Cunch., J.C. Zamora et Lado (\equiv Trichia affinis de Bary), is characterized by the presence of spherical sporangia with light-yellow spore mass. The main difference is that the spores of O. affine have coarse reticulation and are quite similar to the spores of O. favogineum (Fig. 4b), whereas the spores of O. persimile bear a separate groups of large warts not forming a closed network (Fig. 4d).

*Physarum album (Bull.) Chevall.

 \equiv *Physarum nutans* Pers.

as *Physarum nutans* Pers., Tunoshna, birch stump, 29 VII 1916 (LEP 412 [2-b-m]); as *Physarum nutans* Pers., Yaroslavl Governorate, birch wood, 17 VII 1916 (LEP 422 [2-b-n]); as *Physarum nutans* Pers., Yaroslavl Governorate, decaying wood, 12 VIII 1916 (LEP 434 [3-b-m]); as *Physarum nutans* Pers., Tunoshna, wood, 20 VII 1916 (LEP 435 [3-b-m]).

Herbarium specimen LEP 425 is an empty envelope labeled as *P. nutans* with the collection date of 29 VII 1916; specimen LEP 412 is in a box with a field label and contains the fruiting body. From these data, we can conclude that these are two parts of one specimen, therefore we indicate only LEP 412 as a storage unit.

*Physarum auriscalpium Cooke

as *Leocarpus fragilis* Rostaf., Tunoshna, 18 VII 1916 (LEP 601 [2-b-m]). Sporangia of *P. auriscalpium* are severely damaged and are found in the same box with the well-preserved sporangia of *Leocarpus fragilis*.

*Physarum compressum Alb. et Schwein.

as *Physarum compressum*, Tunoshna, aspen wood, 30 V 1916 (LEP 339 [3-b-m]).

**Physarum confertum* T. Macbr.

as *Physarum cinereum* Pers., Tunoshna, old trunks, 16 VIII 1916 (LEP 324 [3-b-m]).

The specimen is heavily damaged by insects. However, it is clearly noticeable that the fruiting bodies are represented by dense groups of dark brown sporangia overlapping each other and interspersed with gray lime.

**Physarum psittacinum* Ditmar.

as *Physarum psittacinum* Ditmar, Yaroslavl Governorate, aspen wood, 21 VI 1916 (LEP 448 [2-b-m]).

**Physarum pusillum* (Berk. et M. A. Curtis) G. Lister

as *Physarum nutans* Pers., Tunoshna, bark, 22 VII 1916 (LEP 402 [3-b-m]).

**Physarum viride* (Bull.) Pers.

as *Physarum viride* Pers., Tunoshna, aspen wood, 17 VII 1916 (LEP 503 [3-b-m]). As indicated on the field label, this specimen also contains fruiting bodies of *P. psittacinum*, but the latter is not given a separate herbarium number; as *Physarum viride* Pers., Tsibirino, birch wood, 16 VI 1916 (LEP 504 [3-b-m]).

**Reticularia lycoperdon* Bull.

as *Reticularia lycoperdon* Bulliard, Yaroslavl Governorate, decaying wood, 26 V 1916 (LEP 1192 [2-b-m]). Fruit bodies are not fully mature; as *Reticularia lycoperdon* Bulliard, Yaroslavl Governorate, birch wood, 26 VII 1916 (LEP 1199 [2-b-m]).

*Reticularia splendens Morgan

as *Enteridium olivaceum* Ehrenb (det. I. P. Javoronkova), as *Reticularia lycoperdon* Bull (det. M. Zelle), Yaroslavl Governorate, pine wood, 10 VI 1916 (LEP 1182 [2-b-m]); as *Reticularia lycoperdon* Bulliard, Yaroslavl Governorate, aspen wood, 18 V 1916 (LEP 1178 [1-b-m]).



Fig. 4. *Oligonema favogineum* and *O. persimile*: a, b – *Oligonema favogineum* (LEP 1425): a – sporangia, b – capillitium and spores (TL); c, d – *Oligonema persimile* (LEP 1326): c – ends of capillitial threads (TL), d – capillitium and spores (TL). Scale bars: a – 1000 μm; b, c – 20 μm; d – 10 μm.

Reticularia splendens is distinguished by large aetalia covered with brown, dense cortex, and a spongy pseudocapillitium represented by perforated plates. The pseudocapillitium of *R. lycoperdon* is represented by coarse, flattened plates extending from the base of the aethalium that branch profusely and terminating in fine sinuous filaments.

**Siphoptychium reticulatum* Leontyev, Schnittler et S. L. Stephenson (Fig. 5)

as *Tubulina cylindrica* DC, Yaroslavl Governorate, old decaying wood, 15 III 1916 (LEP 1128 [5-b-m]).

This species was described in 2019 (Leontyev et al., 2019). Its distinctive feature is the presence of compact pseudoaetalia with a pronounced peridium

from dark red to dark brown (Fig. 5a), with clearly visible light lines between the ends of the lateral parts of the sporangia, which gives the impression of a reticulate structure of the surface of the pseudoaetalia (Fig. 5b). A related species, *S. violaceum* Leontyev, Schnittler et S. L. Stephenson, is characterized by dark purple or dark purple-brown coloring of the peridium surface and by faintly visible light lines along the borders of the sporangia (Leontyev et al., 2019).

