



## A Checklist of Myxomycetes from Kazakhstan

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### Abstract

This paper presents an annotated checklist of myxomycetes recorded from Kazakhstan, comprising 193 species accepted according to the current taxonomy. The checklist synthesizes data from a comprehensive evaluation of 26 relevant publications; species mentioned in these sources were treated as records unless explicitly referencing primary data of another study. Among the major vegetation zones, mountain coniferous forests were most diverse (115 taxa recorded), followed by forest steppe (87), semidesert (71), extra zonal forests in steppe (69), steppe (49), desert (48), and open mountain (25) biomes. Decaying wood was the most frequently reported substrate (157 records), closely followed by plant litter (155). Bark of living trees and shrubs (99) was also important, while living mosses (24) and dung (28) supported fewer, yet often highly specialized, species. Field surveys yielded 109 species, but an additional 48 species were detected via the moist chamber culture technique. Only 36 species were recovered at least once by both methods. These findings demonstrate that field surveys and moist chamber cultures complement each other, recovering distinct species assemblages. The latter method proved to be essential for detecting minute species, particularly those inhabiting desert environments.

**Keywords** – Amoebozoa – biodiversity – Central Asia – regional myxobiota – slime molds – species distribution – taxonomy

### Introduction

Myxomycetes, or plasmodial slime molds, are a group of phagotrophic eukaryotes that belong to the supergroup Amoebozoa and includes more than 1100 described species according to the database of Lado (2005–2025), with the rate of species described as new to science increasing every year (Schnittler et al. 2025). These amoeboid organisms are able to form macroscopic fruiting bodies, making them valuable subjects for research on protist diversity and ecology.

The life cycle of myxomycetes includes two trophic stages. In the first stage, they exist as single-nucleated amoeboid or flagellated cells, functioning as true microorganisms. In the second stage, they form a characteristic multinucleated structure called a plasmodium, which can reach macroscopic dimensions (Martin & Alexopoulos 1969).

Although neither of major ecological importance nor pathogenic to humans (Schnittler et al. 2012), myxomycetes are an important group of organisms in the study of evolutionary processes, phylogenetic relationships, protist systematics and soil microbial ecology (Urich et al. 2008). Their taxonomy is mainly based on the morphological features of their fruiting bodies (sporophores), which can be easily preserved in herbaria (Stephenson et al. 2008). So far, the species concept in the group is entirely based on morphological characters of these sporophores, making these structures key to ecological and geographical research of the group.

Scientific attention to myxomycetes has been mainly focused on regions such as Europe, North and Central America, and East Asia (Schnittler et al. 2017a). These areas have been studied extensively, leading to a substantial expansion in our understanding of their diversity and distribution. However, despite this progress, certain regions, such as Central Asia, remain underexplored.

Until recently, information on the taxonomic composition, ecological characteristics, and geographical distribution of myxomycetes in Kazakhstan was limited to certain ecological groups. Research on epiphytic, coprophilous, bryophilous, and nivicolous species, which form sporophores in the spring near melting snow, has been virtually absent. However, this vast country boasts a wide variety of biomes reaching from deserts to mountain forests and alpine regions (Rakhimova et al. 2023) and should likely host a similarly high diversity in myxomycetes.

Kazakhstan is characterized by a pronounced zonality of natural landscapes, sequentially changing from north to south. In meridional direction, five main natural zones are distinguished: forest-steppe, steppe, semi-desert, desert, and mountain. Arid landscapes (deserts and semi-deserts) occupy approximately 60% of the country's territory (Rachkovskaya et al. 2003, Nazarenko et al. 2025), defining its natural specificity.

The northern regions belong to the forest-steppe zone of the West Siberian Plain, featuring predominantly flat terrain with absolute elevations of 100–200 m, a well-developed river network (Irtysh and Ishim), and numerous closed depressions. The central and western areas include the steppe landscapes of the Kazakh Upland and the Turgay Plateau, characterized by undulating plains with residual elevations of 300–500 m, composed mainly of Paleozoic formations. The southern and southeastern regions are occupied by the mountain systems of the Tian Shan and Dzungarian Alatau, with maximum elevations reaching 6995 m (Pik Khan Tengri). These territories exhibit a distinct altitudinal zonation, ranging from foothill steppes through montane coniferous forests to alpine meadows and a high elevation nival belt (Rakhimova et al. 2023). The western part of the country is represented by the flat landscapes of the Caspian Lowland, dominated by semi-desert and desert formations (see Fig. 1B). Mountainous areas display a significantly higher plant diversity and are often protected within nature reserves. These areas harbor two unique ecological groups of myxomycetes: xylophilic species on coniferous wood (well-studied in older literature, e.g., Golovenko 1957, 1960, 1965, Vasyagina et al. 1977) and the nivicolous myxomycetes (discovered only recently; Azirakhmet et al. 2025).

### **History of the study of Myxomycetes in Kazakhstan**

Systematic research on myxomycetes in Kazakhstan started relatively recently, although the first mention of these organisms in the country dates back to the late 19<sup>th</sup> century (Yachevskiy 1907, Vasyagina et al. 1977). In 1890, N. Sorokin documented the presence of the myxomycete *Fuligo septica* (formerly *Aetaliium septicum*), which marked the first record of a myxomycete in the country (Vasyagina et al. 1977). Later, A. A. Yachevskiy recorded at least one more species (*Mucilago crustacea*, currently known as *Didymium spongiosum* (Leyss.) J.M. García-Martín, J.C. Zamora & Lado) in his monograph, but he often did not give exact localities (Yachevskiy 1907).

A significant contribution followed in 1928 when N. I. Lavrov collected specimens in the southwestern part of the Altai Mountains. This unique material was handed over to I. N. Golovenko, who later conducted extensive research and published several papers (Golovenko 1957, 1965, 1968). Golovenko described several new species of myxomycetes, which are currently not accepted (Lado 2005–2025). She also identified key habitats for myxomycetes in Kazakhstan and studied especially intensely the ecological guild of myxomycetes occurring on decaying wood. Her studies laid the

groundwork for further systematic analysis of this group of organisms in Kazakhstan (Golovenko 1960).

Research on myxomycetes in Kazakhstan advanced significantly between 1947 and 1957, focusing on the Trans-Ili Alatau (Ile Alatau) and Tien Shan regions. During this period, B. I. Kravtsov collected samples in the Zhambyl region (formerly Dzhambul region) in 1949, and N. M. Leonova collected samples between 1953 and 1954 in the Akmola, Aktobe, and Kokshetau regions (formerly the Kokchetav region). These samples were sent to the Department of Botany at Al-Farabi Kazakh National University (formerly S. M. Kirov State University), where department head S. R. Schwartzman led the efforts to process over 140 samples collected from various ecosystems across Kazakhstan. This work identified 38 species of myxomycetes from 21 genera and eight families, including the genus *Ceratiomyxa* (Golovenko 1960), now classified as *Ceratiomyxomycetes* = *Protosporangiida* (Leontyev et al. 2019). An account from 1977 listed 108 species, but several descriptions of new species are not accepted today, and others are now considered as synonyms of other species (Supplementary File 1, Vasyagina et al. 1977).

After a nearly 20-year hiatus, research resumed in 1995. In April and May of that year, field studies were conducted on the Mangyshlak Peninsula in the Mangistau region (western Kazakhstan), near the eastern Caspian Sea coast (around 52.22°E, 44.02°N) (Schnittler & Novozhilov 2000). In this arid region with a sharply continental climate, the life cycle of myxomycetes occurs within a brief period after rainfall, making it challenging to find fruiting bodies in nature. As a result, researchers applied the moist chamber method, which proved effective for studying myxomycetes in arid conditions (Schnittler et al. 2015b). During an expedition in 1998 led by I. N. Safronova, M. Schnittler and Y. K. Novozhilov collected samples for moist chamber cultures along a route covering over 1500 Km. These efforts recorded 513 observations of myxomycetes, representing 27 species (Schnittler & Novozhilov 2000, Schnittler 2001).

From 2004 to 2007, several expeditions were carried out by I. V. Zemlyanskaya and Y. K. Novozhilov in western Kazakhstan (the Almaty, Atyrau, and Mangistau regions) and southeastern Kazakhstan around lakes Balkhash and Zaisan to study myxomycetes biodiversity in desert and steppe zones of Kazakhstan. Extensive material of field-collected herbarium specimens and substrate samples for moist chamber cultures was accumulated; the resulting specimens are now housed in the mycological herbarium of the V. L. Komarov Botanical Institute of the Russian Academy of Sciences (LE). These expeditions yielded a highly unique and rich collection, resulting in several publications, including studies on myxomycetes in the northwestern Caspian Lowland (Novozhilov et al. 2005a, b, c), the Inder Salt Dome area in Atyrau (Zemlyanskaya & Novozhilov 2020, 2023), and southeastern Kazakhstan (Zemlyanskaya & Novozhilov 2018). In addition, two new species were described from these collections. These were *Perichaena polygonospora* (Novozhilov et al. 2008) and *Physarum pseudonotabile* (Novozhilov et al. 2013). Nevertheless, much of the data obtained during these expeditions remain unpublished.

The research on myxomycetes in western Kazakhstan was summarized in an annotated list containing 3,228 records of 111 species from 31 genera and 10 families. The publication provided a detailed species checklist describing collection methods, localities, vegetation types, substrates, and herbarium specimen numbers (Zemlyanskaya et al. 2020). However, this publication did not include data from the Zaysan Depression in eastern Kazakhstan, where 45 species from 15 genera were identified (Zemlyanskaya & Novozhilov 2018), and species records from publications before the 1990-s.

In subsequent years, systematic research on myxomycetes in Kazakhstan declined, with publications mainly reporting isolated findings. Scientists from the Institute of Botany and Phytointroduction in Almaty surveyed the myxomycete biota of the Almaty Region in 2008–2019, consolidating with a few fresh collections a species checklist for the Ile Alatau (Dzhunuskanova & Rakhimova 2021) and for the whole region (Rakhimova et al. 2023). Noteworthy was a record of *Diderma niveum* (Rakhimova et al. 2022), the first for a member of the nivicolous ecological guild. These species form fruiting bodies on plant debris near melting snow (Ronikier & Ronikier 2009, Schnittler et al. 2015a). More nivicolous species, such as *Diderma meyeræ* and *Badhamia* aff.

*albescens* ( $\equiv$  *Physarum albescens*), were collected in 2013 by M. Schnittler in the Ile Alatau Mts. (Azirakhmet et al. 2025) and mentioned in phylogenetic studies of some myxomycete species complexes (Shchepin et al. 2021, 2024).

The latest data on myxomycetes in the Ile Alatau were presented in a dissertation by Gulnaz Sypabekkyzy, completed at Al-Farabi Kazakh National University between 2018 and 2023. While primarily focusing on micromycetes of the Ile Alatau and Kungey Alatau, the study noted the occurrence of three myxomycetes (*Cribraria macrocarpa*, *Fuligo septica*, and *Stemonitis fusca*), all as substrates for mycophilous fungi (Sypabekkyzy 2024).

This review presents an attempt to summarize the knowledge on myxomycete diversity from Kazakhstan into a single annotated checklist, putting the country on the list of many others with published checklists for this group of organisms (e.g., Germany: Schnittler et al. 2011, Costa Rica: Rojas et al. 2010, Russia: Bortnikov et al. 2020).

