Myxomycete diversity and ecology in the arid regions of the Lower Volga River Basin (Russia)

Yuri K. Novozhilov[1], Inna V. Zemlianskaia[2], Martin Schnittler[3], and Steven L. Stephenson[4*]

[1]V.L. Komarov Botanical Institute of the Russian Academy of Sciences, Prof. Popov St. 2, 197376 St. Petersburg, Russia
[2]Volgograd Medical University, Department of Pharmacognosy, 400066, Volgograd, Pavshikh Bortzov Square 1, Russia
[3]Botanical Institute and Botanical Garden, Ernst Moritz Arndt University Greifswald, Grimmer Str. 88, D-17487 Greifswald, Germany
[4]Department of Biological Sciences, University of Arkansas, Fayetteville, AR 72701, USA

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A rapid biodiversity assessment for myxomycetes (plasmodial slime moulds or myxogastrids) was carried out during the 1995 to 2005 field seasons in the desert and steppe regions of the Lower Volga River Basin. The general area investigated represents the northwestern portion of the Caspian Lowland of Russia and adjacent areas of Kazakhstan. Because of the very arid climate of this region of the world, specimens obtained with the use of the moist chamber culture technique formed a major part of the survey. At least 158 species of myxomycetes representing 35 genera were identified from 3227 records that originated from 852 field collections and 2379 collections obtained from 1470 moist chamber cultures prepared with samples of bark from living plants, litter and the dung of herbivorous animals. Both species richness and diversity increased along the gradient of vegetation from sagebrush desert to woodland. The myxomycete biota of this region displays a high level of similarity to those of other arid regions of the world for which data exist but differs considerably from the biotas of temperate, boreal and tropical regions. Seventeen species were recorded for the first time from Russia. Small corticolous (bark-inhabiting) species were found to be characterized by smaller niche breadths than litter-inhabiting species and seem to be more specialized than other ecological groups of myxomycetes. Maximum diversity for corticolous myxomycetes was recorded for plants (e.g., *Calligonum aphyllum* and *Ulmus pumila*) that have deeply furrowed bark. The most specific and poorest corticolous myxomycete biota was recorded for the bark of *Tamarix*.

Key words: biogeography, deserts, distribution, ecology, plasmodial slime moulds, steppes, species inventory

*Corresponding author: S.L. Stephenson; e-mail: slsteph@uark.edu

Introduction

Myxomycetes are regarded primarily as a mesophytic group of organisms. Most of what is known about myxomycete biodiversity has been derived from surveys carried out in temperate and boreal forests of the world. Only a few species lists for arid areas such as the Sinai Desert of northern Africa (Ramon, 1968), the Sahara Desert of northern Africa (Faurel *et al*., 1965), the Sonoran Desert of Arizona in western North America (Evenson, 1961; Blackwell and Gilbertson, 1980, 1984), the Gobi Desert of Asia (Novozhilov and Golubeva, 1986), the Kazakh Desert of Asia (Schnittler and Novozhilov, 2000), and parts of Mexico in southern North America (Lado *et al*., 2002) have been published previously. However, myxomycetes are not uncommon in desert habitats, and a few species are often surprisingly abundant, as reported for the Mangyshlak Peninsula in Kazakhstan (Schnittler, 2001) and semiarid regions of the Colorado Plateau of the western United States (Novozhilov *et al*., 2003). The primary objective of the present study was to assemble taxonomic and distributional data on all of the species of myxomycetes reported from and/or represented by specimens collected in the northwestern portion of the Caspian Lowland.

Materials and methods

Study sites

The general study area encompasses parts of the Rostov, Volgograd, and Astrakhan' provinces, the Kalmykia Republic and several localities in Kazakhstan located between 50° 30' and 45° 04' N latitude (Fig. 1). The major portion of the study area is situated within the Caspian Lowland. Elevations within the lowland range from approximately 28 m below sea level to 20 m above sea level. The Caspian Lowland has a high continental arid climate and is the most drought prone area of Russia. Annual precipitation ranges from about 350 mm in the northwest to no more than 150 mm in the south, with the maximum occurring in summer (70-75% of the annual precipitation). The average annual temperature is 9.2°C. There are two main types of soils. The first type is a light chestnut-coloured steppe soil found in the northern part of the lowland (generally >48° N latitude) and the second type is a dark-brown desert soil that occurs over the remainder of the area investigated. Solidified soils and sands are very typical throughout the general study area. The Volga River flows through the region and forms an oasis—the Volga-Akhtuba floodplain and a wide delta—where it empties into the Caspian Sea. Two vegetation zones are differentiated in the general study area, and these are

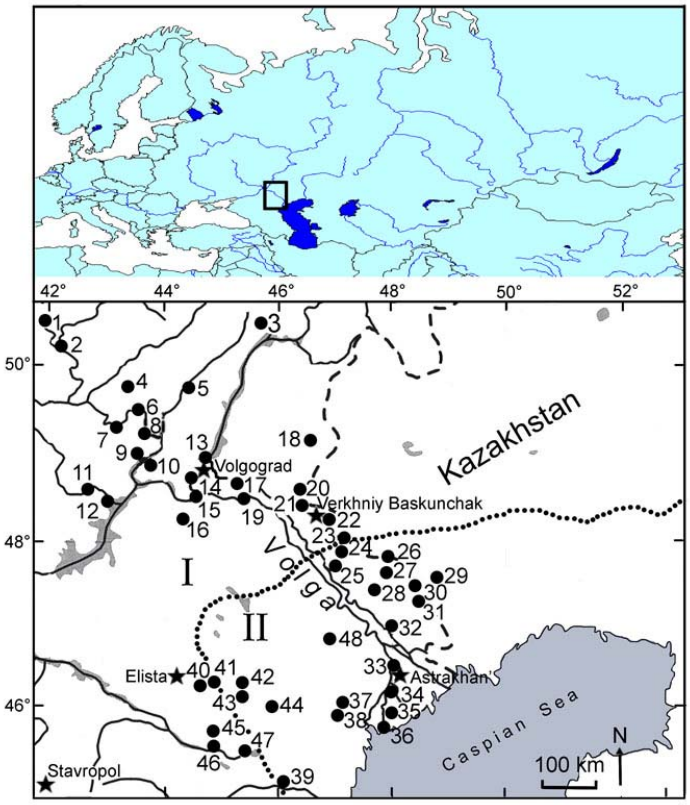

Fig. 1. Map of the northwestern portion of the Caspian Lowland, with sampling localities indicated by black circles. Numbers refer to the localities listed in the text. A dotted line indicates the border between the steppe zone (I) and the desert zone (II) in the general study area (according to Safronova [2002]). The insert shows the geographical position of the general study area (delimited by the rectangle).

indicated with consecutive Roman numbers on the map provided in Fig. 1. A brief description of each zone is given in the section that follows.

I - Steppe (loc. 1-22) with feather-grass communities and **II** - Desert (loc. 23-48). The feather-grass community characterized by *Stipa lessingiana* and *S. sareptana* in the steppe zone and the grass-sagebrush community characterized by *Poa bulbosa* and *Artemisia lercheana* in the desert zone are typical for this entire region (Safronova, 2002). Typically, *Artemisia lercheana* is found on sites with loamy soils, *A. arenaria* on sites with sandy soils, and *A. pauciflora* on sites with solidified soils. Tall shrub communities containing *Calligonum*

aphyllum, *Tamarix ramosissima* and *T. laxa* often occur in sandy landscapes. Of interest as potential substrates for myxomycetes are several members of the *Chenopodiaceae* (e.g., *Salsola laricina* and *Haloxylon aphyllum*) as well as *Atraphaxis spinosa* and *Atriplex cana*. In both vegetation zones, there are different types of intrazonal arboreal communities, including riparian forests with *Populus alba*, *Alnus glutinosa* and *Salix* spp. the most characteristic trees present. On protected sites in gullies within the steppe zone, forest islands consisting mainly of *Acer tatarica*, *A. negundo*, *Crataegus ambigua*, *C. monogyna*, *Malus praecox*, *Pyrus communis*, *Rhamnus cathartica*, *Quercus robur* and *Ulmus campestris* can be found. In the desert zone, communities dominated by *Elaeagnus angustifolia* are widely distributed in sandy depressions. Artificial plantations of *Ulmus pumila* and *Pinus* spp. are found throughout the region. As a general observation, the intrazonal arboreal communities of the steppe and desert zones provide all of the microhabitats for myxomycetes typically found in temperate forests.

Specimens of myxomycetes that had fruited under natural conditions in the field and samples of various substrates to be used to prepare moist chamber cultures were collected from 220 study sites during the period of 1995 to 2004. In most instances, several study sites occurred in the same general locality, and a total of 48 localities were included in the total survey (Fig. 1). Information provided for each locality includes the name of any nearby city or settlement, geographic coordinates and short description of vegetation.

List of localities

I. Steppe zone. Localities situated within the Volgograd region (1-10, 12-18), Rostov (11), and Astrakhan' provinces (19-22): locality **1**: Lukovskaia and Zakhoperskiy, 50°30' N, 41°55' E, different types of intrazonal arboreal communities, **2**: Larinskiy, 50°14' N, 42°13' E, different types of intrazonal arboreal communities, **3**: Bolshenabatovskiy khutor and Shcherbatovka, 50°29' N, 45°39' E, different types of intrazonal arboreal communities and arid pasture, **4**: Padok, 49°47' N, 43°22' E, different types of intrazonal arboreal communities, **5**: Mihailovka, 49°45' N, 44°25' E, single tree of *Salix alba*, the watershed of the Ilovlia River, **6**: Vyezdinskiy, 49°32' N, 43°27' E, intrazonal arboreal vegetation, alder wet groves, with grasses and ferns in the gullies; Kremenskaia, 49°30' N, 43°32' E, oak and elm woodland in a small gully, **7**: Melokletzkiy, 49°19' N, 43°09' E, riparian forest, **8**: Sirotinskaia, 49°14' N, 43°38' E, woodland in the gully, **9**: Yevlampiyevskiy khutor, 48°58' N, 43°36' E; Osinovskiy, N 49°01', E 43°23', intrazonal arboreal vegetation with *Quercus robur*, *Acer* spp., **10**: Golubinskaia, 48°51' N, 43°35' E, riparian poplar forest with *Populus alba* and *P. nigra*; Donskoy khutor, 48°59' N, 43°55' E, riparian poplar forest, **11**: Sekretev, N 48°36', E 42°39', pine plantation and *Salix* groves, **12**: Rychkovo, 48°28' N, 43°01' E, single trees and shrubs, **13**: Pichuga, 48°58' N, 44°42' E, different intrazonal arboreal vegetation, **14**: Volgograd city, 48°35' N, 44°23' E, different intrazonal arboreal vegetation within dry steppe vegetation, **15**: Peskovatka khutor, 48°55' N, 43°46' E, different types of intrazonal arboreal communities and sand land vegetation; Shchuchiy, 48°35' N, 44°39' E, different types of intrazonal arboreal communities;

Volgograd city, 48°30' N, 44°30' E, arboreal intrazonal vegetation, **16:** Tinguta, 48°14' N, 44°20' E, intrazonal arboreal vegetation, **17**: Leninsk, 48°40' N, 45°16' E, riparian forest, **18**: Krasnaia derevnia, 49°09' N, 46°34' E, intrazonal arboreal vegetation; 49°10' N, 46°34' E, zonal dry steppe vegetation with *Artemisia lercheana* and *Poa bulbosa*, **19**: Lopin, 48°30' N, 45°22' E, riparian forest, **20**: Verchniy Baskunchak, 48°35' N, 46°22' E, sagebrush stands of *Artemisia pauciflora* on heavy, fixed and salt-influenced ground, **21**: Nizhnii Baskunchak 48°25' N, 46°25' E, dry steppe, sagebrush and feather-grass dominated communities, **22**: This study region encompasses a rather large area near Nizhniy Baskunchak settlement and the Great Bogdo Mt., between 48°03' and 48°22' N latitude, 46.49 and 46.57 E longitude and includes different type of arboreal intrazonal vegetation.