Stemonitis axifera (Bull.) T. Macbr.

as *Stemonitis fusca* Roth, Yaroslavl Governorate, birch wood (*Betula* sp.), 20 VI 1916 (LEP 946 [4-b-m]). Stemonitis axifera is distinguished by light brown, almost smooth spores in transmitted light, $5.5-7(-7.5) \mu m$ in diameter, while *S. fusca* Roth is characterized by darker, warty-reticulate spores, $7.5-9 \mu m$ in diameter (Martin, Alexopoulos, 1969).

Stemonitopsis typhina (F. H. Wigg.) Nann.-Bremek.

as *Comatricha personi* Rost., Tunoshna, birch decaying wood, 21 VII 1916 (LEP 1037 [4-b-m]); as *Comatricha personi* Rost., Tunoshna, spruce decaying wood, 04 VII 1916 (LEP 1038 [4-b-m]).

Distinctive features of *S. typhina* are the silvery membranous peridium, which is loosely connected to the capillitium, a membranous sheath covering the sporangium stalk, and well-defined groups of warts on the spore surface (Poulain et al., 2011).

*Trichia scabra Rostaf. (Fig. 6a, b).

as *Trichia scabra* Rost., Tunoshna, birch bark, 10 VIII 1916 (LEP 1468 [3-b-m]).

*Trichia varia (Pers. ex J.F. Gmel.) Pers. (Figs 6c, d).

as *Trichia persimilis* Karst, Tunoshna, decaying wood, 17 VIII 1916 (LEP 1446 [5-b-m]); as *Trichia*

persimilis Karst, Tunoshna, decaying wood, 19 VIII 1916 (LEP 1447 [4-b-m]); as *Trichia varia* var. *nigripes* Persoon, Yaroslavl Governorate, birch decaying wood, 16 VIII 1916 (LEP 1514 [4-b-m]).

A unique feature of this species is the presence of two spiral bands on the surface of the elaters (Fig. 6d), whereas in other species of *Trichia* Haller and *Oligonema* Rostaf. the capillitium is decorated with three or more spiral bands.

**Willkommlangea reticulata* (Alb. et Schwein.) Kuntze (Fig. 6e, f).

 \equiv *Cienkowskia reticulata* (Alb. et Schwein.) Rostaf.

as *Cienkowskia reticulata* Rost., Yaroslavl Governorate, bark, 08 VIII 1916 (LEP 511 [5-b-m]); LEP 510 is microscope slide of LEP 511.

Willkommlangea reticulata can be identified in the field by the reticulate plasmodiocarps covered with reddish-brown to light yellow peridium, with deep maroon, round-shaped structures protruding from the surface (Fig. 6f). The capillitium consists of transverse calcified plates that segment the plasmodiocarp, between which a network of yellowish glassy tubes with a few rounded calcareous nodules is formed (Martin, Alexopoulos, 1969).



Fig. 5. *Siphoptychium reticulatum* (LEP 1128): a – pseudoaethalium, b – reticulate surface of the pseudoaethalium. Scale bars: a, b – 1000 μ m.

Non-identified specimens:

as *Ceratiomyxa mucida* Schroeter, Yaroslavl Governorate, wood, 01 VII 1916 (LEP 34 [1-b-m]).

as *Physarum leucopus* Link, Yaroslavl Governorate, birch stump, VII 1916 (LEP 385 [0-e-n]).

as *Physarum viride* Pers., Tunoshna, aspen wood, 16 VII 1916 (LEP 502 [1-b-m]). The specimen is represented by poorly developed sclerotia, which makes its identification impossible. as *Chondrioderma* sp., Tunoshna, dry leaf litter, 16 VIII 1916 (LEP 599 [2-b-m]). The specimen contained several dense, sclerotized fruiting bodies, which can be attributed by their look to *Lamproderma* sp.

as *Spumaria alba* D.C, Yaroslavl Governorate, branches and stems, 06 VII 1916 (LEP 817 [0-e-n]).

as *Lycogala epidendrum* Fries, Yaroslavl Governorate, wood, 1916 (LEP 1281 [2-b-n]). This specimen can be attributed to *Lycogala epidendrum* (L.)

Fr. sensu lato. In 2023, a major revision of the *Lyco-gala* Adans was carried out, resulting in 15 newly described species (Leontyev et al., 2023). Identification at the species level requires studying the structure of scales on the surface of the peridium. Specimen

LEP 1281 is insufficiently preserved, which makes species identification impossible.

as *Trichia decipiens* Macbride, Yaroslavl Governorate, aspen wood, 17 VII 1916 (LEP 1395 [specimen missing]).