## Materials & Methods

Through a systematic literature review, we identified 26 publications documenting myxomycete records in Kazakhstan and sorted them with priority given to primary sources. We then compiled a database of all records (representing each species mention from literature sources, excluding citation-only references) and standardized the available information as follows:

- Administrative regions (Fig. 1A): numbers of records in different parts of Kazakhstan.
- Vegetation zones (Fig. 1B): (1) forest-steppe, the southernmost regions with boreal forests; (2) steppe with (2a) treeless open steppe and (2b) small forest islands in depressions and river valleys, predominantly deciduous; (3) semi-desert with mostly zonal vegetation; and (4) desert with zonal vegetation and small azonal islands of richer vegetation not considered separately and (5) montaneous regions with (5a) mountain coniferous forests, generally above 500 m a.s.l. and (5b) alpine zones above the timberline, especially in the south and east. The five major zones (numbered 1 to 5) are pictured on the map, but the small-scale alpine areas in mountains (1b) and the often tiny forest islands in the steppe region (3b) cannot be shown at this scale. Especially for the latter, many older records cannot be unambiguously assigned to either open steppe or forest islands.

- main **Substrate type**: coarse woody debris at various decay stages, plant litter (mainly ground litter), living mosses (covering coarse woody debris or rocks), bark of living trees and shrubs, weathered dung of herbivorous animals; the latter two substrate types were typically studied using moist chamber cultures.

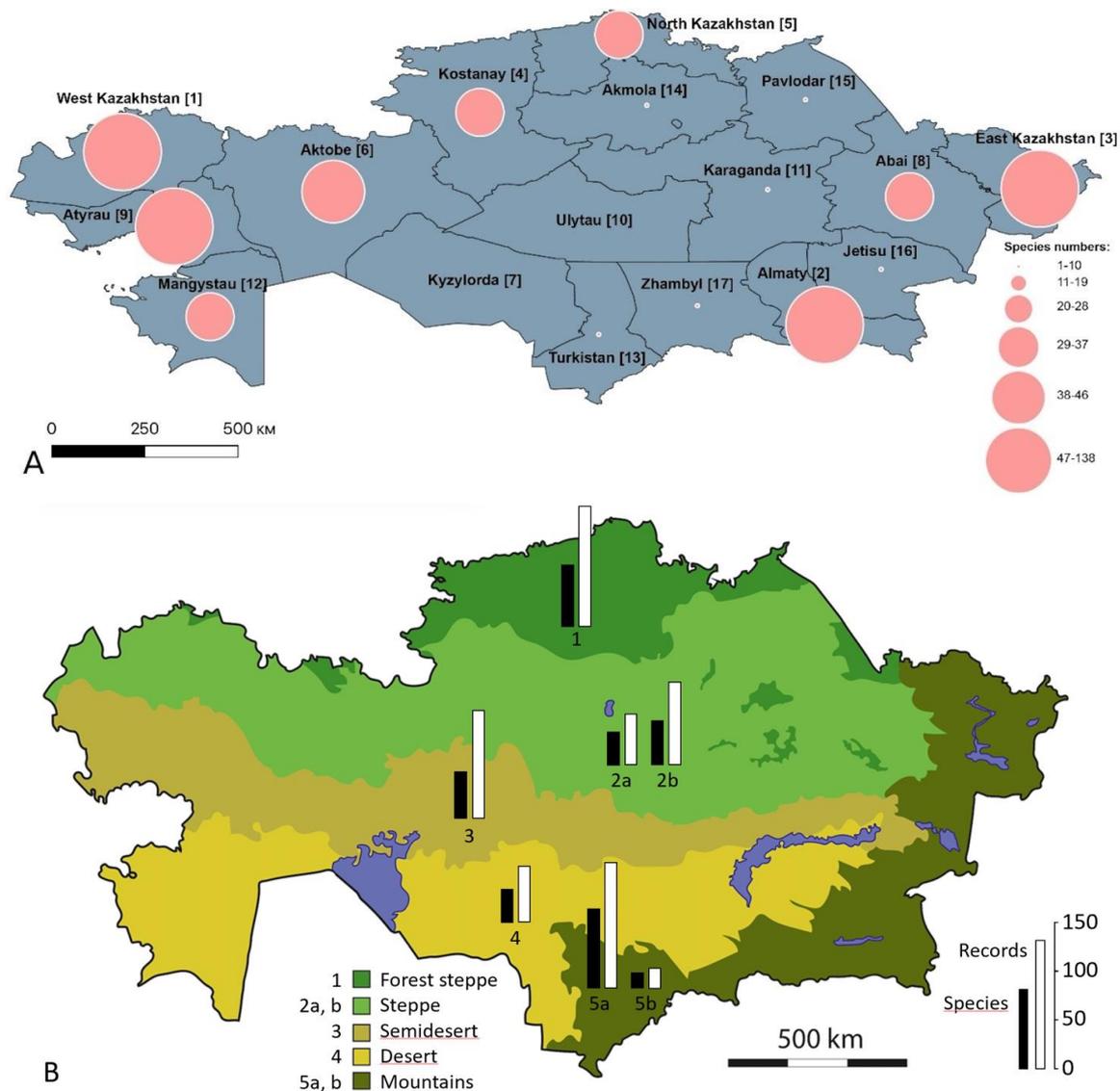
- method of recovery: direct observation/collection in the field (FC) or observation only in substrate cultures (MC) or both.

- ecological guild (a classification system grouping species by primary microhabitat occurrence, defined by combinations of substrate-microclimate conditions): w - xylophilous (decaying wood in forests, usually medium air moisture), m - bryophilous (mosses on wood or rocks in areas with high air moisture), l - lignicolous (on plant litter, usually on the ground under trees, shrubs or herbaceous vegetation), d - coprophilous (on herbivore dung), n - nivicolous (ground plant debris and parts of living plants covered by a contiguous snow cover lasting at least for 2–3 months, fruiting upon snow melt), b - corticolous (bark of living trees and shrubs).

The resulting database was used to produce an annotated species list. For convenience, for some generic names introduced by the latest systematic changes (after 2020) the name used in most monographs (published before 2020) was given. The full database is available as Supplementary File 1. Although occasionally listed, we did not include varieties (like those for the common *Fuligo septica*) in this list, since apparently these names were not used consistently in the literature.

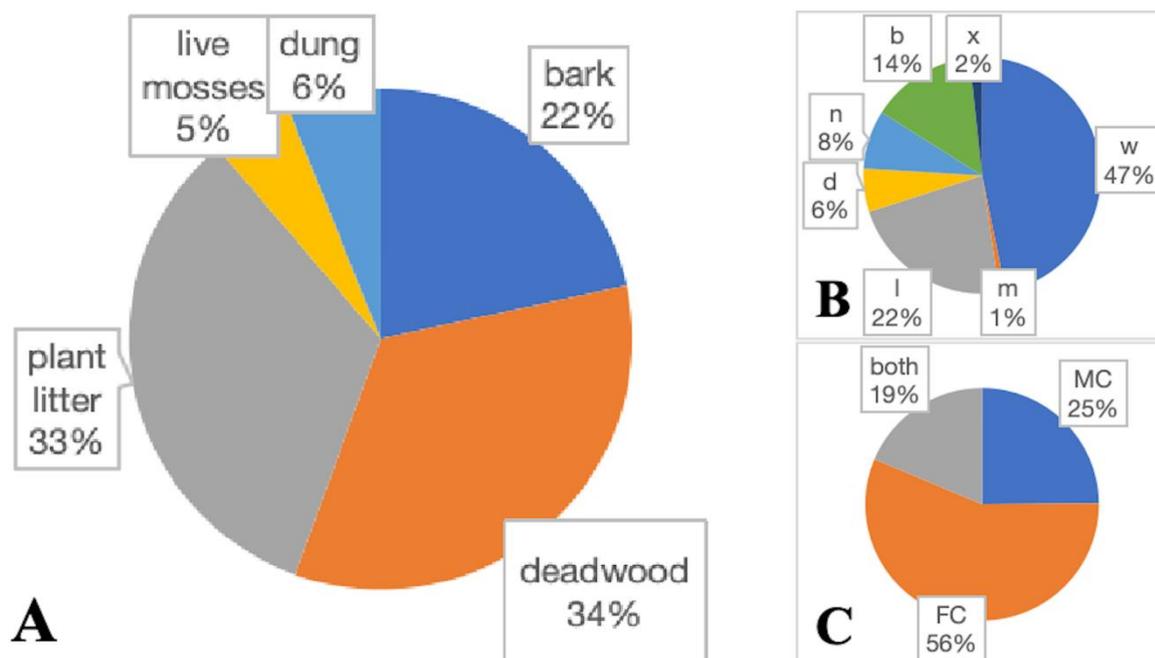
## Results

The survey intensity for the major regions of Kazakhstan is very different, as seen from the number of records (Fig. 1A; Supplementary File 1). Among the biomes, mountain coniferous forests were the richest in species, followed by colline to lowland boreal taiga forests, steppe (including small forest islands, often composed by a few trees only), semidesert, and desert (Fig. 1B)



**Fig. 1** – A Survey intensity across Kazakhstan expressed as the number of known species per administrative region. Circle size is proportional to the number of records. The numbers in square brackets are region numbers used in the annotated species list. B Survey intensity across Kazakhstan by major natural (vegetation) zones, characterized by the number of recorded species. Bar height is proportional to the number of species / records; for numbering see text.

Among the main substrate types, plant litter and coarse woody debris were characterized by the highest number of species, followed by bark, mosses, and dung (Fig. 2A). This picture changed slightly when species were classified according to their ecological guild (Fig. 2B). Xylophilous species (usually found in forested regions on coarse woody debris) are best represented, followed by litter-inhabiting species, which prefer soft plant ground litter. The next large group is the often-minute corticolous species inhabiting the bark of living trees and shrubs. Minor guilds with highly specialized species include the nivicolous myxomycetes (Schnittler et al. 2015a, Azirakhmet et al. 2025), coprophilous (fimicolous) myxomycetes (Calaça et al. 2020, Eliasson & Lundqvist 1989), and the bryophilous myxomycetes, fruiting on moss covers on dead wood and rocks (Schnittler et al. 2010). The two major study methods, field observation and the moist chamber culture technique, complemented each other very well, recovering quite different species assemblages (Fig. 2C): only one in five species was recorded in both the field and in culture.



**Fig. 2** – Statistics for myxomycete species known from Kazakhstan. A Species found in the main substrate types (since one species can occur at several substrate type, numbers exceed the total of species found). B Classification of species into main ecological guilds (w: xylophilous species, decaying wood; m: bryophilous species, mosses on wood or rocks; l: lignicolous species, plant litter; d: coprophilous species, herbivore dung; n: nivicolous species, litter under snow; b: corticolous species, bark of living trees and shrubs; x: unknown). C Species found in moist chambers (MC), in the field (FC), or with both methods.