II. **Desert zone**. Localities situated within the Astrakhan' province (23-26, 27-28), Kazakhastan (26, 29) and Kalmykia (39-48): locality **23**, Verblyuzh'ya, 47°45' N, 46°56' E, desert sagebrush vegetation, **24**. Mikhaylovka, 47°42' N, 46°58' E; Sasykoli, 47°35' N, 47°01' E; Kharabali, 47.25' N, 47.40' E, **25**. Chapchachi, 47°35' N, 47°04' E, desert vegetation; Dosang, 46°55' N, 47°56' E, desert vegetation, **26**. Kazakhstan, Azgir, 47°49' N, 47°55' E, desert vegetation, **27**. Mikhaylovka, 47°36' N, 47°53' E, stands of *Eleagnus angustifolia* in small, sandy depressions, **28**. Kharabali, 47°23' N, 47°50' E, *Haloxylon* plantation with *Artemisia lercheana*; 47°24' N, 47°53' E, elm plantation; Tambovka, 47°21' N, 47°27' E, sagebrush community (*A. lercheana*) on clayish soil; 47°22' N, 47°34' E, sagebrush community (*Artemisia pauciflora*) on weakly salt-influenced soil; 47°22' N, 47°34' E, sagebrush community (*A. lercheana*) on clayish soil, **29**. Kazakhstan, Uschtagan, 47°41' N, 48°36' E, sagebrush (*A. lercheana*) desert community, **30**. Kharabali, 47°28' N, 48°22' E, stands of *Callygonum* and *Tamarix ramosissima* on the sand dunes, **31**. Dosang, 47°16' N, 48°25' E, slightly loose sand dunes with scattered *Calligonum* and *Tamarix* stands, *Artemisia arenaria* and *A. lercheana*, **32**. Dosang, 46°56' N, 47°55' E, zonal desert sagebrush communities (*A. arenaria*, *A. lercheana*) with stands of *Calligonum* and *Tamarix* in sand dunes; 46°55' N, 47°54' E, poplar-elm plantation on sandy soil, **33**. Pastopulovka, 46°30' N, 48°01' E, open poplar forest with *Eleagnus* on sandy soil with *Tamarix* shrubs, 34. Volgo-Kaspiyskiy, 46°12' N, 47°58' E, old stands of *Eleagnus* on sandy soil near the Volga River, **35**. Obraszovo-Travino, 46°00' N, 48° 00' E, grazed half-desert with scattered *Tamarix* shrubs on salty soil; Damchik, 45°52' N, 47°58' E, reed island with small willow stands, **36**. Damchik, 45°48' N, 47°49' E, dry, temporary flooded pastures with *Tamarix* shrubs, weakly salt-influenced soils; 45°48' N, 47°49' E, temporarily flooded meadows; 45°45' N, 47°55' E, older willow floodplain forest, annually flooded, on a small island, **37**. Mikhaylovka, 46°03' N, 47°07' E, stands of *Callygonum* and *Tamarix ramosissima* on the sand dunes, **38**. Zenzeli, 45°54' N, 47°03' E, sagebrush desert with *A. lercheana*, **39**. Acan-Huduk, 45°04' N, 46°04' E, *Stipa capillata* on the old hayfield, **40**. Elista, 46°16' N, 44°38' E, sagebrush desert with *A. lercheana*, **41**. Ulan-Erge, 46°19' N, 44°52' E, sagebrush desert with *A. pauciflora*, **42**: Jaschkul, 46°18' N, 45°21' E, desert community with *Poa bulbosa*, *Salsola laricina*, **43**. Jaschkul, 46°08' N, 45°21' E, sagebrush desert with *A. lercheana*, **44**: Tavn-Gaschun, 46°01' N, 45°53' E, sagebrush desert with *A. lercheana*, **45**: Cholun-Khamur, 45°41' N, 44°52' E, sagebrush desert with *A. lercheana*, **46**: Cholun-Khamur, 45°31' N, 44°52' E, elm plantation; 45°30' N, 44°53' E, sagebrush desert with *A. lercheana*, **47**. Chernosemelskiy, 45°28' N, 45°25' E, sagebrush desert with *A. lercheana*, **48**: Bergin, 46°49' N, 46°54' E, sagebrush desert with *A. lercheana*.

Substrate sampling

A total of 1893 substrate samples were collected for preparation of moist chamber cultures. These included bark from living trees and shrubs (1016 samples), plant litter (620 samples), various types of woody debris (121 samples) and dung (136 samples) of herbivorous animals, such as hare, camel, cow, horse, sheep and some rodents.

Litter was classified into three types. The first type was leafy litter (ll) of such trees as *Quercus*, *Populus* and *Ulmus*, which consisted of decaying leaves forming mats 0.5–2 cm thick beneath shrubs and trees. Twigs of sufficient size to be easily noticed in the field were selectively excluded from samples of leafy litter. The second type was represented by the small twigs (lt) that accumulate in mats 1–5 cm thick under *Artemisia*, *Calligonum* and *Tamarix*. These samples also contained other types of plant debris such as seeds, cone fragments, small twigs and pieces of bark. The third type (lg) consisted of the plant parts of *Stipa lessingiana*, *S. sareptana* and *Poa bulbosa*, all of which grow in dense mats or tussocks. Dead shoots (up to 10 cm thick) from the previous year formed the bulk of these samples.

Dung samples (d) consisted of partially decomposed droppings of various herbivores. Droppings ranged in size from relatively large (2-20 cm) for cattle, camels and horses to relatively small (0.5-1.5 cm) for sheep, saiga antelopes (*Saiga tatarica*) and rodents of the genera *Citellus* and *Lepus*.

Moist chamber cultures

Moist chamber cultures were prepared in the manner described by Härkönen (1977, 1981). All cultures consisted of moist filter paper in Petri dishes (10 cm diam) and were incubated under ambient light and at room temperature (ca 20-24°C) for up to 90 days and examined for the presence of myxomycetes on five occasions (days 2-4, 6-8, 11-14, 20-22, 40-44 and 85-90). A 'collection' is defined herein as one or more fruiting bodies considered to have originated from a single plasmodium (Stephenson, 1989). In virtually all cases, this could be determined without difficulty. For moist chamber cultures, the occurrence of one species in one Petri dish was considered as one collection.

Data analysis

Species diversity (alpha-diversity) was calculated using Shannon's diversity index $H' = -\Sigma P_i \log P_i$, where P_i is the relative abundance (the proportion of the total number of individuals or records represented by a species) of a particular species (Shannon and Weaver, 1963; Magurran, 1988).

Concentration of dominance in different myxomycete assemblages was calculated using Simpson's index. This index is higher for assemblages in which the proportion of species dominance is higher.

For determination, sporocarps were often preserved as permanent slides in lactophenol, and Hoyer's medium and/or glycerol gelatine were used to distinguish between limeless and lime-containing structures. Colour descriptions are given according to Petersen (1996). Sporocarp structures were studied with a JEOL 35c scanning electron microscope (SEM) at St. Petersburg.

Taxonomy

Nomenclature used herein follows that of Lado (2001) and Hernández-Crespo and Lado (2005), except for the genera *Collaria* Nann.-Bremek. and *Stemonitopsis* Nann-Bremek. and the conserved names of several genera (Lado et al., 2005) approved recently by the Committee for Fungi (Gams, 2005) of the IAPT. For each of the new combinations used by Lado (2001), the name cited in Martin and Alexopoulos (1969) also is provided (after "="). Authorities are cited according to Kirk and Ansell (1992), and determinations considered as uncertain are denoted as "cf." (confer). Names of vascular plants are those listed by Czerepanov (1995). After each name, an estimate of abundance as described by Stephenson *et al*. (1993) is given in brackets. This estimate is based upon the proportion of a species in relation to the total number of records recorded in the field and from moist chamber cultures: **R** = rare (< 0.5 % of all records), **O** = occasional (> 0.5-1.5 % of all records), **C** = common (> 1.5-3 % of all records), **A** = abundant (> 3 % of all records). The names of species found only in intrazonal arboreal communities are indicated by an asterisk (*). The symbol "(+)" indicates species for which not all collection numbers are listed. The total numbers of records recorded in the field (fc) or from moist chamber cultures (mc) are provided in brackets (symbols "fc" and "mc"). Next, the distribution of the species in different vegetation zones and microhabitats is listed. Two vegetation zones were differentiated and are indicated by a Roman numeral (**I** for the steppe zone and **II** for the desert zone).

Abbreviations for substrate type are as follows: b = bark of living trees and shrubs; w = large dead woody debris of trees and shrubs; ll = leaf litter; lg = grass litter; lt = small dead twigs of dwarf-shrubs and shrubs; d = dung of herbivorous animals. After a slash, the number of records is given, followed by the locality numbers as given in Fig. 1.

Specimens are deposited in the fungal herbarium of the Komarov Botanical Institute of the Russian Academy of Sciences, Laboratory of Systematics and Geography of Fungi (LE), as well as in the private collection

of the second author (Ze), with duplicates in the collection of the third author (SC) stored at the Herbarium of The Botanische Staatssammlung, München (M). For records of uncertain identification and a number of rare species that occurred regularly in zonal desert treeless communities, brief taxonomic descriptions are provided.

ANNOTATED SPECIES LIST

****Amaurochaete atra*** (Alb. & Schwein.) Rostaf. [**R**, Ze 432, 436, fc-2] **I**: w/2. Loc.: 2.

****Arcyodes incarnata*** (Alb. & Schwein.) O. F. Cooke [**R**, LE 218777 (+), fc-2, mc-5] **I**: b/4, w/3. Loc.: 9, 10, 11, 12, 13, 14, 15.

****Arcyria affinis*** Rostaf. [**R**, Ze 817, fc -1] **I**: w/1. Loc.: 22.

Arcyria cinerea (Bull.) Pers. [**A**, LE 218950 (+), Sc 15226 (+), fc-38, mc-89] **I**: b/62, w/47, ll/7, lg/1, lt/1; **II**: b/3, ll/2, d/4. Loc.: 1, 2, 3, 4, 6, 7, 9, 10, 11, 12, 13, 14, 15, 16, 18, 21, 22, 24, 27, 28, 32, 34, 35, 36.

****Arcyria denudata*** (L.) Wettst. [**O**, LE 218016 (+), fc-21, mc-6] **I**: b/4, w/20, ll/2. Loc.: 1, 2, 6, 10, 14, 15, 16, 19, 22.

****Arcyria incarnata*** (Pers.) Pers. [**O**, LE 218747 (+), fc-36, mc-11] **I**: b/10, w/35, ll/2. Loc.: 1, 3, 4, 6, 9, 11, 13, 14, 15, 16, 19, 22.

****Arcyria insignis*** Kalchbr. & Cooke [**R**, LE 205726 (+), fc-3] **I**: w/3. Loc.: 3, 10, 13.

Arcyria minuta Buchet in Patouillard [**O**, Ze 1103/3 (+), Sc 15179 (+), fc-2, mc-26] **I**: b/8, w/4, d/1; **II**: b/11, w/4. Loc.: 9, 12, 13, 14, 15, 18, 19, 20, 22, 24, 27, 32, 33, 36, 37.

Notes: This is one of the species widely distributed in the desert zone on the bark of trees and shrubs and on woody debris. Sporocarps (Fig. 2) salmon-pink, grouped on a common thin membranous hypothallus. Calyculus small, shallow funnel-shaped, smooth or densely decorated with large rounded or elongated warts, especially near the rim and which are partly united to form a