Fig. 6. *Trichia scabra, T. varia*, and *Willkommlangea reticulata*: a, b – *Trichia scabra* (LEP 1468): a – capillitium (TL), b – capillitium and spores (TL); c, d – *Trichia varia* (LEP 1446): c – sporangia, d – capillitium (TL); e, f – *Willkommlangea reticulata* (LEP 511) – plasmodiocarp under different magnifications. Scale bars: a, d – 20 μm; b – 10 μm; c – 1000 μm; e – 500 μm; f – 200 μm.

Discussion

The diversity of myxomycetes in Russia has been studied unevenly. While for some regions there is

evidence of more than 100–200 species, in many regions sufficient research has not been carried out at all. A striking example is the Yaroslavl Region. Some information about myxomycetes of this re-

gion can be found in the monograph by A. A. Jaczewski, where three species are given for the city of Yaroslavl: Craterium minutum, C. leucocephalum, and Stemonitis fusca Roth. Only one species was recorded for the city of Rybinsk: Arcyria denudata. All specimens were collected by A. A. Jaczewski, only for S. fusca the collector Dmitriev was additionally listed (Yachevskiy, 1907). Unfortunately, the current location of the herbarium specimens cited in this work is unknown. In addition, the boundaries of the administrative units of other regions bordering the Yaroslavl Region have changed over time. For example, Vesyegonsky and Kashinsky districts, previously part of the Tver Governorate, now partially belong to the Yaroslavl Region. Thus, Stemonitopsis typhina, given by A. A. Jaczewski (Yachevskiy, 1907) with the indicated location "Tver Governorate" could be collected within the modern borders of the Yaroslavl Region (Bortnikov et al., 2020).

In the following years, the results of fragmentary studies and occasional findings were published. For the vicinity of the Rakhmanovo village (Pereslavl district), one species is given: Leocarpus fragilis (Barsukova, Dunayev, 1997). In addition, while revising the collection of the Young Naturalists Club at the Zoological Museum of Moscow State University, L. fragilis and Didymium melanospermum (Pers.) T. Macbr. were noted. For these specimens, the place and date of collection were later clarified: 57°1'57.5"N, 38°38'41"E (± 1 km), 25 VIII 1993 (Gmoshinskiy et al., 2020). In 1993, the amoeboid stage of Physarum flagellatum (Alexeieff) Fiore-Donno, Kamono et Caval.-Sm. (≡ Hyperamoeba flagellata Alexeieff) was isolated from the ice of a freshwater reservoir in Yaroslavl (Fiore-Donno et al., 2010).

The list of myxomycetes of the Yaroslavl Region can be supplemented with the results of research conducted at the biological station of Demidov Yaroslavl State University, located in the Uglich district. G. V. Kondakova provides high-quality photographs of six species of slime molds: Ceratiomyxa fruticulosa; Lycogala epidendrum sensu lato (immature aetalia in the photograph, which cannot be identified to the species level in accordance with the concept of Leontyev et al., 2023); L. flavofuscum (species erroneously identified as Reticularia lycoperdon, but the photograph clearly shows the characteristic teardrop-shaped aetalia of a dark gray-green color and a prominent white fibrous hypothallus); Stemonitis axifera; Tubifera cf. dudkae (Leontyev et G. Moreno) Leontyev, G. Moreno et Schnittler (the species is labelled as Tubifera ferruginosa (Batsch) J. F. Gmel., however, the photograph shows imma-

ture sporophores of a soft pink color with a weakly defined structure of individual sporangia, characteristic of Tubifera dudkae, more precise identification of this specimen is difficult due to the impossibility of studying the structure of the pseudoaetalia), and Fuligo septica var. septica (Kondakova, 2024). In addition, F. septica was recorded on the territory of the Pleshcheyevo Lake National Park: vicinity of the village Chashnitsy (Kompleksnaya bioekologicheskaya..., 2016), northern shore of Lake Pleshcheyevo (Kompleksnaya bioekologicheskaya..., 2020) and the Kasarka place (Kompleksnaya bioekologicheskaya..., 2017). Stemonitis axifera was also found in the latter localization (Kompleksnaya bioekologicheskaya..., 2017). The dates of detection of sporophores are not given.

During the revision, of the 14 species previously indicated for the Yaroslavl Region, only four were not confirmed: *Lycogala epidendrum* sensu lato, *Stemonitis fusca, Physarum flagellatum*, and *Tubifera* cf. *dudkae*, for one of which, *P. flagellatum*, the morphology of fruiting body is still unknown (Fiore-Donno et al., 2010), and therefore, it cannot be detected through collection revisions without the use of molecular methods.

Thus, based on all the data at our disposal, we can conclude that at the moment the taxonomic composition of myxomycetes of the Yaroslavl Region is represented by 46 species and 3 intraspecific varieties belonging to 22 genera from 8 families and 6 orders. Of course, the identified species reflect only a small part of the true species diversity of myxomycetes in the region. For comparison, as of 2020, 252 species were known in the Moscow Region, and 207 in the Tver Region, while 455 species were reported for Russia (Bortnikov et al., 2020).

Thus, a critical revision of the collection made it possible to significantly expand the available data on the diversity of myxomycetes of the Yaroslavl Region, and is the first step for their further study in this part of Russia.

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