### Annotated species list

The following annotated checklist first gives the species name according to Lado (2005–2025) from the period 2005–2025, followed by the regions of the country (West Kazakhstan [1], Almaty [2], East Kazakhstan [3], Kostanay [4], North Kazakhstan [5], Aktobe [6], Kyzylorda [7], Abai [8], Atyrau [9], Ulytau [10], Karaganda [11], Mangystau [12], Turkistan [13], Akmola [14], Pavlodar [15], Zhetysu [16], Zhambyl [17]), where the species were found (see Fig. 1), the biomes, the method of recovering (FC: field collection/observation, MC: observation in a moist chamber culture, or both), the main substrate types (bark, deadwood, plant litter, live mosses, dung) and the ecological guild (w: xylophilous species, decaying wood; m: bryophilous species, mosses on wood or rocks; l: lignicolous species, plant litter; d: coprophilous species, herbivore dung; n: nivicolous species, litter under snow; b: corticolous species, bark of living trees and shrubs; x: unknown) into which we classified the species. Information on the numbered sources and their references refer to Table 1. For illustrations of some rare species from nivicolous habitats see Azirakhmet et al. (2025), in addition we illustrate here the rare *Badhamia rhytidosperra*, a species with a preference for desert regions (Fig. 3).

1. *Amaurochaete atra* (Alb. & Schwein.) Rostaf. **Regions:** 1, 2, 3; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe, semidesert; **Method:** FC; **Substrate type:** bark, deadwood; **Guild:** w; **Sources:** 17, 21.
2. *Angioridium sinuosum* (Bull.) Grev. **Regions:** 1, 2, 4, 5; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe, semidesert; **Method:** FC; **Substrate type:** deadwood, plant litter, live mosses; **Guild:** l; **Sources:** 3, 17, 21; **Comment:** syn. *Physarum bivalve* Pers.
3. *Arcyria cinerea* (Bull.) Pers. **Regions:** 1, 3, 6; **Vegetation zones:** mountain coniferous forest,

- extra zonal forest in steppe, semidesert, steppe; **Method:** FC, both; **Substrate type:** bark, deadwood, plant litter; **Guild:** l, w, d; **Sources:** 8, 17, 21; **Comment:** this is a very diverse species complex (Yatsiuk et al. 2024) which needs further investigation.
4. *Arcyria congesta* (Sommerf.) Berk. & Broome. **Regions:** 2, 3, 5; **Vegetation zones:** mountain coniferous forest, forest-steppe; **Method:** FC; **Substrate type:** bark, coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 17; **Comment:** syn. *Arcyodes incarnata* (Alb. & Schwein.) O.F.Cook.
  5. *Arcyria denudata* (L.) Wettst. **Regions:** 1, 2, 3, 4, 5, 6; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe, forest-steppe; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 3, 17, 21.
  6. *Arcyria incarnata* (Pers. ex J.F. Gmel.) Pers. **Regions:** 1, 2, 3, 4, 6; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe, forest-steppe; **Method:** FC; **Substrate type:** bark, coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 3, 17, 21.
  7. *Arcyria minuta* Buchet. **Regions:** 1, 8, 9, 12; **Vegetation zones:** extra zonal forest in steppe, semidesert, desert; **Method:** MC, FC; **Substrate type:** bark, coarse woody debris; ecological **Guild:** w; **Sources:** 8, 13, 19, 21.
  8. *Arcyria occidentalis* (T. Macbr.) G. Lister. **Regions:** 1; **Vegetation zones:** extra zonal forest in steppe; **Method:** FC; **Substrate type:** coarse woody debris; ecological **Guild:** w; **Sources:** 21.
  9. *Badhamia albescens* (Ellis ex T.Macbr.) J.M.García-Martín, J.C.Zamora & Lado. **Regions:** 1, 2, 11; **Vegetation zones:** extra zonal forest in steppe, forest-steppe, subalpine and alpine; **Method:** FC; **Substrate type:** bark, coarse woody debris, plant litter; ecological **Guild:** n; **Sources:** 15, 17, 21; **Comment:** this is another diverse species complex (Shchepin et al. 2021); specimens from Kazakhstan are the most deviating ones in molecular markers (Azirakhmet et al. 2025) and are likely to constitute a species of its own.
  10. *Badhamia capsulifera* (Bull.) Berk. **Regions:** 1, 11; **Vegetation zones:** extra zonal forest in steppe, forest-steppe; **Method:** FC, both; **Substrate type:** bark, coarse woody debris, plant litter, live mosses; ecological **Guild:** l, w; **Sources:** 17, 21.
  11. *Badhamia foliicola* Lister. **Regions:** 1, 2, 3, 8, 9; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe, semidesert, steppe, forest-steppe, desert; **Method:** MC, FC; **Substrate type:** bark, coarse woody debris, plant litter; ecological **Guild:** w, l; **Sources:** 3, 8, 19, 21.
  12. *Badhamia macrocarpa* (Ces.) Rostaf. **Regions:** 1, 6, 9; **Vegetation zones:** extra zonal forest in steppe, semidesert, steppe; **Method:** MC, FC; **Substrate type:** bark, coarse woody debris, plant litter; ecological **Guild:** l, d; **Sources:** 21.
  13. *Badhamia panicea* (Fr.) Rostaf. **Regions:** 1, 2, 3, 6; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe, semidesert, steppe; **Method:** MC, FC; **Substrate type:** bark, coarse woody debris, plant litter, live mosses; ecological **Guild:** l; **Sources:** 3, 17, 21.
  14. *Badhamia rhytidosperma* H.W. Keller & Schokn. **Regions:** 1; **Vegetation zones:** steppe; **Method:** MC; **Substrate type:** bark; ecological **Guild:** l; **Sources:** 21.
  15. *Badhamia spinispora* (Eliasson & N. Lundq.) H.W. Keller & Schokn. **Regions:** 1, 3, 6, 8, 9, 12; biomes: mountains, steppe, semidesert, desert; **Method:** MC; **Substrate type:** bark, coarse woody debris, plant litter, dung; ecological **Guild:** d, b; **Sources:** 8, 19, 21.
  16. *Badhamia utricularis* (Bull.) Berk. **Regions:** 1, 2, 3, 6, 8, 9; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe, steppe, forest-steppe, desert; **Method:** MC, FC; **Substrate type:** bark, coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 17, 19, 21.
  17. *Badhamia verrucospora* G. Moreno, D.W. Mitch. & Novozh. **Regions:** 3; **Vegetation zones:** extra zonal forest in steppe, semidesert, desert; **Method:** MC; **Substrate type:** bark, plant litter, dung; ecological **Guild:** w; **Sources:** 19.
  18. *Badhamia viridescens* Meyl. **Regions:** 2; **Vegetation zones:** mountain coniferous forest;

- Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** w, d; **Sources:** 17.
19. *Badhamiopsis ainoae* (Yamash.) T.E. Brooks & H.W. Keller. **Regions:** 1; **Vegetation zones:** semidesert; **Method:** FC; **Substrate type:** bark, coarse woody debris; ecological **Guild:** b; **Sources:** 21
  20. *Brefeldia maxima* (Fr.) Rostaf. **Regions:** 2; **Vegetation zones:** mountain coniferous forest; **Method:** FC; **Substrate type:** coarse woody debris; ecological **Guild:** w; **Sources:** 3.
  21. *Calomyxa metallica* (Berk.) Nieuwl. **Regions:** 1, 6; **Vegetation zones:** semidesert; **Method:** MC; **Substrate type:** bark, plant litter; ecological **Guild:** b, w; **Sources:** 21.
  22. *Ceratiomyxa fruticulosa* (O.F. Mull.) T. Macbr. **Regions:** 2, 3, 4, 6; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe; **Method:** FC; **Substrate type:** bark, coarse woody debris; ecological **Guild:** w; **Sources:** 3, 17, 21.
  23. *Claustria didermoides* (Pers.) Fr. **Regions:** 1, 2, 9; **Vegetation zones:** extra zonal forest in steppe, semidesert, steppe, forest-steppe, desert; **Method:** MC, FC; **Substrate type:** bark, coarse woody debris, plant litter, dung; ecological **Guild:** l; **Sources:** 13, 17, 21; **Comment:** syn. *Physarum didermoides*(Pers.) Rostaf.
  24. *Collaria arcyrionema* (Rostaf.) Nann.-Bremek. ex. Lado. **Regions:** 3; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 17.
  25. *Collaria lurida* (Lister) Nann.-Bremek. **Regions:** 1; **Vegetation zones:** semidesert / steppe; **Method:** FC, both; **Substrate type:** bark, coarse woody debris, plant litter; ecological **Guild:** l; **Sources:** 8, 21.
  26. *Comatricha ellae* Hark. **Regions:** 1; **Vegetation zones:** steppe; **Method:** FC; **Substrate type:** coarse woody debris; ecological **Guild:** w; **Sources:** 21.
  27. *Comatricha laxa* Rostaf. **Regions:** 1, 8, 9, 12; **Vegetation zones:** semidesert, steppe, forest-steppe, desert; **Method:** MC, FC; **Substrate type:** bark, coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 8, 13, 19, 21.
  28. *Comatricha nigra* (Pers. ex J.F. Gmel.) J. Schröt. **Regions:** 1, 2, 3; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe, semidesert, forest-steppe; **Method:** MC, FC; **Substrate type:** bark, coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 3, 8, 17, 21.
  29. *Comatricha pulchella* (C. Bab.) Rostaf. **Regions:** 1, 2, 3, 9, 12; **Vegetation zones:** mountain coniferous forest, semidesert, forest-steppe, desert; **Method:** MC, FC; **Substrate type:** bark, coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 13, 17, 21.
  30. *Comatricha tenerrima* (M.A. Curtis) G. Lister. **Regions:** 1; **Vegetation zones:** forest-steppe; **Method:** FC; **Substrate type:** coarse woody debris; ecological **Guild:** w; **Sources:** 21.
  31. *Craterium aureum* (Schumach.) Rostaf. **Regions:** 2, 4; **Vegetation zones:** mountain coniferous forest, forest-steppe; **Method:** FC; **Substrate type:** coarse woody debris, plant litter, live mosses; ecological **Guild:** l, w; **Sources:** 17.
  32. *Craterium leucocephalum* (Pers. ex J.F. Gmel.) Ditmar. **Regions:** 1, 2, 4; **Vegetation zones:** mountain coniferous forest, forest-steppe; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** l, w; **Sources:** 3, 17, 21.
  33. *Craterium minutum* (Leers) Fr. **Regions:** 4; **Vegetation zones:** forest-steppe; **Method:** FC; **Substrate type:** plant litter; ecological **Guild:** l; **Sources:** 17.
  34. *Cribraria argillacea* (Pers. ex J.F. Gmel.) Pers. **Regions:** 3, 6; **Vegetation zones:** mountain coniferous forest, forest-steppe; **Method:** FC; **Substrate type:** bark, coarse woody debris; ecological **Guild:** w; **Sources:** 17.
  35. *Cribraria cancellata* (Batsch) Nann.-Bremek. **Regions:** 1, 2, 3, 4, 6; **Vegetation zones:** mountain coniferous forest, forest-steppe; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 3, 17, 21.
  36. *Cribraria macrocarpa* Schrad. **Regions:** 2, 3; **Vegetation zones:** mountain coniferous forest; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** w; **Sources:**