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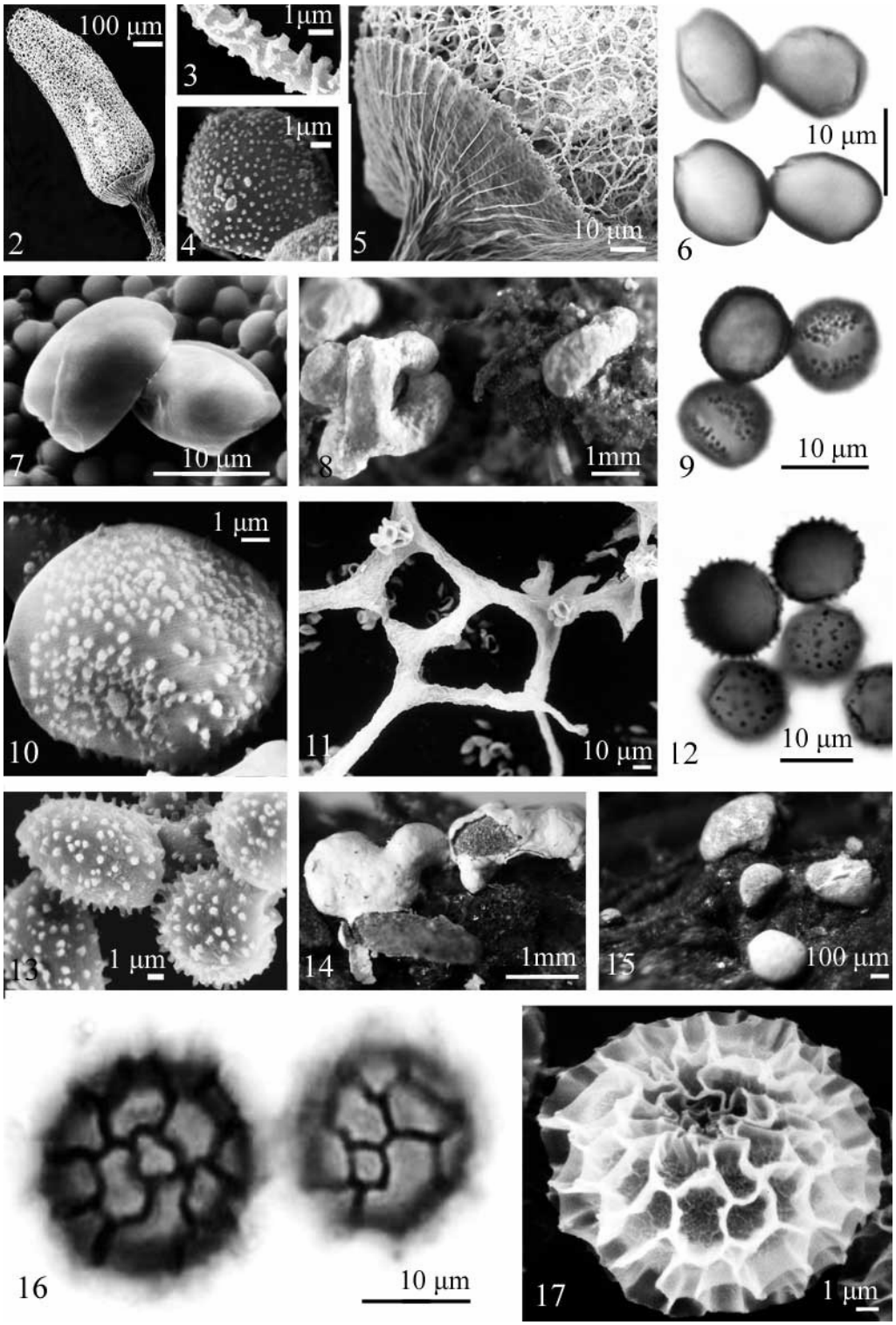
Figs 2-5. *Arcyria minuta* (SC 15401). 2. Sporocarp by SEM. 3. Capillitium by SEM. 4. Spore by SEM. 5. Calyculus and capillitium by SEM. **Figs 6-8.** *Badhamia apiculospora* (LE 219388). 6. Spores by TL with an apiculus at ends and a ridge along of spore. 7. Spores and lime granules by SEM. 8. Sporocarps by dissection microscope. **Figs 9-11.** *Badhamia goniospora* (LE 218577). 9. Spores by TL encircled by a narrow pale band. 10. Spore by SEM. 11. Capillitium by SEM. **Figs 12-14.** *Badhamia spinispora*. (LE 205465). 12. Spores by TL with spines widely-spaced on spore surface. 13. Spores by SEM. 14. Sporocarps by dissection microscope. **Figs 15-17.** *Didymium sp*. (LE 220327). 15. Sporocarp by dissection microscope. 16. Spore by TL ornamented with a deep reticulum. 17. Spore by SEM with prominently basic banded-reticulum and the secondary reticulum inside the basic reticulum.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broken net with irregular meshes (Fig. 5). Capillitium 3-5 µm diam, with large meshes and few free ends, attached to the calyculus, expanding 1.5 times the original size, densely decorated with spines, half-rings, reticulations and warts (Fig. 3), sometimes with bifid tips and up to 1.5 µm high, the basal threads almost smooth. Spore-mass salmon-pink. Spores (6-)8-10(-12) µm diam with a few scattered inconspicuous warts and warts grouped in complexes (Fig. 4).

****Arcyria obvelata*** (Oeder) Onsberg [**O**, LE 218011 (+), fc-21] **I**: w/21. Loc.: 2, 3, 6, 9, 11, 13, 14, 15, 19, 22.

Arcyria pomiformis (Leers) Rostaf. [**O**, LE 205688 (+), Sc 14918 (+), fc-15, mc-28] **I**: b/25, w/12, ll/1, lg/2; **II**: b/3. Loc.: 3, 6, 7, 9, 11, 13, 15, 21, 22, 32, 33.

****Arcyria stipata*** (Schwein.) Lister [**R**, Ze 484, fc-1] **I**: w/1. Loc.: 4.

****Badhamia affinis*** Rostaf. [**R**, Sc 15239, mc-1] **I**: b/1. Loc.: 22.

Badhamia apiculospora (Härk.) Eliasson & N. Lundq. [**O**, LE 219388 (+), mc-25] **I**: b/17, w/2, ll/2, lt/1; **II**: b/3. Loc.: 9, 10, 14, 15, 18, 24.

Notes: Sporocarps sessile, subglobose to pulvinate on a broad base, convex, irregular, greyish white, 0.25–1.0 mm diam, crowded into small colonies 1–2 mm across (Fig. 8). Peridium single, calcareous, light buff to white (21, 60; Petersen, 1996), opaque, lime distributed rather densely, rugulose, brittle, fairly evenly thick; inner surface pale yellow. Dehiscence irregular. Capillitium consisting of large, calcareous, irregular nodes, white or yellowish with short calcareous tubules, "badhamioid" type, pseudocolumella absent or present, forming a discrete body in centre of the sporocarp. Spore mass black. Spores free, smooth, thick-walled elliptical, slightly angular in outline, with an apiculus (or two) and a ridge along of spore (Figs. 6, 7), dark brown, smooth, 10.5–12(13) x 13–15 (16) µm diam.

****Badhamia capsulifera*** (Bull.) Berk. [**R**, LE 218079, LE 218392, fc -2] **I**: b/1, w/1. Loc.: 15, 4.

Badhamia foliicola Lister [**O**; Ze 1092/2 (+), fc-6, mc-13] **I**: b/6, w/1, ll/6, lt/1; **II**: b/3, w/1, lt/1. Loc.: 9, 14, 15, 18, 19, 22, 24, 36, 37, 38.

****Badhamia goniospora*** Meyl. [**R**, LE 218577, Ze 841, fc-2] **I**: b/1, w/1. Loc.: 13, 14.

Our specimens have the typical characters of this species. Spores free, globose, minutely and closely spinulose, purplish brown, encircled by a narrow pale band (Figs. 9, 10) (11-)12-14(-16) µm diam. Capillitium a delicate

network of slender tubules sparsely charged with lime, sometimes nearly limeless and appearing pale yellow (Fig. 11).

****Badhamia macrocarpa*** (Ces.) Rostaf. [**R**, LE 218371 (+), fc-6, mc-3] **I**: b/5, w/2, ll/2. Loc.: 3, 4, 9, 13, 14, 15, 22.

****Badhamia panicea*** (Fr.) Rostaf. [**R**, LE 218225 (+), fc-5] **I**: b/1, w/4. Loc.: 6, 11, 15.

****Badhamia populina*** Lister & G. Lister [**R**, LE 218367 (+), fc-4] **I**: b/2, w/2. Loc.: 4.

Badhamia spinispora (Eliasson & N. Lundq.) H.W. Keller & Schokn. [**A**, LE 220054 (+), Ze 1013/1 (+), mc-146] **I**: b/52, ll/1, lt/10, d/1; **II**: b/56, w/2, ll/2, lg/1, lt/10, d/11. Loc.: 9, 10, 12, 13, 14, 16, 18, 24, 26, 28, 29, 38, 41, 42, 43, 45, 46.

Notes: Our material is quite typical for this species. Sporocarps are primarily plasmodiocarpous (Fig. 14), irregularly branched or reticulate, up to 6 mm long, sometimes sporocarpous or occurring as short, straight plasmodiocarps <1 mm long. Peridium double, the outer layer filled with white lime, smooth to rugulose and connected to the membranous, slightly iridescent, hyaline, inner layer (Fig. 14). Spore-mass black. Spores reddish brown, globose to ellipsoid and then 12-16 x 11-13 µm including ornamentation, conspicuously spinose, the spines widely-spaced (Fig. 12) and up to 1 µm high with rounded ends (Fig. 13). Our records are the first for Russia, but this species may be more widespread than available records indicate, especially in arid regions.

****Badhamia utricularis*** (Bull.) Berk. [**R**, Ze 2105/4 (+), fc-2, mc-3] **I**: b/3, w/2. Loc.: 3, 13, 14.

****Comatricha alta*** Preuss [**R**, LE 218512, fc-1] **I**: w/1. Loc.: 15.

****Comatricha elegans*** (Racib.) G. Lister [**R**, Ze 141/372/5 (+), fc-4, mc-2] **I**: b/2, w/4. Loc.: 3, 4, 9, 11, 15.

****Comatricha ellae*** Härk. [**R**, Ze 138/369/1 (+), fc-1, mc-2] **I**: b/2, w/1. Loc.: 11, 15, 22.

Comatricha laxa Rostaf. [**C**, Ze 1103/1 (+), Sc 14855 (+), fc-7, mc-55] **I**: b/18, w/7, lg/1; **II**: b/24, w/8, lt/4. Loc.: 9, 10, 14, 15, 18, 19, 22, 24, 25, 26, 27, 28, 29, 31, 32, 33, 34, 35, 36, 37, 46.

Notes: Our collections consist of two forms. All specimens obtained from bark and litter collected in treeless communities are morphologically intermediate between *Paradiacheopsis cribrata* and typical specimens of *Comatricha laxa* collected from decayed wood. The corticolous form has

sporocarps (0.35)-0.5-0.8-(1) mm tall that form small groups, scattered, with stalks reaching one to one and a half times the sporotheca diam. Sporotheca globose to weakly ovoid, (0.15)-0.2-0.3-(0.35) mm in diam, dark blackish brown. Stalk fibrous at the base, with an inconspicuous hypothallus, under the microscope opaque, black, turning to olivaceous-yellow at the base, (0.2)-0.3-0.5-(0.6) mm high, extending into a columella equalling one to two thirds of the height of the sporotheca. Capillitium stiff and coarse, branching from the whole length of the columella, dark black to brown, outer threads pale brown. Peridium absent, no conspicuous collar. Spores dull olivaceous brown in mass, lacking reddish tints, globose, olivaceous brown under transmitted light, with regularly arranged warts up to 0.2 mm high, (10)-11-12.7-(13) µm in diam.

The wood-inhabiting form is characterized by sporocarps with a total height of 1.2-2. Sporotheca cylindrical or slightly attenuate upwards, becoming long-conical on weathering, rounded at the base, dark brown, 0.8-1.3 mm tall and ca. 0.25 mm diam. Capillitium lax, brown, rather flexuose, primary branches joined to the columella along its whole length, pointing upwards, branched and anastomosed into an net with 1-3 meshes across the radius.

The first of these two forms is seemingly a common species in arid areas (Schnittler and Novozhilov, 2000; Novozhilov *et al*., 2003; unpubl. data from central and western Kazakhstan).

Comatricha lurida Lister [**R**, Ze 138/369/1 (+), mc-2] **I**: b/1; **II**: b/1. Loc.: 14, 24.

Comatricha nigra (Pers. ex J. F. Gmel.) J. Schröt. [**C**, Ze 108/979/2 (+), fc-16, mc-57] **I**: b/6, w/65; **II**: b/2. Loc.: 1, 2, 3, 4, 6, 9, 10, 11, 13, 14, 15, 19, 22, 33.

Comatricha pulchella (C. Bab.) Rostaf. [**O**, Ze 126/357/1 (+), Sc 14975 (+), fc-14, mc-12] **I**: b/2, w/1, ll/14; **II**: b/4, ll/5. Loc.: 11, 20, 22, 32, 33.

****Comatricha typhoides*** (Bull.) Rostaf. [**R**, Ze 200 (+), fc-3] **I**: w/3. Loc.: 4, 14.

****Craterium aureum*** (Schumach.) Rostaf. [**R**, LE 218605, fc-1] **I**: w/1. Loc.: 3.

Craterium leucocephalum (Pers. ex J. F. Gmel.) Ditmar [**O**, LE 218002 (+), fc-23, mc-3] **I**: b/1, w/8, ll/16; **II**: w/1. Loc.: 1, 3, 9, 13, 14, 15, 16, 22, 24.

****Craterium minutum*** (Leers) Fr. [**R**, LE 218548, LE 204539, fc-2] **I**: w/1, ll/1. Loc.: 13, 15.

****Cribraria argillacea*** (Pers.) Pers. [**R**, LE 218199 (+), fc-4] **I**: w/4. Loc.: 6, 13, 15.

****Cribraria aurantiaca*** Schrad. [**R**, LE 218164 (+), fc-8] **I**: w/8. Loc.: 3, 6, 13, 15.

****Cribraria cancellata*** (Batsch) Nann.-Bremek. [**O**, LE 218091 (+), fc-20] **I**: w/20. Loc.: 4, 6, 13, 14, 15.

****Cribraria languescens*** Rex [**R**, Ze 298, fc-1] **I**: w/1. Loc.: 6.

****Cribraria rufa*** (Roth) Rostaf. [**R**, Ze 84, fc-1] **I**: w/1. Loc.: 3.

****Cribraria tenella*** Schrad. [**R**, Ze 321, fc-1] **I**: w/1. Loc.: 6.

****Cribraria violacea*** Rex [**R**, Ze 2837/1 (+), fc-2, mc-3] **I**: w/3, ll/1; **II**: ll/1. Loc.: 3, 9, 16, 25.

****Diachea leucopodia*** (Bull.) Rostaf. [**R**, Ze 81, fc-1] **I**: ll/1. Loc.: 3.

****Diachea subsessilis*** Peck [**R**, Ze 680, fc-2] **I**: ll/2. Loc.: 13, 15.

****Dianema corticatum*** Lister [**R**, LE 220333, fc-1, mc-1] **I**: b/1, w/1. Loc.: 11, 46.

Diderma deplanatum Fr. [**R**, Ze 1439/1, 1439/2, mc-2] **II**: lt/2. Loc.: 24.

****Diderma globosum*** Pers. [**R**, Ze 638, fc-1] **I**: ll/1. Loc.: 15.

Didymium anellus Morgan [**C**, Ze 1021/1 (+), Sc 14969 (+), fc-2, mc-31] **I**: b/9, w/1, ll/5, lg/3, d/1; **II**: b/12, w/2, ll/8, lg/4, lt/8, d/12. Loc.: 9, 10, 13, 14, 15, 16, 18, 21, 22, 23, 24, 25, 26, 28, 29, 31, 32, 33, 35, 38, 43, 44.

Didymium bahiense Gottsb. [**R**, Sc 15233, mc-1] **I**: b/1. Loc.: 22.

****Didymium clavus*** (Alb. & Schwein.) Rabenh. [**R**, LE 218034 (+), fc-4] **I**: w/1, ll/2, d/1. Loc.: 15, 22.

****Didymium crustaceum*** Fr. [**R**, Ze 141 (+), fc-10] **I**: w/5, ll/5. Loc.: 15, 22.

Didymium difforme (Pers.) Gray [**A**, Ze 10/715/1 (+), Sc 15200 (+), mc-101] **I**: b/43, w/5, ll/8, lg/1, lt/12, d/6; **II**: b/17, w/1, ll/1, lg/1, lt/2, d/4. Loc.: 3, 9, 10, 12, 13, 15, 16, 18, 21, 24, 25, 26, 28, 29, 31, 37, 37, 43.

Didymium dubium Rostaf. [**R**, Ze 1493/2 (+), fc-6, mc-5] **I**: b/3, w/1, ll/5; **II**: ll/2. Loc.: 3, 9, 13, 15, 22, 28.

****Didymium flexuosum*** Yamash. [**R**, Ze 2830/2 (+), mc-2] **I**: ll/1, w/1. Loc.: 9, 16.

Didymium inconspicuum Nann.-Bremek. & D. W. Mitch. [**R**, Ze 1493/4 (+), mc-5] **II**: b/1, w/1, ll/1, lt/1, d/1. Loc.: 26, 28, 29.

Didymium iridis (Ditmar) Fr. [**O**, Ze 106/977/1 (+), Sc 15218, fc-2, mc-26] **I**: b/15, w/2, ll/1, lt/1, d/1; **II**: b/6, w/1, lt/1. Loc.: 6, 9, 10, 13, 14, 18, 22, 24, 25, 26, 28.

****Didymium megalosporum*** Berk. & M. A. Curtis [**R**, Ze: 615, fc-1] **I**: ll/1. Loc.: 15.

Didymium melanospermum (Pers.) T. Macbr. [**R**, Ze: 132/872/2 (+), fc-5, mc-1] **I**: b/1, w/1, ll/3, one collection on living mosses. Loc.: 4, 6, 15, 18, 22.

****Didymium mexicanum*** G. Moreno, Lizárraga & Illana [**R**, Ze 1104/1 (+), mc-1] **II**: w/1, lt/6. Loc.: 24, 37.

****Didymium minus*** (Lister) Morgan [**R**, Ze 372 (+), fc-5, mc-3] **I**: b/2, w/2, ll/4. Loc.: 3, 6, 12, 15.

Didymium nigripes (Link) Fr. [**R**, Ze 373 (+), fc-6, mc-3] **I**: b/2, ll/7. Loc.: 6, 14, 15.

Didymium squamulosum (Alb. & Schwein.) Fr. [**C**, Ze 102 (+), Sc 15500, fc-46, mc-25] **I**: b/12, w/18, ll/31, lg/1, lt/1, d/2; **II**: b/3, ll/1, lt/2. Loc.: 3, 4, 6, 7, 8, 9, 12, 13, 14, 15, 18, 22, 23, 26, 31, 32, 36.

Didymium sp. [**R,** LE 220327, 220334, Ze 614 (+) mc-6]. **I**: b/2, **II**: b/2, ll/2. Loc.: This taxon was first recorded from a locality in the steppe community, 48°34'43" N, 44°21'04" E, located at an elevation of 100 m above sea level; isolated in moist chamber culture on the dead twigs of *A. lercheana*, coll. 24.07.2001, I.V. Zemlianskaia. A second record was from Shcherbatovskiy National Park, 50°29'36" N, 45°41'33" E; on bark of an apple tree and on litter of a pear tree.

Notes: This appears to be a new species of *Didymium*. Sporocarps scattered or gregarious, snow-white (60, Petersen, 1996) or ash grey (56, Petersen, 1996) forming subglobose or pulvinate slightly flattened sporangia, 0.5-1.5 mm diam, varying to short plasmodiocarps up to 3 mm long (Fig. 15). Peridium single, thin, membranous, sparsely to densely powdered with white lime polygonal minute crystals and scales, sometimes nearly limeless. Columella absent. Capillitium absent. Spore-mass dark brown. Spores globose or slightly elongated, 13-16 μm diam, including the ornamentation, very dark purplish brown, fuscous (3, Petersen, 1996), prominently banded-reticulate with regular large 3-4 meshes across the hemisphere (Fig. 16); the bands forming a border ca. 1.5-2 μm high in optical section; as viewed under SEM a

secondary reticulum with smaller meshes covering the epispore is visible inside the basic reticulum (Fig. 17). Plasmodium hyaline to yellowish-milky.

On the basis of the structure of the peridium and colour of the spore mass, it was suspected that this material represented a species of *Didymium*. The majority of *Didymium* species have a well-developed capillitium, but some species appear to lack a capillitium. *Didymium atrichum* Henney & Alexop. in Henney, Alexopoulos & Scheetz (1980) and *D. nullifilum* (Kowalski) M.L. Farr (1982) are good examples of species with a reduced capillitium. None of the described species of *Didymium* with reduced capillitium appear to be closely related to this species, which differs in the unique structure of the spore ornamentation. *Didymium atrichum* has reticulate or spinulose spores but its spores are much smaller (10-11 µm diam) and only faintly reticulate under oil immersion. *Didymium nullifilum* another species with a reduced capillitium, has spores 8-10 µm diam covered with widely scattered spines up to 1 µm high.

A number of taxa with banded-reticulate spores have been described throughout many genera of myxomycetes, but this type of spore ornamentation is rare among species of *Didymium*. No described species of *Didymium* appears to be closely related to *D. subreticulosporum* Oltra, G. Moreno & Illana. *Didymium subreticulosporum* (Lizarraga *et al*., 1998) has banded-retuculate spores, but all other species of *Didymium* have spinulose, verrucose or faintly reticulate spores. Moreover, *D. subreticulosporum* has stipitate sporocarps and its spores are much smaller (9-11 µm diam). In contrast our species has sessile sporocarps and large prominently banded-reticulate spores (13-16 µm), with the secondary reticulum covering the epispore. This type of spore ornamentation has never been observed among the myxomycetes.

Didymium trachysporum G. Lister [**C**, Ze 1007/1 (+), mc-54] **I**: b/23, w/2, ll/9, lg/1, lt/1; **II**: b/16, lt/2. Loc.: 3, 4, 6, 7, 8, 12, 13, 14, 15, 18, 22, 23, 26, 31, 32, 36.

Notes: This was the most common *Didymium* in the general study area. Our specimens have the typical characters of the species. Sporotheca hemispheric or pulvinate on a constricted base, scattered, 0.1-0.6 mm diam, white or cream (Fig. 20). Peridium double, the outer layer a smooth or wrinkled crust of compacted lime crystals, the inner layer membranous, hyaline, iridescent. Spores 9-10 µm diam, dark purplish brown, coarsely and irregularly verrucose (Figs. 18, 19), the warts often arranged in lines to form an imperfect reticulation.

Echinostelium arboreum H. W. Keller & T. E. Brooks [**R**, Sc 15023 (+), mc-3] **I**: b/1, w/1; **II**: b/1. Loc.: 21, 22, 32.

Notes: Small to large colonies of single sporocarps, stout in habit, stalked, golden yellow-brown, shiny under dissecting microscope. Sporotheca globose or urn-shaped, 30-50 µm in diam (Fig. 22). Stalk 120-150 µm long, about two thirds of the total length filled with darker granules (Fig. 21), 10-15 µm in diam at the base, tapering to 2.5-3.5 µm on top. Peridium often persistent (Fig. 22), smooth and colourless in transmitted light, leaving at least a conspicuous collar (Fig 23). No particular dehiscence lines were visible, but sutures during sporocarp development allowed the peridium, usually not connected with the capillitial threads, to fall away in mature sporocarps. Capillitium arising from one point at the centre of the sporotheca with a few perpendicular, stiff branches, these mostly dichotomous 1(-2) times more forked, at the tips about 1 µm in diam (Fig. 23). Spores-mass rose (4B4) to olivaceous (5B4) brown, very pale olivaceous (4A3) under the microscope, globose, (5.5)-6.5-8-(9) µm in diam, minutely roughened (asperulate) under oil immersion, spinulose (delicately spiny) under SEM, evenly covered with somewhat distant spines (Fig. 24).

Echinostelium colliculosum K. D. Whitney & H. W. Keller [**O**, Ze 2794/1, Sc 14843 (+), mc-19] **I**: b/8, w/1, lt/2. **II**: b/8. Loc.: 14, 15, 22, 23, 31, 32, 33, 35, 36.