- 16, 17.
37. *Cribraria mirabilis* (Rostaf.) Masee. **Regions:** 3; **Vegetation zones:** mountain coniferous forest; **Method:** FC; **Substrate type:** coarse woody debris; ecological **Guild:** w; **Sources:** 17.
  38. *Cribraria piriformis* Schrad. **Regions:** 3; **Vegetation zones:** mountain coniferous forest; **Method:** FC; **Substrate type:** coarse woody debris; ecological **Guild:** w; **Sources:** 17.
  39. *Cribraria splendens* (Schrad.) Pers. **Regions:** 3; **Vegetation zones:** mountain coniferous forest; **Method:** FC; **Substrate type:** coarse woody debris; ecological **Guild:** w; **Sources:** 17.
  40. *Cribraria violacea* Rex. **Regions:** 1, 3, 6; **Vegetation zones:** semidesert, steppe, desert; **Method:** MC; **Substrate type:** bark, plant litter; ecological **Guild:** w, b; **Sources:** 19, 21.
  41. *Cribraria vulgaris* Schrad. **Regions:** 3; **Vegetation zones:** mountain coniferous forest; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 17.
  42. *Dianema corticatum* Lister. **Regions:** 1, 6, 9, 12; **Vegetation zones:** semidesert, steppe, desert; **Method:** MC; **Substrate type:** bark, coarse woody debris, plant litter; ecological **Guild:** w, b; **Sources:** 21.
  43. *Dianema harveyi* Rex. **Regions:** 3; **Vegetation zones:** semidesert; **Method:** MC; **Substrate type:** plant litter; ecological **Guild:** w; **Sources:** 19.
  44. *Dictydiaethalium plumbeum* (Schumach.) Rostaf. **Regions:** 5; **Vegetation zones:** mountain coniferous forest; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 3.
  45. *Diderma hemisphaericum* (Bull.) Hornem. **Regions:** 3; **Vegetation zones:** desert; **Method:** MC; **Substrate type:** plant litter; ecological **Guild:** l; **Sources:** 19.
  46. *Diderma meyeri* H. Singer, G. Moreno, Illana & A. Sánchez. **Regions:** 2; **Vegetation zones:** subalpine and alpine; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** n; **Sources:** 1.
  47. *Diderma montanum* (Meyl.) Meyl. **Regions:** 2; **Vegetation zones:** mountain coniferous forest; **Method:** FC; **Substrate type:** coarse woody debris; ecological **Guild:** w; **Sources:** 3.
  48. *Diderma niveum* (Rostaf.) E. Sheld. **Regions:** 2, 3; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe, steppe; **Method:** FC; **Substrate type:** coarse woody debris, plant litter, live mosses; ecological **Guild:** n; **Sources:** 3, 12, 17, 23; **Comment:** this species is reported as strictly nivicolous, but other *Diderma* spp. are often misidentified as *D. niveum*. Records should be critically revised, best applying barcoding (see Shchepin et al. 2024).
  49. *Diderma radiatum* (L.) Morgan. **Regions:** 2, 3; **Vegetation zones:** mountain coniferous forest, subalpine and alpine; **Method:** FC; **Substrate type:** coarse woody debris, plant litter, live mosses; ecological **Guild:** w; **Sources:** 3, 17.
  50. *Diderma testaceum* (Schrad.) Pers. **Regions:** 2; **Vegetation zones:** mountain coniferous forest; **Method:** FC; **Substrate type:** coarse woody debris, plant litter, live mosses; ecological **Guild:** l; **Sources:** 3.
  51. *Diderma tigrinum* (Schrad.) Prikhodko, Shchepin, Novozh., López-Vill., G. Moreno & Schnittler. **Regions:** 2; **Vegetation zones:** mountain coniferous forest; **Method:** FC; **Substrate type:** coarse woody debris, plant litter, live mosses; ecological **Guild:** m, w; **Sources:** 3; **Comment:** syn. *Lepidoderma tigrinum* (Schrad.) Rostaf.
  52. *Didymium anellus* Morgan. **Regions:** 1, 3, 6, 8, 9, 12; **Vegetation zones:** extra zonal forest in steppe, semidesert, steppe, forest-steppe, desert; **Method:** MC, FC; **Substrate type:** bark, coarse woody debris, plant litter, dung; ecological **Guild:** l; **Sources:** 13, 19, 21.
  53. *Didymium annulisporum* H.W. Keller & Schokn. **Regions:** 12; **Vegetation zones:** desert; **Method:** MC; **Substrate type:** dung; ecological **Guild:** l, b; **Sources:** 13.
  54. *Didymium clavus* (Alb. & Schwein.) Rabenh. **Regions:** 1, 2; **Vegetation zones:** mountain coniferous forest, semidesert; **Method:** FC; **Substrate type:** bark, coarse woody debris, plant litter, live mosses; ecological **Guild:** l; **Sources:** 17, 21.
  55. *Didymium comatum* (Lister) Nann.-Bremek. **Regions:** 8; **Vegetation zones:** steppe; **Method:**

- MC; **Substrate type:** plant litter; ecological **Guild:** 1, d; **Sources:** 19.
56. *Didymium crustaceum* Fr. **Regions:** 1; **Vegetation zones:** extra zonal forest in steppe, semidesert, steppe; **Method:** MC, FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** 1; **Sources:** 21.
57. *Didymium difforme* (Pers.) Gray. **Regions:** 1, 2, 3, 5, 6, 8, 9, 12; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe, semidesert, steppe, forest-steppe, desert; **Method:** MC, FC; **Substrate type:** bark, coarse woody debris, plant litter, dung; ecological **Guild:** 1, d; **Sources:** 13, 17, 19, 21; **Comment:** this species has a nivicolous form with larger plasmodiocarps; the records mentioned here concern most likely the lowland form. Molecular investigations are needed to test if we deal with two different taxa here.
58. *Didymium dubium* Rostaf. **Regions:** 1, 2, 3, 8, 9; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe, semidesert, forest-steppe, desert, subalpine and alpine; **Method:** MC, FC; **Substrate type:** bark, coarse woody debris, plant litter; ecological **Guild:** n; **Sources:** 1, 19, 21; **Comment:** a very variable species complex, see as well comments under *D. pseudodecipiens* ad. int.
59. *Didymium inconspicuum* Nann.-Bremek. & D.W. Mitch. **Regions:** 3, 9, 12; **Vegetation zones:** mountain coniferous forest, semidesert, desert; **Method:** MC; **Substrate type:** bark, coarse woody debris, plant litter, dung; ecological **Guild:** 1; **Sources:** 19, 21.
60. *Didymium iridis* (Ditmar) Fr. **Regions:** 1, 9; **Vegetation zones:** semidesert, steppe; **Method:** MC; **Substrate type:** bark, coarse woody debris, plant litter, dung; ecological **Guild:** 1; **Sources:** 21.
61. *Didymium macrospermum* Rostaf. **Regions:** 2; **Vegetation zones:** subalpine and alpine; **Method:** FC; **Substrate type:** coarse woody debris, plant litter, live mosses; ecological **Guild:** x; **Sources:** 17; **Comment:** an enigmatic species described in 1874, no contemporary records are available.
62. *Didymium melanospermum* (Pers.) T. Macbr. **Regions:** 2, 3; **Vegetation zones:** mountain coniferous forest, steppe, subalpine and alpine; **Method:** FC; **Substrate type:** plant litter; ecological **Guild:** 1; **Sources:** 17.
63. *Didymium mexicanum* G. Moreno, Lizarraga & Illana. **Regions:** 1; **Vegetation zones:** semidesert, forest-steppe; **Method:** MC, FC; **Substrate type:** plant litter; ecological **Guild:** 1; **Sources:** 21; **Comment:** records of this species, originally described from deserts of the new world, would need a confirmation supported by barcoding.
64. *Didymium nigripes* (Link) Fr. **Regions:** 1, 4, 5, 9; **Vegetation zones:** semidesert, forest-steppe; **Method:** MC, FC; **Substrate type:** bark, coarse woody debris, plant litter, live mosses; ecological **Guild:** 1; **Sources:** 17, 21.
65. *Didymium phloiogenum* (M.Blackw. & Alexop.) J.M. García-Martín & Lado. **Regions:** 1, 9, 12; **Vegetation zones:** extra zonal forest in steppe, semidesert, steppe, desert; **Method:** MC; **Substrate type:** bark, plant litter; ecological **Guild:** b; **Sources:** 13, 21; **Comment:** syn. *Protophysarum phloiogenum* M. Blackw. & Alexop. See Schnittler (2001) for an ecological characterization of this tiny corticolous species.
66. *Didymium "pseudodecipiens"* ad int. **Regions:** 2; **Vegetation zones:** subalpine and alpine; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** n; **Sources:** 1; **Comment:** this tentatively described species belongs to the complex of *Didymium dubium*, all species are nivicolous. See Azirakhmet et al. (2025) for a description.
67. *Didymium serpula* Fr. **Regions:** 2; **Vegetation zones:** mountain coniferous forest; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** 1; **Sources:** 17.
68. *Didymium spongiosum* (Leyss.) J.M. García-Martín, J.C. Zamora & Lado. **Regions:** 1, 2, 3, 4, 5, 6, 13; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe, forest-steppe, desert, subalpine and alpine regions; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** 1; **Sources:** 3, 17, 21; **Comment:** syn. *Mucilago crustacea* F.H. Wigg.
69. *Didymium squamulosum* (Alb. & Schwein.) Fr. **Regions:** 1, 2, 3, 6, 7, 9, 12; **Vegetation zones:**