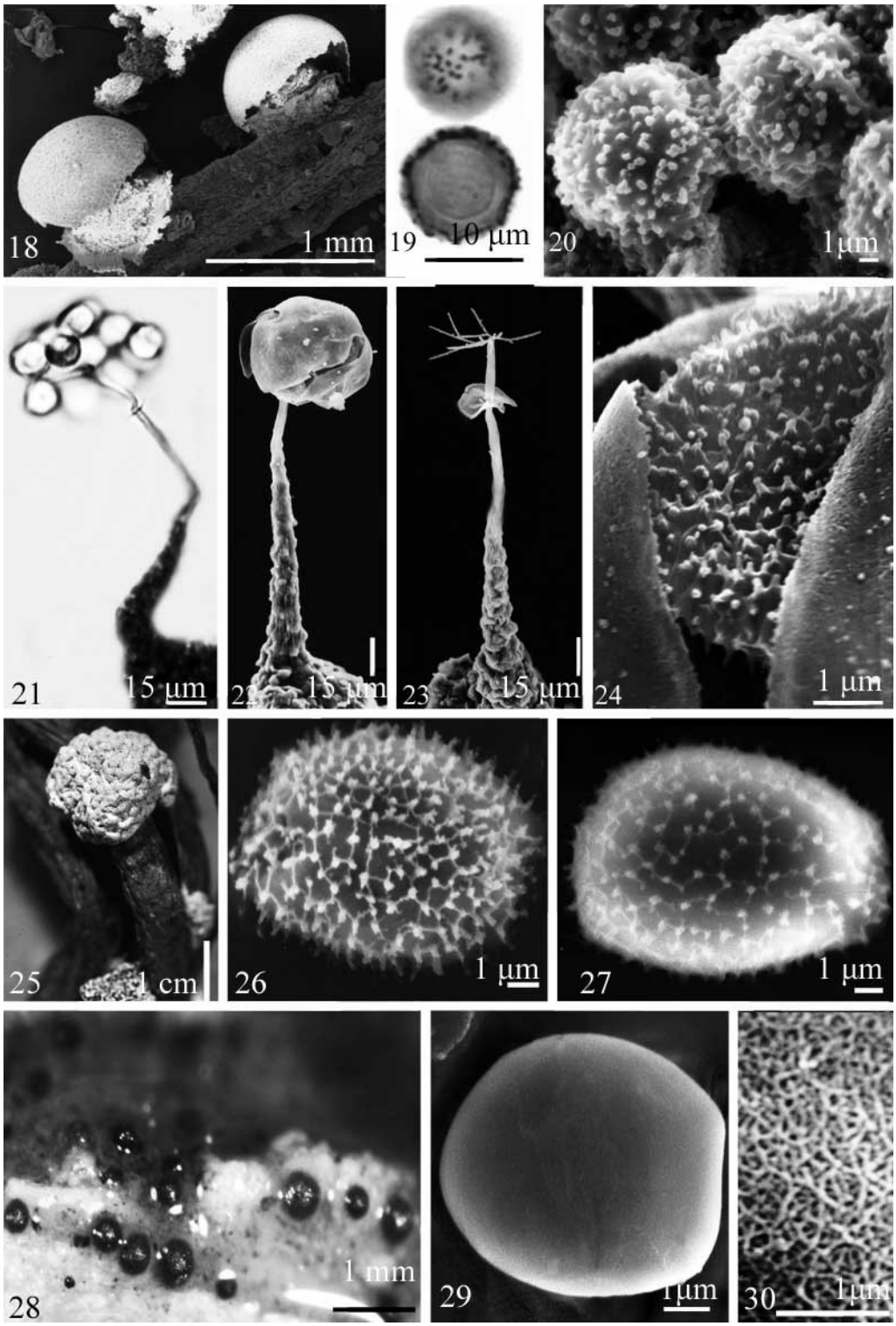
Echinostelium minutum de Bary [**O**, Ze 2105/1 (+), Sc 14866 (+), mc-23] **I**: b/10, lg/3, lt/2; **II**: b/8. Loc.: 9, 14, 15, 16, 20, 21, 22, 31, 32, 34, 36.

****Enerthenema papillatum*** (Pers.) Rostaf. [**R**, LE 205762 (+), fc-6] **I**: w/6. Loc.: 2, 4, 9, 15.

Fuligo cinerea (Schwein.) Morgan [**A**, Ze: 1/60/1 (+), Sc 15115 (+), fc-1, mc-200] **I**: b/69, lg/2, lt/51, d/5; **II**: b/25, w/1, ll/6, lg/3, lt/21, d/18. Loc.: 3, 9, 10, 12, 13, 14, 15, 16, 18, 20, 21, 22, 24, 25, 26, 28, 29, 32, 34, 35, 37, 38, 42, 43, 45, 46, 48.

Notes: The SEM micrographs (Figs. 26, 27) show that considerable variation exists in the spore ornamentation. The small aethalia (Fig. 25) of this species are almost invariably associated with litter and dung.

Figs 18-20. *Didymium trachysporum* (LE 219212). 18. Spores by TL with coarsely and irregularly distributed verruca. 19. Spores by SEM. 20. Sporocarps by SEM. **Figs 21-24.** *Echinostelium arboreum* (LE 205466). 21. Dehiscing sporocarp by TL. 22. Closed sporocarp by SEM. 23. Dehiscing sporocarp by SEM showing columella, capillitium and peridium remaining as a basal collar. 24. Detail of peridium and spore by SEM with dense even spines. **Figs 25-27.** *Fuligo cinerea* (LE 219966). 25. Sporocarps by dissection microscope. 26-27. Spores by SEM. **Figs 28-30.** *Licea denudescens* (LE 205452). 28. Sporocarps in moist chamber under dissection microscope. 29. Spore by SEM. 30. Spore ornamentation by SEM.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1µm

****Fuligo septica*** (L.) F. H. Wigg. [**R**, Ze 454 (+), fc-6] **I**: w/5, one collection on living grasses.

Hemitrichia clavata (Pers.) Rostaf. [**R**, Ze 100 (+), fc-17] **I**: w/16, ll/1. Loc. 1, 3, 6, 14, 15.

****Hemitrichia intorta*** (Lister) Lister [**R**, LE 218600, fc-1] **I**: w/1. Loc.: 14.

****Hemitrichia leiocarpa*** (Cooke) Lister [**R**, Ze 89/805/4, mc-1] **I**: b/1. Loc.: 12.

Kelleromyxa fimicola (Dearn. & Bisby) Eliasson [**R**, Sc 15447 (+), mc-3] **I**: d/2; **II**: d/1. Loc.: 21, 22, 25.

Notes: Sporocarps scattered, gregarious or clustered. Sporothecae shiny black, spindle-shaped, erect on a constricted base, 0.1-0.5 mm high, 0.05-0.25 mm wide. Peridium rather thick, cartilaginous, smooth. Dehiscence by separation of the two sides along what appears to be a preformed suture, or occasionally irregular. Spore-mass dull dark brown. Spores smoky, hyaline, with faint pinkish contents and a thick wall, evenly ornamented by spines, these (11-)13-15(-l6) µm diam. With strong preference for dung.

****Lamproderma arcyrioides*** (Sommerf.) Rostaf. [**R**, Ze 815, fc-1] **I**: ll/1. Loc. 22.

****Lamproderma arcyrionema*** Rostaf. [**R**, Ze 244 (+), fc-7, mc-1] **I**: w/7, ll/1. Loc.: 6, 13.

****Lamproderma columbinum*** (Pers.) Rostaf. [**R**, LE 219411, fc-1] **I**: ll/1. Loc.: 13.

****Lamproderma scintillans*** (Berk. & Broome) Morgan [**R**, LE 205649 (+), fc-4] **I**: w/2, ll/2. Loc.: 3, 6, 13.

****Leocarpus fragilis*** (Dicks.) Rostaf. [**R**, Ze 846, fc-1] **I**: ll/1. Loc.: 15.

Licea belmontiana Nann.-Bremek. [**O**, Ze 1500/4 (+), Sc 15425 (+), fc-1, mc-15] **I**: b/2, ll/1, lg/3; **II**: b/1, ll/2, lg/2, lt/3, d/2. Loc.: 22, 25, 26, 28, 31, 32.

Notes: The distinguishing characteristics of this species are the smooth peridium without tubercles, the apical plate acting as a lid and the basal plates forming petaloid lobes, as well as the dark brown spore-mass with spores rosy to brown under transmitted light, reaching only 10-13 µm in diam.

****Licea biforis*** Morgan [**R**, Ze 2812/7, 2817/6, mc-2] **I**: b/2. Loc.: 9.

Licea chelonoides Nann.-Bremek. [**R**, Ze 1429/3, mc-1] **II**: b/1. Loc.: 24.

Licea denudescens H. W. Keller & T. E. Brooks [**R**, Ze 702, Sc 14897 (+), mc-11] **I**: b/4; **II**: b/7. Loc.: 22, 25, 28, 32, 33, 36.

Notes: Our specimens have the typical characters of this species and match a description given by Keller & Brooks (1977). The moist sporangia have the appearance of shiny yellowish brown (9, Petersen, 1996) or dark olivaceous (2, Petersen, 1996) balls in a drop of clear gelatine (Fig. 28). The thicker outer layer of the peridium consists of material that is gelatinous when moist (Fig. 31) and finally weathers away by exposure to rain over a period of time. The inner layer of the peridium is densely ornamented with tiny warts and papillae (Fig. 32). The spores are glossy brown or dark olivaceous in mass, concolorous by transmitted light, thick-walled with a paler area, smooth under the light microscope and low magnification by SEM (Fig. 29), 10–13 µm in diam, under high magnification by SEM the spore wall complete and evenly ornamented by very dense reticulum (Fig. 30).

Licea kleistobolus G. W. Martin [**R**, Ze 141/372/3 (+), fc-1, mc-3] **I**: b/2, w/1; **II**: b/1. Loc.: 3, 11, 22, 36.

****Licea minima*** Fr. [**R**, Ze 2859/1, mc-1] **I**: b/1. Loc.: 9.

Licea nannengae Pando & Lado [**O**, Ze: 1424/5 (+), mc-7] **I**: b/4, w/1, lt/5; **II**: lt/2. Loc.: 9, 13, 14, 15, 24, 46.

Notes: Sporocarps scattered to gregarious, 0.05-0.2 mm diam, sessile, nearly globose on a somewhat narrowed to broad base, without platelets but with small ridges when dry (Fig. 33). Peridium brown to yellow-ochraceous (7, Petersen, 1996) with deposits of granular refuse matter which, when they are scanty, reveal the membranous inner layer (Fig. 34, 35), which is translucent, shiny and slightly iridescent, by transmitted light, with a smooth inner surface (Fig. 35), pale olive. Dehiscence by fragmentation of the peridium but without preformed lines of dehiscence. Spore-mass dark brown. Spores globose, olivaceous-brown (16, Petersen, 1996), smooth under the light microscope but verruculose under SEM (Fig. 36), thin-walled with an even thinner, paler area, 9.5-13.5 µm in diam.

This species is distinguished from *L. belmontiana* by its lack of platelets and olivaceous spores without a rose tint.

****Licea operculata*** (Wingate) G. W. Martin [**R**, Ze 218924 (+), mc-4] **I**: b/4. Loc.: 9, 11, 13, 16.

Licea parasitica (Zukal) G. W. Martin [**R**, Ze 2105, Sc 14875, mc-3] **I**: b/2; **II**: b/1. Loc.: 14, 22, 31.

Licea pusilla Schrad. [**R**, Ze 1423/3 (+), mc-3] **II**: b/2, lt/1. Loc.: 24, 29.

Licea scyphoides Keller & Brooks [**R,** LE 219531, mc-1] **II**: b/1. Loc.: 15.

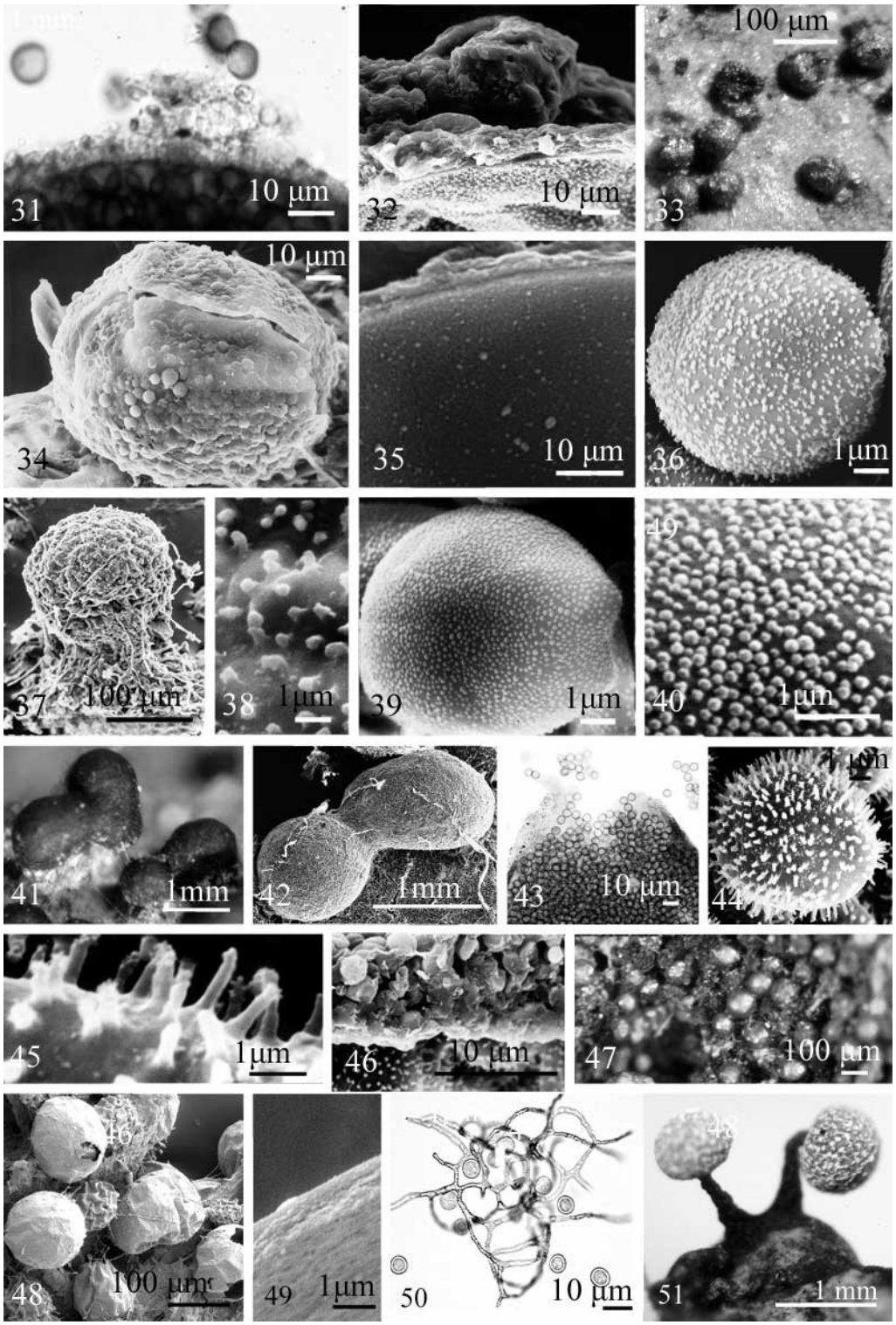
Notes: The single specimen, collected on the bark of *Acer negundo*, consists of well-matured sporocarps and conforms very closely to the descriptions provided by Keller and Brooks (1977) and Wrigley de Basanta and Lado (2005). Sporocarps 200-300 µm tall on a dark, stipe short 30-80 µm long, with abundant dark olive refuse matter (Fig. 37). Peridium membranous, forming a distinct boundary with the stalk, pale olivaceous brown by transmitted light, minutely papillose on the inner surface (Fig. 38), with deposits of refuse matter on the upper surface of the sporotheca (Fig. 37). Dehiscence by an equatorial circumscissile fissure but not as well pronounced as in *L. operculata*. Spore-mass golden brown. Spores pale brownish yellow, free, globose, smooth or minutely roughened, with a thinner, paler area by TL, closely and distinctly verruculose by SEM (Figs. 39, 40), 11.5-13 µm diam.