- mountain coniferous forest, semidesert, steppe, forest-steppe; **Method:** MC, FC; **Substrate type:** bark, coarse woody debris, plant litter, live mosses, dung; ecological **Guild:** l; **Sources:** 13, 17, 19, 21.
70. *Didymium trachysporum* G. Lister. **Regions:** 1, 3, 8, 9, 12; **Vegetation zones:** semidesert, steppe, desert; **Method:** MC; **Substrate type:** bark, coarse woody debris, plant litter, dung; ecological **Guild:** l; **Sources:** 19, 21.
71. *Echinostelium arboreum* H.W. Keller & T.E. Brooks. **Regions:** 1, 12; **Vegetation zones:** mountain coniferous forest, semidesert, steppe, forest-steppe, desert; **Method:** MC; **Substrate type:** bark, coarse woody debris; ecological **Guild:** b; **Sources:** 13; **Comment:** see Schnittler (2001) for an ecological characterization of this tiny corticolous species.
72. *Echinostelium brooksii* K.D. Whitney. **Regions:** 6; **Vegetation zones:** semidesert; **Method:** MC; **Substrate type:** bark; ecological **Guild:** b; **Sources:** 21; **Comment:** see Schnittler (2001) for an ecological characterization of this and the following three *Echinostelium* spp., all are corticolous and form minute sporocarps visible only in moist chamber cultures.
73. *Echinostelium coelocephalum* T.E. Brooks & H.W. Keller. **Regions:** 9; **Vegetation zones:** desert; **Method:** MC; **Substrate type:** bark; ecological **Guild:** b; **Sources:** 21.
74. *Echinostelium colliculosum* K.D. Whitney & H.W. Keller. **Regions:** 1, 3, 6, 8, 9, 12; **Vegetation zones:** extra zonal forest in steppe, semidesert, steppe, forest-steppe, desert; **Method:** MC; **Substrate type:** bark, coarse woody debris, plant litter; ecological **Guild:** b; **Sources:** 13, 19, 21.
75. *Echinostelium elachiston* Alexop. **Regions:** 9; **Vegetation zones:** semidesert, steppe; **Method:** MC; **Substrate type:** bark, coarse woody debris; ecological **Guild:** b; **Sources:** 21.
76. *Echinostelium minutum* de Bary. **Regions:** 1, 3, 6, 8, 9, 12; **Vegetation zones:** semidesert, steppe, forest-steppe, desert; **Method:** MC; **Substrate type:** bark, coarse woody debris, plant litter, dung; ecological **Guild:** b, w; **Sources:** 13, 19, 21; **Comment:** this is the largest species of the genus and can be occasionally observed in the field.
77. *Enteridium olivaceum* Ehrenb. **Regions:** 2, 3, 14; **Vegetation zones:** mountain coniferous forest, forest-steppe; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 3, 17. **Comment:** syn. *Reticularia olivacea* (Ehrenb.) Fr.
78. *Fuligo cinerea* (Schwein.) Morgan. **Regions:** 1, 3, 6, 8, 9, 12; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe, semidesert, steppe, forest-steppe, desert; **Method:** MC; **Substrate type:** bark, coarse woody debris, plant litter, dung; ecological **Guild:** l, d; **Sources:** 13, 19, 21.
79. *Fuligo intermedia* T. Macbr. **Regions:** 1, 2; **Vegetation zones:** mountain coniferous forest, forest-steppe; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 17, 21.
80. *Fuligo muscorum* Alb. & Schwein. **Regions:** 3; **Vegetation zones:** mountain coniferous forest; **Method:** FC; **Substrate type:** plant litter; ecological **Guild:** l; **Sources:** 3.
81. *Fuligo septica* (L.) F.H. Wigg. **Regions:** 1, 2, 3, 4, 5, 6, 11, 14, 15; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe, semidesert, forest-steppe, desert, subalpine and alpine; **Method:** FC; **Substrate type:** bark, coarse woody debris, plant litter, dung; ecological **Guild:** w; **Sources:** 3, 16, 17, 21, 23, 24.
82. *Gulielmina vermicularis* (Schwein.) García-Cunch., J.C. Zamora & Lado. **Regions:** 1, 3, 8, 9, 12; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe, semidesert, steppe, forest-steppe, desert; **Method:** MC, FC; **Substrate type:** bark, coarse woody debris, plant litter, dung; ecological **Guild:** w, b; **Sources:** 13, 19, 21; **Comment:** syn. *Perichaena vermicularis* (Schwein.) Rostaf.
83. *Hemitrichia abietina* (Wigand) G. Lister. **Regions:** 3; **Vegetation zones:** subalpine and alpine; **Method:** FC; **Substrate type:** bark; ecological **Guild:** w; **Sources:** 17.
84. *Hemitrichia clavata* (Pers.) Rostaf. **Regions:** 2, 3; **Vegetation zones:** mountain coniferous forest, forest-steppe; **Method:** FC; **Substrate type:** bark, coarse woody debris, plant litter, live mosses; ecological **Guild:** w; **Sources:** 17.

85. *Hemitrichia decipiens* (Pers.) García-Cunch., J.C. Zamora & Lado. **Regions:** 2, 3; **Vegetation zones:** mountain coniferous forest, forest-steppe; **Method:** FC; **Substrate type:** bark, coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 17, 23.
86. *Hemitrichia karstenii* (Rostaf.) Lister. **Regions:** 1, 2, 6; **Vegetation zones:** forest-steppe, subalpine and alpine; **Method:** MC, FC; **Substrate type:** bark, coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 17, 21.
87. *Hemitrichia leiotricha* (Lister) G. Lister. **Regions:** 3; **Vegetation zones:** mountain coniferous forest, forest-steppe; **Method:** FC; **Substrate type:** bark, live mosses; ecological **Guild:** w; **Sources:** 17.
88. *Hemitrichia minor* G. Lister. **Regions:** 3; **Vegetation zones:** mountain coniferous forest; **Method:** FC; **Substrate type:** bark, coarse woody debris, plant litter; ecological **Guild:** w, b; **Sources:** 17.
89. *Hemitrichia pardina* (Minakata) Ing. **Regions:** 1, 3, 6, 9; **Vegetation zones:** extra zonal forest in steppe, semidesert, forest-steppe, subalpine and alpine; **Method:** MC; **Substrate type:** plant litter; ecological **Guild:** l; **Sources:** 19, 21.
90. *Hemitrichia serpula* (Scop.) Rostaf. ex Lister. **Regions:** 2, 5; **Vegetation zones:** mountain coniferous forest, forest-steppe; **Method:** FC; **Substrate type:** bark, coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 17.
91. *Heterotrichia ferruginea* (Saut.) Yatsiuk, Leontyev & Schnittler. **Regions:** 2, 3, 5; **Vegetation zones:** mountain coniferous forest, forest-steppe; **Method:** FC; **Substrate type:** bark, coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 3, 17; **Comment:** syn. *Arcyria ferruginea* Saut.
92. *Heterotrichia insignis* (Kalchbr. & Cooke) Yatsiuk, Leontyev & Schnittler. **Regions:** 1, 3; **Vegetation zones:** mountain coniferous forest, forest-steppe; **Method:** FC; **Substrate type:** bark, coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 17, 21; **Comment:** syn. *Arcyria insignis* Kalchbr. & Cooke.
93. *Heterotrichia obvelata* (Oeder) Yatsiuk, Leontyev & Schnittler. **Regions:** 2, 3, 4, 5; **Vegetation zones:** mountain coniferous forest, forest-steppe; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 3, 17; **Comment:** syn. *Arcyria obvelata* (Oeder) Onsberg.
94. *Heterotrichia oerstedii* (Rostaf.) Yatsiuk, Leontyev & Schnittler. **Regions:** 2, 3, 5; **Vegetation zones:** mountain coniferous forest, forest-steppe; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 17; **Comment:** syn. *Arcyria oerstedii* Rostaf.
95. *Heterotrichia pomiformis* (Leers) Yatsiuk, Leontyev & Schnittler. **Regions:** 1, 9; **Vegetation zones:** semidesert, forest-steppe; **Method:** MC, FC; **Substrate type:** bark, coarse woody debris; ecological **Guild:** w; **Sources:** 8, 21; **Comment:** syn. *Arcyria pomiformis* (Leers) Rostaf.
96. *Kelleromyxa fimicola* (Dearn. & Bisby) Eliasson. **Regions:** 1, 8; **Vegetation zones:** semidesert, steppe; **Method:** MC; **Substrate type:** dung; ecological **Guild:** d; **Sources:** 19, 21.
97. *Lamproderma aeneum* Mar. Mey. & Poulain. **Regions:** 2; **Vegetation zones:** subalpine and alpine; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** n; **Sources:** 1.
98. *Lamproderma arcyrioides* (Sommerf.) Rostaf. **Regions:** 2; **Vegetation zones:** extra zonal forest in steppe; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** b; **Sources:** 17.
99. *Lamproderma columbinum* (Pers.) Rostaf. **Regions:** 2, 3; **Vegetation zones:** mountain coniferous forest; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** m, w; **Sources:** 3, 17.
100. *Lamproderma cucumer* (Meyl.) Nowotny & H. Neubert. **Regions:** 2; **Vegetation zones:** mountain coniferous forest; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** n; **Sources:** 1; **Comment:** one of the species of the *L. ovoideum* complex;

future revisions will show if it deserves recognition. Usually recognized by elongated, sausage-shaped sporocarps.

101. *Lamproderma echinosporum* Meyl. **Regions:** 2; **Vegetation zones:** mountain coniferous forest; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** n; **Sources:** 1.
102. *Lamproderma ovoideochinulatum* Mar. Mey. & Poulain. **Regions:** 2; **Vegetation zones:** mountain coniferous forest; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** n; **Sources:** 1; **Comment:** another species of the *L. ovoideum* complex represented by a different group of DNA barcodes. The distinguishing morphological character is spores ornamented with longer spines than in *L. ovoideum*.
103. *Lamproderma ovoideum* Meyl. **Regions:** 2; **Vegetation zones:** mountain coniferous forest; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** n; **Sources:** 1.
104. *Lamproderma sauteri* Rostaf. **Regions:** 2; **Vegetation zones:** mountain coniferous forest; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** n; **Sources:** 1.
105. *Lamproderma scintillans* (Berk. & Broome) Morgan. **Regions:** 1, 6; **Vegetation zones:** semidesert, forest-steppe; **Method:** MC, FC; **Substrate type:** bark, coarse woody debris, plant litter; ecological **Guild:** l; **Sources:** 21.
106. *Lamproderma zonatopulchellum* Yatsiuk, Leontyev, López-Vill. & Schnittler. **Regions:** 2; **Vegetation zones:** mountain coniferous forest; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** n; **Sources:** 1; **Comment:** a recently described species (Yatsiuk et al. 2024); rare but widely distributed.
107. *Leocarpus fragilis* (Dicks.) Rostaf. **Regions:** 2, 4, 6; **Vegetation zones:** mountain coniferous forest, forest-steppe; **Method:** FC; **Substrate type:** coarse woody debris, plant litter, live mosses; ecological **Guild:** l; **Sources:** 3, 17.
108. *Licea belmontiana* Nann.-Bremek. **Regions:** 1, 3, 8, 9; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe, semidesert, forest-steppe, desert; **Method:** MC; **Substrate type:** bark, plant litter; ecological **Guild:** w, b; **Sources:** 19, 21.
109. *Licea biforis* Morgan. **Regions:** 1, 3, 12; **Vegetation zones:** extra zonal forest in steppe, semidesert; **Method:** MC; **Substrate type:** bark, plant litter; ecological **Guild:** w, b; **Sources:** 13, 19, 21.
110. *Licea castanea* G. Lister. **Regions:** 8; **Vegetation zones:** forest-steppe; **Method:** MC; **Substrate type:** plant litter; ecological **Guild:** w; **Sources:** 19.
111. *Licea chelonoides* Nann.-Bremek. **Regions:** 9; **Vegetation zones:** semidesert; **Method:** MC; **Substrate type:** bark; ecological **Guild:** w, b; **Sources:** 21.
112. *Licea denudescens* H.W. Keller & T.E. Brooks. **Regions:** 1, 3, 6, 8, 9, 12; **Vegetation zones:** extra zonal forest in steppe, semidesert, steppe, desert, subalpine and alpine; **Method:** MC; **Substrate type:** bark, coarse woody debris, plant litter, dung; ecological **Guild:** w, b; **Sources:** 13, 19, 21.
113. *Licea kleistobolus* G.W. Martin. **Regions:** 1, 3, 8, 9, 12; **Vegetation zones:** mountain coniferous forest, semidesert, steppe, forest-steppe, desert; **Method:** MC; **Substrate type:** bark, plant litter; ecological **Guild:** w, b; **Sources:** 13, 19, 21.
114. *Licea minima* Fr. **Regions:** 3; **Vegetation zones:** mountain coniferous forest; **Method:** FC; **Substrate type:** bark, coarse woody debris; ecological **Guild:** w; **Sources:** 17.
115. *Licea nannengae* Pando & Lado. **Regions:** 1, 3, 6, 8, 9, 12; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe, semidesert, steppe, forest-steppe, desert; **Method:** MC; **Substrate type:** bark, coarse woody debris, plant litter, dung; ecological **Guild:** w, b; **Sources:** 19, 21.
116. *Licea operculata* (Wingate) G.W. Martin. **Regions:** 6, 9; **Vegetation zones:** semidesert, desert; **Method:** MC; **Substrate type:** plant litter; ecological **Guild:** w, b; **Sources:** 21.
117. *Licea parasitica* (Zukal) G.W. Martin. **Regions:** 1, 3, 6, 8, 9, 12; **Vegetation zones:** mountain