Licea tenera E. Jahn [**R**, Ze 2128/2 (+), mc-2] **I**: lg/1, lt/1. Loc. 14.

Notes: This species approaches *Perichaena liceoides* in habit and substrate preferences. Our specimens of *L. tenera* have a peridium in which the outer layer lacks the granular deposits as found in *P. liceoides* but is characterized by amorphous deposits. Spores minutely roughened (asperulate), requiring oil immersion to observe, spinulose (delicately spiny) under SEM, spines 0.2–0.3 µm high. See comments for *Perichaena liceoides*. This is another example of a strictly coprophilous myxomycete.

****Licea testudinacea*** Nann.-Bremek. [**R**, LE 218930 (+), mc-1] **I**: b/1. Loc.: 16.

Figs 31-32. *Licea denudescens* (LE 205452). 31. Spores and peridium with hyaline, gelatinous outer layer by TL. 32. Two adhering layers of peridium by SEM, outer layer with refuse material and inner layer marked by papillae. **Figs 33-36.** *Licea nannengae* (SC 15472, LE 218891). 33. Sporocarps in moist chamber under dissection microscope. 34. Sporocarp by SEM. 35. Inner surface of peridium by SEM. 36. Spore by SEM. **Figs 37-40.** *Licea scyphoides* (LE 219531). 37. Sporocarp by SEM. 38. Inner surface of peridium by SEM. 39. Spore by SEM. 40. Ornamentation of spore by SEM. **Figs 41-46.** *Perichaena liceoides* (LE 205582). 41. Sporocarps by dissection microscope. 42. Sporocarp with rough peridium containing granular material by SEM. 43. Detail of sporocarp by TL. 44. Spore by SEM. 45. Spore ornamentation by SEM showing long spines and small verruca on spore surface. 46. Detail of edge of peridium with granules of lime by SEM. **Figs 47-50.** *Perichaena luteola* (sc 15618). 47. Sporocarps by dissection microscope. 48. Sporocarps by SEM. 49. Detail of peridium by SEM. 50. Capillitium and spores by TL. **Fig. 51.** *Physarum notabile* (LE 205514). Sporocarps in moist chamber under dissection microscope.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50
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51
1 mm

****Lycogala epidendrum*** (L.) Fr. [**O**, LE 218008 (+), fc-22] **I**: b/1, w/20, ll/1. Loc.: 1, 3, 4, 6, 7, 9, 10, 11, 13, 15.

****Lycogala exiguum*** Morgan [**R**, LE 218203, fc-1] **I**: w/1. Loc.: 8.

****Lycogala flavofuscum*** (Ehrenb.) Rostaf. [**R**, LE 218218 (+), fc-3] **I**: b/2, w/1. Loc.: 15, 22.

Macbrideola cornea (G. Lister & Cran) Alexop. [**R**, Ze 2854/1, mc-1] **I**: b/1. Loc.: 9.

Macbrideola oblonga Pando & Lado [**O**, Sc 14844 (+), mc-36] **I**: b/7, w/2; **II**: b/25, w/2. Loc.: 20, 22, 24, 25, 28, 31, 32, 33, 34, 36.

Notes: Comparisons with material obtained from Kazakhstan (Schnittler and Novozhilov, 2000; Zemlianskaia, Adamonyte, Krivomaz and Novozhilov, unpubl. data), Mongolia (Schnittler and Novozhilov, unpubl. data), the Orenburg area of Russia (Novozhilov, unpubl. data), the Colorado Plateau of the western United States (Novozhilov *et al*., 2003) allow us to assign our specimens to *M. oblonga*. Common in arid regions.

****Metatrichia vesparia*** (Batsch) Nann.-Bremek. [**O**, Ze 241 (+), fc-18] **I**: w/17, ll/1. Loc.: 1, 3, 6, 13, 14, 15, 22.

****Mucilago crustacea*** F. H. Wigg. [**O**, LE 218009 (+), fc-26] **I**: b/1, w/7, ll/14, lt/1, three collections on living grasses. Loc. 1, 4, 6, 9, 11, 12, 13, 14, 15.

****Oligonema flavidum*** (Peck) Peck [**R**, Ze 271 (+), fc-8] **I**: w/8. Loc.: 6.

Oligonema schweinitzii (Berk.) G. W. Martin [**R**, Ze 3/272/3 (+), fc-1, mc-4] **I**: b/3 w/1, lt/1. Loc.: 14, 15, 16.

****Paradiacheopsis cribrata*** Nann.-Bremek. [**R**, Ze 154/385/2 (+), mc-2] **I**: b/2. Loc.: 9, 15.

****Paradiacheopsis solitaria*** (Nann.-Bremek.) Nann.-Bremek. [**R**, Ze 2146/1 (+), mc-2] **I**: b/2. Loc.: 9, 22.

Perichaena chrysosperma (Curr.) A. Lister [**C**, Ze 10/31/1, Sc 15204, fc-3, mc-66] **I**: b/47, w/9, ll/6, lt/3, d/1; **II**: ll/3. Loc.: 3, 9, 11, 12, 13, 14, 15, 16, 18, 22, 25, 27, 33.

Perichaena corticalis (Batsch) Rostaf. [**A**, Ze 100/971/2 (+), Sc 15497 (+), fc-7, mc-280] **I**: b/119, w/16, ll/16, lg/2, lt/22, d/5; **II**: b/41, w/4, ll/6, lg/7, lt/21, d/28. Loc.: 9, 10, 11, 12, 13, 14, 15, 16, 18, 22, 23, 24, 25, 26, 28, 29, 31, 32, 33, 36, 38, 40, 41, 42, 43, 44, 45, 46, 47.

Perichaena depressa Lib. [**A**, Ze 10/11/1 (+), Sc 15481 (+), mc-229] **I**: b/75, w/25, ll/21, lg/1, lt/15, d/3; **II**: b/30, w/8, ll/8, lg/3, lt/26, d/14. Loc.: 9, 10, 12, 13, 14, 15, 16, 18, 20, 21, 22, 24, 25, 26, 28, 29, 31, 32, 33, 34, 35, 36, 38, 42, 43, 44, 45, 46, 47, 48.

Perichaena liceoides Rostaf. [**A**, Ze: 10/71/2 (+), Sc 15424 (+), mc-106] **I**: b/31, w/4, ll/5, lt/12, d/6; **II**: b/17, ll/9, lg/3, lt/6, d/13. Loc.: 9, 12, 13, 14, 15, 16, 18, 20, 21, 22, 23, 24, 25, 26, 27, 32, 33, 35, 45, 46, 47, 48.

Notes: Our material consists of sporocarps (Fig. 41) that lack a capillitium. Prominent differences between this species and *L. tenera* include the structure of the peridium and spore ornamentation. The membranous layer of the peridium of *P. liceoides* is densely covered with rounded granular deposits 2.5-4 μm in diam (Figs 42, 43, 46). Spores have two types of ornamentation, the first consisting of spines 0.8-1.0 μm high with small lateral appendices up to 8 per spine and the second consisting of very small verrucae scattered among the spines (Figs 44, 45). This species appears to be common in arid regions, where it has been found on litter and dung of herbivorous animals (Novozhilov *et al*., 2003; unpubl. observations from Big Bend National Park in Texas, Mongolia and Kazakhstan).

Perichaena luteola (Kowalski) Gilert [**R**, Sc 15618, mc-1] **I**: d/1. Loc.: 22.

Notes: The distinguishing characters of this species are the transparent thin peridium with smooth inner surface (Figs. 47-49), olive shiny globose sporocarps with a bright yellow spore mass that looks as a dense globe within the sporocarp when observed with a dissecting microscope (Fig. 48). Capillitium yellow, composed of a network of branched and anastomosed tubules 1-4 μm diam (Fig. 50), with a few free ends that are weakly attached to the peridium. This is a strictly coprophilous myxomycete.

Perichaena minor (G. Lister) Hagelst. [**R**, Ze 106/297/1 (+), mc-6] **I**: b/1, ll/1, lg/1; **II**: w/1, lt/2. Loc.: 14, 16, 24.

Perichaena pedata (Lister & G. Lister) G. Lister ex E. Jahn [**R**, Ze 2850/8, mc-1] **I**: ll/1. Loc.: 9.

****Perichaena quadrata*** T. Macbr. [**O**, LE 218834 (+), fc-1, mc-25] **I**: b/18, w/3, ll/4, lt/1. Loc.: 9, 12, 13, 15, 16, 18, 22, 26, 46.

Perichaena vermicularis (Schwein.) Rostaf. [**C**, LE 218938 (+), Sc 14839 (+), fc-15, mc-81] **I**: b/27, w/9, ll/13, lg/1, lt/4, d/1; **II**: b/13, w/3, ll/10, lt/13, d/2. Loc.: 9, 10, 12, 13, 14, 15, 16, 18, 21, 22, 24, 25, 26, 28, 31, 32, 33, 34, 35, 36, 46.

***Physarum album** (Bull.) Chevall. = *Physarum nutans* Pers. [**O**, Ze 161 (+), fc-33] **I**: b/3, w/29, ll/1. Loc.: 3, 4, 6, 11, 13, 14, 15, 19, 22.

***Physarum bitectum** G. Lister [**R**, LE 218803, mc-1] **I**: w/1. Loc.: 22.

Physarum bivalve Pers. [**R**, Ze 177 (+), fc-3, mc-3] **I**: w/2, b/2, ll/1, one collection on living mosses. Loc.: 6, 9, 11, 13, 14, 16.

Physarum cinereum (Batsch) Pers. [**C**, Ze 1009/2 (+), Sc 15446 (+), fc-4, mc-44] **I**: b/6, w/2, ll/3, lg/8, d/2; **II**: b/8, w/3, lg/1, lt/12, d/3. Loc.: 15, 18, 20, 21, 22, 24, 26, 28, 29, 32, 38, 41, 42, 43.

Physarum compressum Alb. & Schwein. [**O**, Ze 103/157/2 (+), Sc 15180 (+), mc-31] **I**: b/7, w/1 d/1; **II**: b/15, w/2, lt/1, d/4. Loc.: 9, 13, 15, 16, 22, 24, 28, 32, 33, 36, 38.

***Physarum conglomeratum** (Fr.) Rostaf. [**R**, Ze 294, fc-1] **I**: w/1. Loc.: 6.

Physarum decipiens M. A. Curtis [**C**, Ze 1/735/1 (+), Sc 14888 (+), mc-77] **I**: b/49, ll/1, d/1; **II**: b/16, w/3, ll/2, lt/4, d/1. Loc.: 9, 10, 12, 14, 15, 16, 18, 20, 22, 25, 31, 32, 33, 34, 36.

***Physarum diderma** Rostaf. [**R**, Ze 178 (+), fc-1, mc-2] **I**: b/1, one field collection on soil; **II**: b-1. Loc.: 11, 12, 26.

Physarum didermoides (Pers.) Rostaf. [**O**, Ze 1023/3 (+), Sc 15220 (+), mc-29] **I**: b/7, ll/2, lg/1, d/1; **II**: b/11, ll/1, lg/1, lt/3, d/2. Loc.: 9, 12, 13, 18, 21, 22, 24, 26, 27, 28, 29, 32, 33, 36, 38, 43.

***Physarum flavicomum** Berk. [**R**, Ze 266 (+) fc-2] **I**: w/2. Loc.: 6, 13.

Physarum gyrosum Rostaf. [**R**, Ze 9312/3 (+) mc-1] **I**: lt/1. Loc.: 14.

Physarum leucophaeum Fr. [**O**, Ze 1093/6, Sc 14928 (+), fc-24, mc-27] **I**: b/9, w/17, ll/5, lt/4, three collections on living mosses; **II**: b/4, w/1, lg/2, lt/6. Loc.: 1, 3, 6, 9, 11, 13, 15, 16, 18, 19, 21, 22, 24, 26, 28, 29, 37, 38, 46.

***Physarum leucopus** Link [**R**, Ze 654, fc-1] **I**: ll/1. Loc.: 13.

Physarum notabile T. Macbr. [**A**, Ze 177/917/1 (+), Sc 14842 (+), fc-3, mc-223] **I**: b/45, w/7, ll/7, lg/11, lt/5, d/7, one collection on lichens originated from moist chamber culture; **II**: b/60, w/7, ll/9, lg/14, lt/36, d/17. Loc.: 9, 10, 12, 13, 14, 15, 18, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 31, 32, 33, 34, 35, 36, 38, 46, 47, 48.

Notes: This species is the most abundant myxomycete in arid areas (Novozhilov and Golubeva, 1986; Schnittler and Novozhilov, 2001; Novozhilov

et al., 2003; unpublished data from central and western Kazakhstan and the Orenburg region of Russia) and occurs on all types of substrates. Three forms, which were described in detail from material collected on the Mangyshlak Peninsula (Schnittler and Novozhilov, 2001), were represented in our collections from the Low Volga River Basin. The majority of our specimens include forms with globose sporotheca (Fig. 51).

Physarum nudum T. Macbr. [**R**, Ze 48/707/3 (+), mc-2] **I**: b/1, w/1. Loc.: 22.

Notes: Our specimens agree with the description of *P. nudum* and cannot be placed elsewhere with more certainty. They could be confused with a limeless form of *P. cinereum*, but the latter species is associated with a different microhabitat (litter).

****Physarum ovisporum*** G. Lister [**R**, LE 219209 (+), mc-2] **I**: b/2. Loc.: 18.

****Physarum pezizoideum*** (Jungh.) Pavill. & Lagarde [**R**, LE 218217 (+), fc-6] **I**: b/2, w/4. Loc.: 6.

Physarum pusillum (Berk. & M. A. Curtis) G. Lister [**R**, Ze 1080/3 (+), mc-5] **I**: b/1; **II**: b/1, w/1, lg/1. Loc.: 22, 37, 38, 44.

Physarum sessile Brândza [**R**, Sc 15111 (+), mc-3] **I**: ll/1, lg/1; **II**: b/1. Loc.: 21, 25, 27.

****Physarum straminipes*** Lister [**R**, LE 218025 (+), fc-8, mc-1] **I**: b/1, w/4, ll/4. Loc.: 13, 22.

Physarum vernum Sommerf. [**R**, Ze 134/874/3 (+), fc-5, mc-5] **I**: b/3, w/2, ll/2, d/1; **II**: b/1, lt/1. Loc.: 13, 15, 18, 22, 28, 29.

*

Physarum virescens Ditmar in Sturm [**R**, Ze 399, fc-1] **I**: w/1. Loc.: 14.

****Physarum viride*** (Bull.) Pers. [**R**, Ze 246 (+), fc-9] **I**: w/9. Loc.: 3, 4, 6, 11, 15.

Protophysarum phloiogenum M. Blackw. & Alexop. [**R**, Ze 12046/1 (+), Sc 14863, mc-5] **II**: b/2, w/2, lt/1. Loc.: 24, 28, 32.

****Reticularia intermedia*** Nann.-Bremek. [**R**, Ze 604, fc-1] **I**: w/1. Loc.: 15.

****Reticularia lycoperdon*** Bull. [**R**, Ze 479 (+), fc-4] **I**: w/4. Loc.: 6, 14, 15.

****Reticularia splendens*** Morgan [**R**, Ze 183 (+), fc-6] **I**: b/1, w/5. Loc.: 3, 6, 11, 14.

Reticularia cf. sp. [**R**, LE 220333, mc-1] **II**: b/1. Loc.: 11.

Notes: This taxon is represented by several small but well-matured sporocarps from the bark of *Pinus sylvestris*, collected from the steppe zone in a pine plantation. Sporocarps are 1-5 mm in diam and consist of closely interwoven sporangia, deep olive (2, Petersen, 1996), with these forming a close network of tufts, sometimes so closely massed as to approach an aethalium, enclosed in a smooth very thin (shiny yellowish) transparent cortex (Fig. 52), without any deposits. Capillitium and pseudocapillitium are absent. Spore mass curry-yellow (12, Petersen, 1996). Spores pale olive (2, Petersen, 1996) in clusters of 5-25, turbinate and covered with verrucae on the outside, smooth on the inside of the cluster, 10-13 μm diam (Figs. 53, 54).

This new taxon apparently could be referred to either *Reticularia* or *Licea*. The habit of the sporocarp, structure of the peridium, shape, color and ornamentation of spores resemble *R. olivacea*, but this species has a dense system of perforated pseudocapillitium. Applying the currently used generic delimitation of *Licea*, our specimens have to be accommodated in the genus *Licea* due to the lack of a capillitium or pseudocapillitium. We can not find any traces of either a capillitium and pseudocapillitium even after an intensive examination under SEM, and for this reason our specimens would be formally placed in *Licea*. However, to reach any final conclusion about the taxonomic position of this taxon, it will be necessary to have more material.

****Stemonaria irregularis*** (Rex) Nann.-Bremek. [**R**, Ze 624, fc-1] **I**: w/1. Loc.: 15.

****Stemonaria longa*** (Peck) Nann.-Bremek., R. Sharma & Y. Yamam. [**R**, Sc 15583, mc-4] **I**: b/3, w/1. Loc.: 27.

****Stemonitis axifera*** (Bull.) T. Macbr. [**O**, Ze 11 (+), fc-31, mc-2] **I**: b/3, w/30. Loc.: 1, 3, 6, 7, 9, 10, 13, 15, 19.

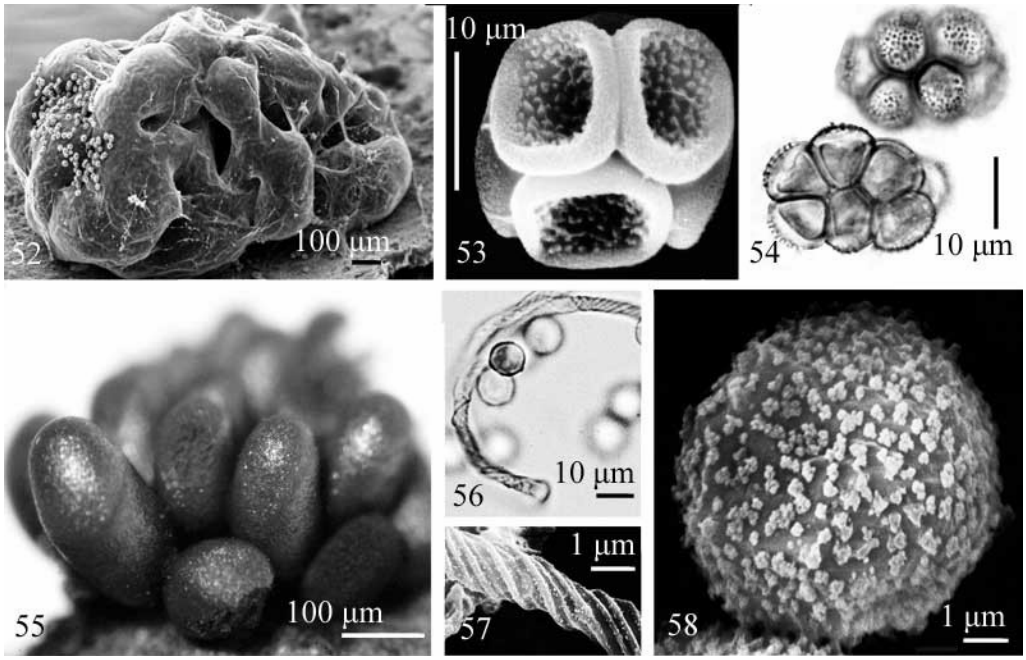
Stemonitis fusca Roth [**O**, Ze 108/979/1 (+), Sc 15442 (+), fc-21, mc-14] **I**: b/13, w/20, lt/1; **II**: w/1. Loc.: 3, 6, 7, 9, 10, 13, 14, 15, 16, 20, 22, 25.

Stemonitis hyperopta Meyl. [**R**, Ze 16 (+), fc-7, mc-2] **I**: b/2, w/7. Loc.: 9, 10, 13, 15, 22.

****Stemonitis lignicola*** Nann.-Bremek. [**R**, Ze 657 (+), fc-2] **I**: w/2. Loc.: 13, 15.

****Stemonitis nigrescens*** Rex [**R**, Ze 19 (+), fc-1, mc-3] **I**: b/3, w/1. Loc.: 9, 13, 15.

****Stemonitis pallida*** Wingate [**R**, Ze 561 (+), fc-3] **I**: w/3. Loc.: 15, 22.



Figs 52-54. *Reticularia* sp. (LE 237000). 52. Sporocarp by SEM. 53. Spore clusters by SEM with collapsed spore walls. 54. Spore clusters by TL with densely verruculose on free side and elsewhere smooth. **Figs 55-58.** *Trichia brunnea* (LE 205465). 55. Habit by dissection microscope. 56. Capillitium with two loose spirals and with slightly swollen tips by TL. 57. Capillitium by SEM. 58. Spore by SEM.

****Stemonitis smithii*** T. Macbr. [**R**, Ze 276 (+), fc-4] **I**: w/4. Loc.: 6, 15, 46.

Stemonitis splendens Rostaf. [**O**, LE 219431 (+), fc-42] **I**: b/10, w/29, three collections found on living grasses. Loc.: 1, 3, 4, 5, 6, 9, 10, 13, 14, 15, 17, 22.

****Symphytocarpus flaccidus*** (Lister) Ing & Nann.-Bremek. [**R**, LE 218645, Sc 15579, mc-1, fc-2] **I**: b/1; **II**: b/1. Loc.: 5, 33.

Trichia brunnea J. J. Cox [**R**, Ze 89/805/6, Sc 15448, mc-2] **I**: b/1, d/1. Loc.: 12, 22.

Notes: Our material consists of small groups of sporangia, these sessile on a restricted base (Fig. 55), shiny brown, 0.3-0.8 mm broad, 0.8-1 mm high. Peridium single, somewhat iridescent, membranous, translucent, with a circumscissile line of dehiscence. Capillitium olivaceous, composed of simple or sparsely branched elaters (Fig. 56), elaters smooth, with two loose spirals and small papillae by SEM (Fig. 57), 2.0-3.0 µm diam with slightly swollen tips (Fig. 56), 2.5-3.0 µm diam. Spore-mass brown. Spores olivaceous by

transmitted light, prominent verrucose observed under SEM (Fig. 58), 10-11 µm diam.