- coniferous forest, extra zonal forest in steppe, semidesert, steppe, forest-steppe, desert; **Method:** MC; **Substrate type:** bark, coarse woody debris, plant litter, dung; ecological **Guild:** w, b; **Sources:** 19, 21.
118. *Licea pusilla* Schrad. **Regions:** 1, 9; **Vegetation zones:** semidesert; **Method:** MC; **Substrate type:** bark, plant litter; ecological **Guild:** w, b; **Sources:** 21.
119. *Licea rugosa* Nann.-Bremek. & Y. Yamam. **Regions:** 8; **Vegetation zones:** steppe; **Method:** MC; **Substrate type:** plant litter; ecological **Guild:** w, l; **Sources:** 19.
120. *Licea tenera* E. Jahn. **Regions:** 1, 3; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe, desert; **Method:** MC, FC; **Substrate type:** bark, coarse woody debris, plant litter, dung; ecological **Guild:** l, d; **Sources:** 17, 19, 21.
121. *Licea variabilis* Schrad. **Regions:** 3; **Vegetation zones:** mountain coniferous forest; **Method:** FC; **Substrate type:** bark, coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 17.
122. *Lindbladia tubulina* Fr. **Regions:** 3; **Vegetation zones:** forest-steppe; **Method:** FC; **Substrate type:** bark, coarse woody debris, plant litter, live mosses; ecological **Guild:** w; **Sources:** 17.
123. *Lycogala epidendrum* (L.) Fr. **Regions:** 1, 2, 3, 4, 5, 6, 16; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe, forest-steppe; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 3, 21, 23, 24; **Comment:** this name stands here for the whole complex, not *L. epidendrum* s. str., as the collections have not been revised in the light of recent papers of Leontyev et al. (2023, 2025).
124. *Lycogala exiguum* Morgan. **Regions:** 2; **Vegetation zones:** mountain coniferous forest; **Method:** FC; **Substrate type:** coarse woody debris; ecological **Guild:** w; **Sources:** 17.
125. *Lycogala flavofuscum* (Ehrenb.) Rostaf. **Regions:** 1, 2, 3, 4, 5, 6, 15; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe, forest-steppe; **Method:** FC; **Substrate type:** coarse woody debris; ecological **Guild:** w; **Sources:** 3, 17, 21.
126. *Macbrideola cornea* (G. Lister & Cran) Alexop. **Regions:** 1; **Vegetation zones:** extra zonal forest in steppe, semidesert; **Method:** MC; **Substrate type:** bark; ecological **Guild:** b; **Sources:** 21.
127. *Macbrideola oblonga* Pando & Lado. **Regions:** 1, 3, 6, 8, 9, 12; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe, semidesert, steppe, forest-steppe, desert; **Method:** MC; **Substrate type:** bark, coarse woody debris, plant litter; ecological **Guild:** b; **Sources:** 13, 19, 21.
128. *Meriderma carestiae* (Ces. & De Not.) Mar. Mey. & Poulain. **Regions:** 2; **Vegetation zones:** subalpine and alpine; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** n; **Sources:** 1.
129. *Meriderma cribrarioides* (Fr.) Mar. Mey. & Poulain. **Regions:** 2; **Vegetation zones:** subalpine and alpine; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** n; **Sources:** 1.
130. *Metatrichia floriformis* (Schwein.) Nann.-Bremek. **Regions:** 3; **Vegetation zones:** mountain coniferous forest; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 17.
131. *Metatrichia vesparia* (Batsch) Nann.-Bremek. ex G.W. Martin & Alexop. **Regions:** 2, 3, 4, 5, 6, 14; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe, steppe, forest-steppe; **Method:** FC; **Substrate type:** bark, coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 3, 17, 21.
132. *Nannengaella alpina* (Lister & G.Lister) J.M. García-Martín, J.C. Zamora & Lado. **Regions:** 3; **Vegetation zones:** mountain coniferous forest; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** n; **Sources:** 17; **Comment:** syn. *Physarum alpinum* (Lister & G.Lister) G.Lister.
133. *Nannengaella contexta* (Pers.) J.M. García-Martín, J.C. Zamora & Lado. **Regions:** 2, 3, 4, 5, 6; **Vegetation zones:** mountain coniferous forest, steppe, forest-steppe; **Method:** FC; **Substrate type:** coarse woody debris, plant litter, live mosses; ecological **Guild:** l; **Sources:** 17; **Comment:** syn. *Physarum contextum* (Pers.) Pers.

134. *Nannengaella sulphurea* (Alb. & Schwein.) J.M. García-Martín, J.C. Zamora & Lado. **Regions:** 5; **Vegetation zones:** forest-steppe; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** l, w; **Sources:** 17; **Comment:** syn. *Physarum sulphureum* Alb. & Schwein.
135. *Neodiderma spumarioides* (Fr. & Palmquist) X.F. Li, B. Zhang & Yu Li. **Regions:** 1, 2, 13; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe, subalpine and alpine; **Method:** FC; **Substrate type:** coarse woody debris, plant litter, live mosses; ecological **Guild:** l; **Sources:** 3, 17, 21; **Comment:** syn. *Diderma spumarioides* (Fr. & Palmquist) Fr.
136. *Oligonema affine* (de Bary) García-Cunch., J.C. Zamora & Lado. **Regions:** 2, 3; **Vegetation zones:** mountain coniferous forest, forest-steppe; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 17; **Comment:** syn. *Trichia affinis* de Bary.
137. *Oligonema favogineum* (Batsch) García-Cunch., J.C. Zamora & Lado. **Regions:** 2, 3; **Vegetation zones:** mountain coniferous forest, forest-steppe; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 3, 17; **Comment:** syn. *Trichia favoginea* (Batsch) Pers.
138. *Oligonema flavidum* (Peck) Peck. **Regions:** 1; **Vegetation zones:** forest-steppe; **Method:** FC; **Substrate type:** coarse woody debris; ecological **Guild:** w; **Sources:** 21.
139. *Oligonema persimile* (P. Karst.) García-Cunch., J.C. Zamora & Lado. **Regions:** 2, 3; **Vegetation zones:** mountain coniferous forest; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 17; **Comment:** syn. *Trichia persimilis* P.Karst.
140. *Oligonema schweinitzii* (Berk.) G.W. Martin. **Regions:** 1, 3, 5; **Vegetation zones:** extra zonal forest in steppe, forest-steppe; **Method:** FC; **Substrate type:** bark, coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 17, 21.
141. *Ophiotheca chrysosperma* Curr. **Regions:** 1, 2, 6, 8, 9; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe, semidesert, steppe; **Method:** MC, FC; **Substrate type:** bark, coarse woody debris, plant litter; ecological **Guild:** w, b; **Sources:** 17, 19, 21; **Comment:** syn. *Perichaena chrysosperma* (Curr.) Lister.
142. *Ophiotheca pedata* (Lister & G.Lister) García-Cunch., J.C. Zamora & Lado. **Regions:** 1, 6, 12; **Vegetation zones:** extra zonal forest in steppe, semidesert, desert; **Method:** MC; **Substrate type:** plant litter; ecological **Guild:** l; **Sources:** 21; **Comment:** syn. *Perichaena pedata* (Lister & G. Lister) Lister ex E. Jahn.
143. *Paradiacheopsis cribrata* Nann.-Bremek. **Regions:** 12; **Vegetation zones:** extra zonal forest in steppe, desert; **Method:** MC; **Substrate type:** bark; ecological **Guild:** b; **Sources:** 21.
144. *Paradiacheopsis fimbriata* (G. Lister & Cran) Hertel ex Nann.-Bremek. **Regions:** 3; **Vegetation zones:** mountain coniferous forest; **Method:** FC; **Substrate type:** coarse woody debris; ecological **Guild:** b; **Sources:** 17.
145. *Perichaena corticalis* (Batsch) Rostaf. **Regions:** 1, 2, 3, 6, 8, 9, 12; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe, semidesert, steppe, desert; **Method:** MC, FC; **Substrate type:** bark, coarse woody debris, plant litter, dung; ecological **Guild:** w, b; **Sources:** 13, 17, 19, 21.
146. *Perichaena depressa* Lib. **Regions:** 1, 2, 3, 6, 8, 9, 12; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe, semidesert, steppe, forest-steppe, desert, subalpine and alpine; **Method:** M C, FC; **Substrate type:** bark, coarse woody debris, plant litter, dung; ecological **Guild:** l; **Sources:** 13, 17, 19, 21.
147. *Perichaena liceoides* Rostaf. **Regions:** 1, 2, 3, 6, 8, 9, 12; **Vegetation zones:** mountain coniferous forest, semidesert, steppe, forest-steppe, desert; **Method:** MC, FC; **Substrate type:** bark, coarse woody debris, plant litter, dung; ecological **Guild:** d, w; **Sources:** 13, 17, 19, 21.
148. *Perichaena luteola* (Kowalski) Gilert. **Regions:** 1, 3, 8, 9; **Vegetation zones:** semidesert, steppe, desert; **Method:** MC; **Substrate type:** plant litter, dung; ecological **Guild:** d, l; **Sources:** 19, 21.
149. *Perichaena polygonospora* Novozh., Zemly., Schnittler & S.L. Stephenson. **Regions:** 1, 2, 3,

- 9, 11; **Vegetation zones:** extra zonal forest in steppe, steppe, desert; **Method:** MC; **Substrate type:** bark, plant litter; ecological **Guild:** b; **Sources:** 9, 19, 21.
150. *Perichaena quadrata* T. Macbr. **Regions:** 1, 3, 8, 9, 12; **Vegetation zones:** extra zonal forest in steppe, semidesert, steppe, forest-steppe, desert, subalpine and alpine; **Method:** MC; **Substrate type:** bark, coarse woody debris, plant litter, dung; ecological **Guild:** w, b; **Sources:** 19, 21.
151. *Physarum album* (Bull.) Chevall. **Regions:** 1, 2, 3, 4, 6; **Vegetation zones:** forest-steppe, subalpine and alpine; **Method:** FC; **Substrate type:** bark, coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 3, 17, 21; **Comment:** syn. *Physarum nutans* Pers.
152. *Physarum altaicum* Lavrov. **Regions:** 3; **Vegetation zones:** mountain coniferous forest; **Method:** FC; **Substrate type:** coarse woody debris; ecological **Guild:** x; **Sources:** 17; **Comment:** an enigmatic species, no contemporary records are available.
153. *Physarum apiculosporum* Hark. **Regions:** 1, 3, 9; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe, semidesert, desert; **Method:** MC; **Substrate type:** bark, coarse woody debris, plant litter, dung; ecological **Guild:** d; **Sources:** 8, 19, 21.
154. *Physarum cinereum* (Batsch) Pers. **Regions:** 1, 2, 3, 5, 9, 12, 17; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe, semidesert, forest-steppe, desert; **Method:** MC, FC; **Substrate type:** bark, coarse woody debris, plant litter, dung; ecological **Guild:** l; **Sources:** 3, 13, 17, 19, 21, 24.
155. *Physarum compressum* Alb. & Schwein. **Regions:** 1, 2, 3, 4, 9; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe, semidesert, forest-steppe, desert; **Method:** MC, FC; **Substrate type:** bark, coarse woody debris, plant litter; ecological **Guild:** l; **Sources:** 3, 17, 19, 21.
156. *Physarum confertum* T. Macbr. **Regions:** 12; **Vegetation zones:** mountain coniferous forest, semidesert; **Method:** MC; **Substrate type:** bark; ecological **Guild:** l; **Sources:** 13.
157. *Physarum decipiens* M.A. Curtis. **Regions:** 1, 3, 6, 8, 9, 12; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe, semidesert, forest-steppe, desert; **Method:** MC, both; **Substrate type:** bark, coarse woody debris, plant litter; ecological **Guild:** b, w; **Sources:** 13, 19, 21.
158. *Physarum diderma* Rostaf. **Regions:** 2, 3, 4, 12; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe, semidesert, steppe; **Method:** MC, FC; **Substrate type:** bark, coarse woody debris, plant litter; ecological **Guild:** l, w; **Sources:** 3, 17, 19, 21.
159. *Physarum famintzinii* Rostaf. **Regions:** 3; **Vegetation zones:** mountain coniferous forest; **Method:** FC; **Substrate type:** coarse woody debris; ecological **Guild:** w; **Sources:** 17.
160. *Physarum flavicomum* Berk. **Regions:** 3; **Vegetation zones:** mountain coniferous forest; **Method:** FC; **Substrate type:** coarse woody debris, plant litter, live mosses; ecological **Guild:** w; **Sources:** 17.
161. *Physarum gyrosum* Rostaf. **Regions:** 1, 12; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe, semidesert, desert; **Method:** MC; **Substrate type:** bark, coarse woody debris, plant litter, dung; ecological **Guild:** l, d; **Sources:** 21.
162. *Physarum leucophaeum* Fr. **Regions:** 1; **Vegetation zones:** forest-steppe; **Method:** FC; **Substrate type:** bark, coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 21
163. *Physarum leucopus* Link. **Regions:** 1, 4; **Vegetation zones:** extra zonal forest in steppe, forest-steppe; **Method:** MC, FC; **Substrate type:** bark, coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 17, 21.
164. *Physarum megalosporum* T. Macbr. **Regions:** 1; **Vegetation zones:** forest-steppe; **Method:** MC; **Substrate type:** bark; ecological **Guild:** x; **Sources:** 21.
165. *Physarum pseudonotabile* Novozh., Schnittler & Okun. **Regions:** 1, 3, 6, 8, 9, 12; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe, semidesert, steppe, forest-steppe, desert; **Method:** MC, FC; **Substrate type:** bark, coarse woody debris, plant litter, dung; ecological **Guild:** d, l; **Sources:** 10, 19, 21; **Comment:** widely distributed in steppe and semi desert, readily fruiting in moist chambers (Novozhilov et al. 2013).

166. *Physarum pusillum* (Berk. & M.A. Curtis) G. Lister. **Regions:** 1; **Vegetation zones:** extra zonal forest in steppe; **Method:** MC; **Substrate type:** coarse woody debris; ecological **Guild:** l; **Sources:** 21.
167. *Physarum rubiginosum* Fr. & Palmquist. **Regions:** 3; **Vegetation zones:** subalpine and alpine; **Method:** FC; **Substrate type:** coarse woody debris, plant litter, live mosses; ecological **Guild:** w; **Sources:** 17.
168. *Physarum straminipes* Lister. **Regions:** 1, 6; **Vegetation zones:** forest-steppe; **Method:** MC; **Substrate type:** bark, plant litter; ecological **Guild:** l; **Sources:** 21.
169. *Physarum vernum* Sommerf. **Regions:** 1, 2, 9; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe, semidesert, forest-steppe; **Method:** MC, FC; **Substrate type:** bark, coarse woody debris, plant litter; ecological **Guild:** n; **Sources:** 1, 21.
170. *Physarum viride* (Bull.) Pers. **Regions:** 2, 3, 4, 5; **Vegetation zones:** mountain coniferous forest, forest-steppe; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 3, 17.
171. *Polyschismium carestianum* (Rabenh.) A. Ronikier, J.M. García-Martin, A. Kuhnt, J.C. Zamora, M. de Haan, Janik & Lado. **Regions:** 2; **Vegetation zones:** mountain coniferous forest; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** n; **Sources:** 1; **Comment:** syn. *Lepidoderma carestianum* (Rabenh.) Rostaf.
172. *Reticularia lycoperdon* Bull. **Regions:** 2, 3, 4, 5, 6, 15; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe, forest-steppe; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 3, 17.
173. *Reticularia splendens* Morgan. **Regions:** 2, 3; **Vegetation zones:** mountain coniferous forest, steppe; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 17.
174. *Stemonitis axifera* (Bull.) T. Macbr. **Regions:** 1, 2, 3, 4, 5, 6; **Vegetation zones:** mountain coniferous forest, forest-steppe; **Method:** FC; **Substrate type:** bark, coarse woody debris, plant litter, live mosses; ecological **Guild:** w; **Sources:** 3, 17, 21.
175. *Stemonitis flavogenita* E. Jahn. **Regions:** 3, 4; **Vegetation zones:** mountain coniferous forest, forest-steppe; **Method:** FC; **Substrate type:** bark, coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 17.
176. *Stemonitis fusca* Roth. **Regions:** 1, 2, 3, 4, 5, 9; **Vegetation zones:** mountain coniferous forest, semidesert, steppe, forest-steppe, subalpine and alpine; **Method:** MC, FC; **Substrate type:** bark, coarse woody debris, plant litter, live mosses; ecological **Guild:** w; **Sources:** 3, 16, 17, 21.
177. *Stemonitis herbatica* Peck. **Regions:** 6; **Vegetation zones:** forest-steppe; **Method:** FC; **Substrate type:** coarse woody debris; ecological **Guild:** w, l; **Sources:** 21.
178. *Stemonitis pallida* Wingate. **Regions:** 1; **Vegetation zones:** forest-steppe; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** w, l; **Sources:** 21.
179. *Stemonitis splendens* Rostaf. **Regions:** 1, 2, 3, 4, 5, 6, 15; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe, forest-steppe; **Method:** FC; **Substrate type:** bark, coarse woody debris, plant litter, live mosses; ecological **Guild:** w; **Sources:** 3, 17, 21.
180. *Stemonitis virginiensis* Rex. **Regions:** 12; **Vegetation zones:** extra zonal forest in steppe; **Method:** MC; **Substrate type:** bark; ecological **Guild:** w; **Sources:** 13.
181. *Stemonitopsis hyperopta* (Meyl.) Nann.-Bremek. **Regions:** 1; **Vegetation zones:** extra zonal forest in steppe; **Method:** FC; **Substrate type:** coarse woody debris; ecological **Guild:** w; **Sources:** 21.
182. *Stemonitopsis typhina* (F.H.Wigg.) Nann.-Bremek. **Regions:** 2, 3, 5; **Vegetation zones:** mountain coniferous forest, forest-steppe; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 3, 17; **Comment:** syn. *Comatricha typhoides* (Bull.) Rostaf.
183. *Symphytocarpus confluens* (Cooke & Ellis) Ing & Nann.-Bremek. **Regions:** 1, 2, 3; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe; **Method:** FC; **Substrate type:**

- bark, coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 17, 21.
184. *Trichia alpina* (R.E. Fr.) Meyl. **Regions:** 2; **Vegetation zones:** subalpine and alpine; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** n; **Sources:** 1.
185. *Trichia botrytis* (J.F. Gmel.) Pers. **Regions:** 2, 3; **Vegetation zones:** mountain coniferous forest; **Method:** FC; **Substrate type:** bark, coarse woody debris, plant litter; ecological **Guild:** w, l; **Sources:** 17; **Comment:** a species complex, see Bortnikov et al. (2023).
186. *Trichia contorta* (Ditmar) Rostaf. **Regions:** 1, 2, 3, 6; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 3, 17, 21.
187. *Trichia scabra* Rostaf. **Regions:** 2, 3, 5; **Vegetation zones:** mountain coniferous forest, forest-steppe; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 17.
188. *Trichia subfusca* Rex. **Regions:** 3; **Vegetation zones:** mountain coniferous forest; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 17.
189. *Trichia varia* (Pers. ex J.F. Gmel.) Pers. **Regions:** 2, 3, 4, 5, 11; **Vegetation zones:** mountain coniferous forest, forest-steppe; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 3, 17, 24.
190. *Tubifera ferruginosa* (Batsch) J.F. Gmel. **Regions:** 2, 3, 4, 5, 6, 11; **Vegetation zones:** mountain coniferous forest, extra zonal forest in steppe, forest-steppe; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 17; **Comment:** a species complex, reports before 2015 can only be assigned to the whole complex, see Leontyev et al. (2015).
191. *Willkommlangea reticulata* (Alb. & Schwein.) Kuntze. **Regions:** 5; **Vegetation zones:** forest-steppe; **Method:** FC; **Substrate type:** coarse woody debris, plant litter; ecological **Guild:** w; **Sources:** 17.

**Table 1** Literature sources reporting records of 193 myxomycete species from 26 papers covering Kazakhstan (full citations appear in the reference list). Abbreviations: Coll = specimen collection technique, FC = field collection, MC = moist chamber culture; Rec = records (number of records considered for this checklist).

Source number	References	Comment	Coll	Rec
1	Azirakhmet et al. (2025)	Reports first survey for nivicolous myxomycetes from Kazakhstan	FC	16
2	Golovenko (1957)	All records listed are included in Golovenko (1960).	FC	0
3	Golovenko (1960)	The first checklist for myxomycetes from Kazakhstan.	FC	72
4	Golovenko (1965)	All records included in Vasyagina et al. (1977).	FC	0

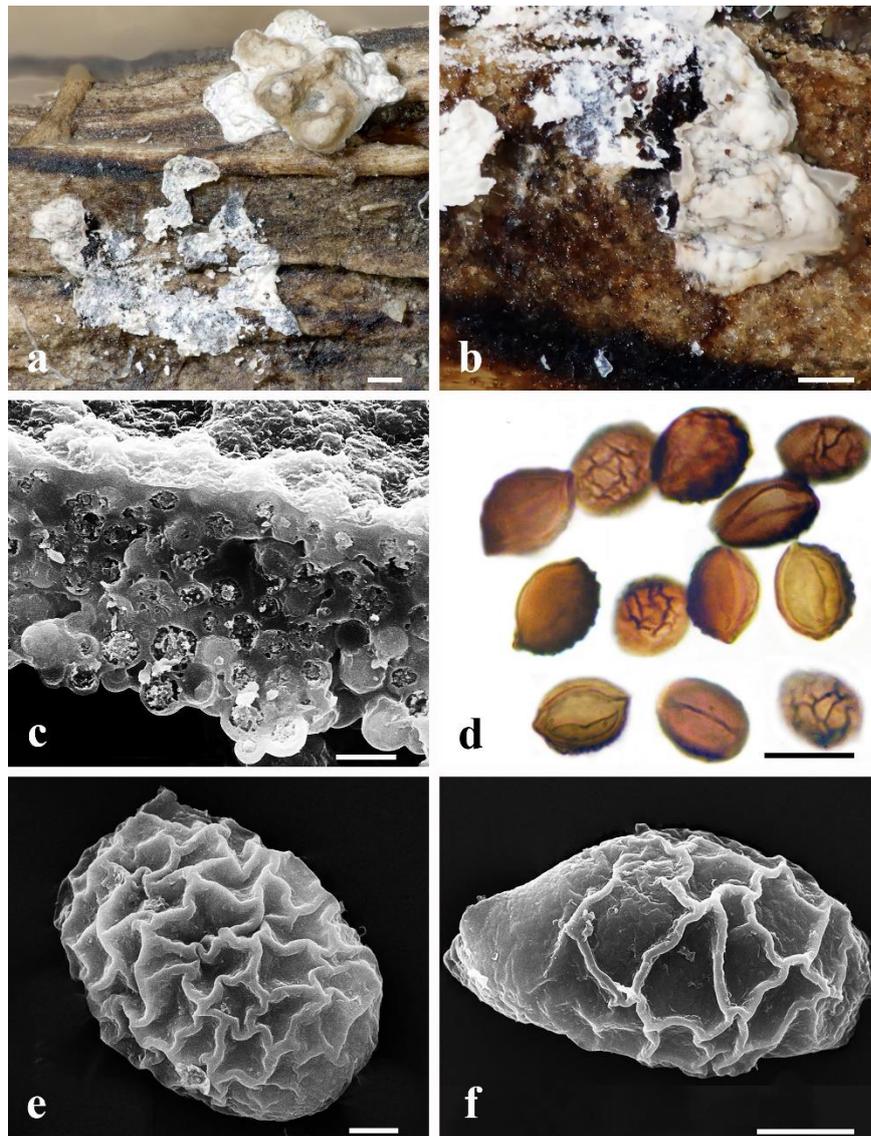
**Table 1** Continued.

Source number	References	Comment	Coll	Rec
5	Golovenko (1968)	All records included in Vasyagina et al. (1977).	FC	0
6	Novozhilov et al. (2005a)	All records included in Zemlyanskaya et al. (2020).	MC	0
7	Novozhilov et al. (2005b)	All records included in Zemlyanskaya et al. (2020).	MC	0
8	Novozhilov et al. (2005c)	Most records included in Zemlyanskaya et al. (2020).	MC	9
9	Novozhilov et al. (2008)	Description of two new myxomycete species from Kazakhstan.	MC	2
10	Novozhilov et al. (2013)	Description of one new species from Kazakhstan, some records included in Zemlyanskaya et al. (2020).	MC	1
11	Novozhilov et al. (2015)	All records included in Zemlyanskaya et al. (2020).	MC	0

12	Rakhimova et al. (2022)	One nivicolous species, <i>Diderma niveum</i> , reported	FC	1
13	Schnittler & Novozhilov (2000)	Detailed study of myxomycetes from the Mangyschlak peninsula based on the moist chamber culture technique; for the ecology of species, see Schnittler (2001)	MC	33
14	Schnittler (2001)	Ecological study; for species list and descriptions, see Schnittler & Novozhilov (2000).	MC	0
15	Shchepin et al. (2021)	One species, <i>Badhamia albescens</i> , characterized molecularly; see description in Azirakhmet et al. (2025).	FC	1
16	Sypabekkyzy (2024)	A mycological study reporting three myxomycete species.	FC	3
17	Vasyagina et al. (1977)	A detailed account on the myxomycete biota of Kazakhstan, including as well all records reported by Golovenko (1960).	FC	212
18	Zemlyanskaya & Novozhilov (2023)	Records already published in Zemlyanskaya et al. (2020).	MC	0
19	Zemlyanskaya & Novozhilov (2018)	A regional study adding numerous new records.	MC	106
20	Zemlyanskaya & Novozhilov (2020)	Records already published in Zemlyanskaya et al. (2020).	MC	0
21	Zemlyanskaya et al. (2020)	A detailed checklist of the hitherto known myxomycetes from western Kazakhstan.	FC/ MC	376
22	Yachevskiy (1907)	All records are included in Golovenko (1960).	FC	0
23	Dzhunuskanova & Rakhimova (2021)	Species checklist for Ile Alatau; most records listed are included in Vasyagina et al. (1977).	FC	4
24	Rakhimova et al. (2023)	Species checklist for Almaty Region; most records listed are included in Vasyagina et al. (1977) or Dzhunuskanova & Rakhimova (2021).	FC	4
25	Shchepin et al. (2024)	All records are included in Azirakhmet et al. (2025).	FC	0
26	Borg Dahl et al. (2018)	All records are included in Azirakhmet et al. (2025).	FC	0

## Discussion

Early research on myxomycetes in Kazakhstan primarily targeted forested regions, where field collecting is possible (Golovenko 1965, 1968). Later, the steppes and deserts of western Kazakhstan were surveyed (Schnittler & Novozhilov 2000, Schnittler 2001, Zemlyanskaya & Novozhilov 2018, 2020, 2023). In these arid ecosystems, field collections are rather rare and restricted to forest islands; therefore, the moist chamber culture technique (Gilbert & Martin 1933) was the main research tool. This technique works more effectively in dry regions compared to humid forests (Schnittler et al. 2015b), enabling recovery of minute corticolous (e.g., *Didymium phloiogenum*) and fimicolous species (e.g., *Kelleromyxa fimicola*). More recently, research in the Ile Alatau mountains in 2013 recovered nivicolous myxomycetes (Azirakhmet et al. 2025). Despite these advances, many regions remain underexplored (Fig. 1A).



**Fig. 3** — Micromorphological characteristics of *Badhamia rhytidosperma*. a Sporocarps viewed under a dissection microscope (DM). b Opened sporocarp (DM). c Peridium with lime globules viewed under a scanning electron microscope (SEM). d Spores viewed under a light microscope showing the characteristic wrinkles. e-f Spores (SEM). Scale bars: a = 200  $\mu\text{m}$ , b = 100  $\mu\text{m}$ , c, e = 2  $\mu\text{m}$ , d = 10  $\mu\text{m}$ , f = 5  $\mu\text{m}$ .

Among the 193 documented species, two (*Didymium macrospermum* Rostaf. and *Physarum altaicum* Lavrov) were reported from Kazakhstan only once, more than 65 years ago; they have never been encountered by us, and we do not know any mention of these species in the recent literature. Additionally, four taxa described from Kazakhstan by Golovenko (1960) – *Cienkowskia transiliensis*, *Lamproderma columbinum* var. *equiseti*, *Stemonitis minor*, and *S. sophia* – are not recognized in current taxonomy and consequently excluded from this checklist.

Analysis of species distribution across biomes, substrate types, and ecological guilds (Fig. 2A–C) confirms mountain forests to be the most diverse habitats for myxomycetes – consistent with global patterns (e.g., Schnittler et al. 2021). By contrast, deserts harbor lower diversity but sustain specialized corticolous (e.g., minute *Echinostelium* spp., Novozhilov et al. 2005b, c, Schnittler et al. 2013) and coprophilous species facilitated by widespread pastoralism. The latter guild fruits on herbivore dung (cattle, horse, sheep, goat, and camel). Developmental cycles differ markedly between these guilds: minute corticolous species mature in several days in moist chamber cultures, whereas coprophilous taxa require up to two months (Schnittler 2001). This underscores the critical

importance of moist chamber technique for studying myxomycetes in arid regions, as demonstrated in other studies (China, Taklimakan: Schnittler et al. 2012; Oman, Rub-el-Khali: Schnittler et al. 2015b).

Most of the records of this study were determined with traditional morphological methods. However, in the last two decades molecular methods, first applied by Fiore-Donno et al. (2005), have greatly changed myxomycete systematics, and barcoding techniques (Schnittler et al. 2017b, 2020, Novozhilov et al. 2025) became available. Three recent trends have to be mentioned:

1. Phylogenetic analyses revealed widespread parallel evolution (see discussion in Leontyev et al. 2019) and demonstrated non-monophyly in traditionally recognized orders and species-rich genera (Trichiales: García-Cunchillos et al. 2022, Physarales: García-Martín et al. 2023, Ronikier et al. 2022, Prikhodko et al. 2023). This taxonomic instability necessitates frequent nomenclatural revisions.

2. Barcoding based on the 18S rDNA marker was developed after 2010 (Schnittler et al. 2017a). For Kazakhstan, only 15 nivicolous species have been barcoded (Azirakhmet et al. 2025). Consequently, most pre-molecular records require verification. From our experience, we cannot rule out that older, not barcoded records, like *Diderma niveum* (Golovenko 1960, Rakhimova et al. 2022) may represent other nivicolous species of this genus (see revision of this genus by Shchepin et al. 2024).

3. Investigations with independently inherited nuclear markers confirm frequent cryptic speciation, revealing reproductively isolated lineages representing putative biological species (*Badhamia albescens*: Shchepin et al. 2021; *Hemitrichia serpula*: Dagamac et al. 2017; *Meriderma* spp.: Feng et al. 2016; *Trichia varia*: Feng & Schnittler 2015). Where molecular evidence (published or unpublished) indicates that a morphologically defined species represents a complex of cryptic lineages, we include taxonomic annotations. These advances suggest that species numbers in myxomycetes may be underestimated by a factor of 2–3, consistent with case studies (Feng & Schnittler 2017, Inoue et al. 2024).

The latest revisions of some species complexes (e.g., Leontyev et al. 2015, 2023, 2025, Bortnikov et al. 2023) cannot be applied to species records from the older literature; nevertheless, the species list compiled herein shows that the myxomycete biota of Kazakhstan is quite rich – most traditionally circumscribed genera were found, as shown in the following list with species numbers per genus:

Ceratiomyxales: *Ceratiomyxa* 1.

Liceales: *Cribraria* 8, *Lindbladia* 1, *Dictydiaethalium* 1, *Tubifera* 1, *Reticularia* 2, *Lycogala* 3, *Licea* 14.

Echinosteliales: *Echinostelium* 6.

Trichiales: *Dianema* 2, *Calomyxa* 1, *Perichaena* 6, *Arcyria* 6, *Metatrachia* 2, *Hemitrichia* 8, *Trichia* 6, *Oligonema* 5.

Physarales: *Kelleromyxa* 1, *Fuligo* 4, *Willkommlangea* 1, *Leocarpus* 1, *Badhamiopsis* 1, *Badhamia* 11, *Craterium* 3, *Physarum* 20, *Diderma* 7, *Didymium* 19.

Stemonitidales: *Brefeldia* 1, *Amaurochaete* 1, *Symphytocarpus* 2, *Macbrideola* 2, *Paradiacheopsis* 2, *Lamproderma* 11, *Meriderma* 2, *Comatracha* 6, *Stemonitis* 7, *Stemonitopsis* 2.

This checklist, thus, serves as a baseline, but it should be noted that many historic records require critical revision. Further studies should be directed to (1) critically evaluate old records in the light of modern taxonomy, preferentially employing barcoding, (2) disentangle species complexes with molecular markers, and (3) target the understudied regions of the country, preferably by surveys combining field collecting and the moist chamber culture method.

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## Accessibility of data

The herbarium specimens of myxomycetes used in this study are deposited in the following herbaria: the Volgograd Herbarium, the V.L. Komarov Herbarium of the Russian Academy of Sciences, St. Petersburg (LE), and the Herbarium of the Institute of Botany and Landscape Ecology at the University of Greifswald (GFW). All specimens have registration numbers available upon request. Species records from literature are available in Supplementary File 1. Collection data and corresponding bibliographic information are provided in the References section.

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### Supplementary File

[https://docs.google.com/spreadsheets/d/18-nJrRoTZPs3DK-p79pCpPg3xu4b\\_01d/edit?usp=sharing&ouid=114351694417193133260&rtpof=true&sd=true](https://docs.google.com/spreadsheets/d/18-nJrRoTZPs3DK-p79pCpPg3xu4b_01d/edit?usp=sharing&ouid=114351694417193133260&rtpof=true&sd=true)