****Trichia contorta*** (Ditmar) Rostaf. [**R**, Ze 159 (+), fc-6, mc-1] **I**: w/5, ll/2. Loc.: 9, 10, 13, 14, 15, 22.

****Trichia contorta*** var. ***karstenii*** (Rostaf.) Ing [**R**, LE 218033 (+), fc-10] **I**: b/2, ll/8. Loc. 22.

****Trichia decipiens*** (Pers.) T. Macbr. [**R**, LE 218220 (+), fc-3] **I**: w/3. Loc.: 4, 6, 15.

****Trichia favoginea*** (Batsch) Pers. [**R**, Ze 279 (+), fc-12] **I**: w/12. Loc.: 3, 6.

****Trichia scabra*** Rostaf. [**R**, LE 205978, Ze 98, fc-2] **I**: w/2. Loc.: 3.

****Trichia varia*** (Pers.) Pers. [**R**, LE 218057 (+), fc-4] **I**: w/3, ll/1. Loc.: 15, 22.

****Tubulifera arachnoidea*** Jacq. = *Tubifera ferruginosa* (Batsch) J. F.Gmel. [**R**, LE 218013 (+), fc-3] **I**: w/6. Loc.: 1, 6, 11, 13, 14.

****Tubulifera casparyi*** (Rostaf.) Lado = *Tubifera casparyi* (Rostaf.) T. Macbr. [**R**, LE 219474, fc-1] **I**: w/1. Loc.: 19.

Myxomycete diversity

The present survey yielded a total of 3227 records (852 field collections and 2379 records originating from 1470 moist chamber cultures), from which 158 species representing 35 genera (including *Ceratiomyxa fruticulosa*, traditionally regarded as a myxomycete but now placed with the protostelids [Protosteliomycetes]) were identified. As a whole, species diversity of the Lower Volga River Basin is high (H' = 3.9) and the Simpson's dominance index is rather low (D = 0.04). At least 113 (72%) of the 158 taxa are classified as rare for whole area. Most of these species were collected in the field on woody debris and leaf litter in intrazonal arboreal habitats located in gully and riparian forests, where conditions are rather similar to those in temperate deciduous forests. In treeless zonal steppe habitats on grass litter, only one specimen of *Fuligo cinerea* was found. This contrasts markedly with the number of taxa found in gully and riparian forests and artificial tree plantations, where 78 species were recorded in the field. In desert regions in zonal habitats, no field collections were obtained. From the 92 species collected in intrazonal arboreal habitats, 62 species from 26 genera were

recorded in the field exclusively, and most species found there are lignicolous (52 species, 278 records) or inhabitants of leaf litter (18 species, 46 records). Common species found in the field (recorded more then 5 times) and confined exclusively to wood debris were *Arcyria obvelata*, *Cribraria aurantiaca*, *C. cancellata*, *Enerthenema papillatum*, *Ceratiomyxa fruticulosa*, *Hemitrichia clavata*, *Lycogala epidendrum*, *Metatrichia vesparia*, *Oligonema flavidum*, *Physarum album*, *Physarum viride*, *Trichia favoginea* and *Tubulifera arachnoidea*. Prominent examples of litter-inhabiting species were *Craterium leucocephalum*, *C. minutum*, *Didymium crustaceum*, *D. minus*, *Mucilago crustacea* and *Trichia contorta* var. *karstenii*. All of these species are widely distributed and often abundant in temperate deciduous forests and are also well known from the taiga. This suggests that the zonal limits of myxomycete distribution are relative. During the transition towards steppe, forest species disappear gradually. In the forest zone they are found in a variety of microhabitats in watersheds and in damp depressions. In the steppe zone they also occur in appropriate situations in intrazonal arboreal habitats where there is a rich supply of woody debris and leaf litter.

Surprisingly, in spite of the harsh climatic conditions associated with zonal treeless open steppe and desert communities, species richness is rather high. For example, 40 species originating from 571 records were found in different treeless sagebrush steppe and desert communities dominated by *Artemisia arenaria*, *A. lercheana* and *A. santonica*. In zonal steppe and desert communities, we recorded a total of 63 species, originating from 509 and 808 records, respectively. All species, excluding one field collection in steppe, were obtained from moist chamber cultures.

The distribution of species differs considerably in intrazonal habitats and in zonal open steppe and desert habitats. The high species richness in intrazonal habitats is due primarily to the general rarity of lignicolous species and litter-inhabiting species in steppe. As the specificity of the environment increases with the prevailing conditions of the open zonal habitats of steppe and desert, the number of rare species decreases and the proportion of abundant species increases. This follows the pattern that species dominance in zonal desert and steppe habitats with extreme conditions is higher ($D = 0.07$) than in the more stable and diverse habitats of intrazonal habitats, such as those found in gully and riparian forests in steppe ($D = 0.03$).

The most abundant species in treeless steppe and desert zonal habitats (>3% of all 1317 records) were *Badhamia spinispora*, *Comatricha laxa*, *Didymium anellus*, *D. difforme*, *D. trachisporum*, *Fuligo cinerea*, *Perichaena corticalis*, *P. depressa*, *P. liceoides*, *P. vermicularis*, *Physarum cinereum*, *Ph. decipiens* and *Ph. notabile*. Species richness (50 species recorded in each zone)

and diversity (H' = 3.0) were equal in zonal habitats of steppe and desert. The species composition was also very similar. However, *Arcyria minuta* and *Macbrideola oblonga* were found to be relatively common in desert but rare in steppe.

Myxomycete species richness and diversity varied considerably on different substrates (Table 1). The bark of living trees and shrubs were characterized by the highest diversity (H' = 3.5, S/G = 3.9) and species richness (83 species representing 21 genera). The mean value for the number of species per culture was 2.1 ± 0.1 (Table 1). Up to 8 species per culture were observed. On all of substrates examined in this present study, from 2 to 8 dominant species, all having a high frequency of occurrence, were always recorded. For example, on the bark of *Tamarix* (67 records) the dominant species were *Arcyria minuta* (18%) and *Comatricha laxa* (28%); on the bark of *Calligonum* (44 records) the dominant species were *Macbrideola oblonga* (16%), *Physarum notabile* (16%), and *Ph. decipiens* (11%); and on the bark of *Artemisia lercheana* (350 records) *Badhamia spinispora* (22%), *Perichaena corticalis* (17%), and *Fuligo cinerea* (10%) were dominant.

Table 1. Comparison of the assemblages of species of bark-, wood-, litter- and dung-inhabiting myxomycetes of the Lower Volga River Basin (data were obtained only from moist chamber cultures).

	Mc	PMc	R	S/Mc ± SE	S	G	S/G	H´	D
Bark	1016	959	1404	2.14 ± 0.05	83	21	3.9	3.5	0.04
Wood	121	74	161	2.21 ± 0.14	44	17	2.6	3.0	0.06
Litter	620	339	640	1.89 ± 0.06	53	18	2.9	3.0	0.07
Dung	136	98	174	1.80 ± 0.10	23	9	2.5	2.4	0.1

Note: Mc = number of moist chamber cultures prepared; PMc = number of positive moist chamber cultures; R = number of records; S/Mc = mean number species per culture ± SE; S = number of species; G = number of genera; S/G = species/genus ratio; H´ = Shannon's diversity index; D = Simpson's dominance index.

In desert regions, litter plays an important role as a microhabitat for myxomycetes. It is known that plant litter mineralizes rather quickly in deserts (Dobrovol'skaya *et al*., 1997) due to the high abundance of hydrolytic bacteria, which are a source of food for myxomycetes. Litter (620 moist chamber cultures) was less productive than bark and was characterized by lower diversity (H' = 3.0, S/G = 2.9) and species richness (53 species representing 18 genera). The mean value for the number of species per moist chamber culture prepared with litter was 2.8 ± 0.3 (Table 1), and as many as 6 species per culture were observed. Among the 53 species recorded from litter in moist chamber cultures, the dominant litter-inhabiting forms were species of *Perichaena*.

From all 782 records of the 7 species of *Perichaena* recovered from moist chamber cultures in the present study, 233 records including all 7 species came from litter. Other typical litter-inhabiting species were *Fuligo cinerea* (82 records) and *Physarum notabile* (83 records).

Among the three main substrates investigated by means of the moist chamber culture technique, dung was characterized by the lowest diversity (H' = 2.4) and a species-poor myxomycete biota (23 species representing 9 genera). The average number of species per moist chamber culture prepared with dung was 1.4 ± 0.3 (Table 1). As many as 5 species per culture were observed. The assemblage of myxomycetes associated with dung was rather restricted but distinctive in species composition. Of the members this assemblage, only *Kelleromyxa fimicola and Trichia brunnea* appear to be obviously obligate coprophilous. For the most part, species such as *Perichaena liceoides* and *P. depressa* that were found on dung also were common on litter.

The most common coprophilous species were *Fuligo cinerea* (23 records, 13% of 176 records on dung) and *Perichaena liceoides* (19 records, 11%). These species are characterized by a long period (up to 3 months) of development in moist chamber cultures and form larger, sessile sporocarps with a well-developed peridium (*F. cinerea*) or numerous colonies *P. liceoides*. It is interesting to note that the assemblage of coprophilous species from desert habitats of the Low Volga River Basin differed considerably from those found in northern taiga and tundra, where *Didymium difforme*, *Ph. bivalve* and *Leocarpus fragilis* were encountered regularly on dung (Novozhilov, unpubl. data) and the species (*F. cinerea*) represented by the most records in desert occurs only sporadically. The proportion of dominants is almost identical for assemblages of corticolous species (9 species as dominants, 18% of all species on bark) and assemblages of litter-inhabiting species (10 species, 24%), and the proportion increases sharply for assemblages of coprohilous species (9 species, 41%), where the maximum index of dominance (D = 0.1) was observed.

Community coefficient values, calculated for pairwise combinations of sets of data from other study sites in arid areas ranged from 0.61 for the myxomycete biota of the Mangyshlak Peninsula (Schnittler and Novozhilov, 2000) to 0.73 for myxomycete biota of the Colorado Plateau (Novozhilov *et al*., 2003). These rather high values indicate relatively high levels of similarity among the myxomycete biotas of deserts and semi-deserts.

Our data allow us to make some general conclusions about the distribution and occurrence of myxomycetes in arid regions of the Low Volga River Basin. Many common forest lignicolous and litter-inhabiting species extend far into the steppe zone, utilising intrazonal habitats of gullies and riparian forests. In zonal open treeless habitats, there is a distinct assemblage of

species-dominants with high frequency (>3%), the composition of which varies considerably on different substrates. Species diversity of myxomycetes decreases dramatically from the bark of living plants to the different types of litter and dung substrates. Differences in the composition of species-dominants on the same substrates in steppe and desert habitats were not found. In general, species richness and diversity decrease from north to south, primarily due to the disappearance of the rare species found in intrazonal forest habitats of regions of steppe. The myxomycete species composition of steppe and desert communities of the Low Volga River Basin is characterized by a high enough level of similarity with the species composition of other arid regions of the world to suggest that these taxa comprise a complex of xerotolerant species, which are probably widely distributed in steppe and desert habitats throughout the world, many of which are still poorly investigated.

Data analysis

As has been demonstrated by Schnittler (2001), the moist chamber culture technique is essential for the study of myxomycete ecology in deserts. Collectively, 1893 moist chamber cultures were used for assessment of the myxomycete biodiversity of the Low Volga River Basin. However, a full set of the environmental parameters needed for ecological analysis, including the type of substrate, light intensity, wind exposure, water retention of the substrate in question, pH and the type of bark texture, were recorded for only 295 moist chamber cultures prepared with substrate samples collected in 1998 during an expedition to the deserts of the northwestern Caspian Lowland (Russia) within of the Low Volga River Basin. For this reason, only the results obtained from this set of data could be used for canonical correspondence analysis (CCA, Ter Braak 1986, 1987) and estimation of niche breath. The methods used for data analysis were described in detail by Schnittler (2001) and Schnittler *et al*. (2002). The eigenvalues that were calculated, which ranged between 0 and 1, represent a measure of the degree to which species distribution can be explained by the respective ordination axis (Ter Braak, 1987). Calculations were carried out with the program PcOrd 4.17 and SygmaPlot 2002, vers.8 (ser. N 7988483).

Values for niche breadth (NB) *sensu* Whittaker *et al*. (1973) were calculated as described in Stephenson (1988), using the formula $NB = 1/\sum P_{ij}^{2}$. The sum refers to the number of states for the environmental parameter defining a niche dimension, with P_{ij} as the proportion of species *i* associated with state *j* divided by the total abundance of species *i* across all states (Feinsinger *et al*., 1981). Each moist chamber culture, representing a sample collected from one microhabitat in one sampling plot, was assigned to a position along each

environmental parameter that could be measured or determined for the microhabitat in question.

Numbers of records or total abundance were used as a measure of abundance for a particular species. Parameters used to define niche dimensions were the type of substrate, light intensity, wind exposure, water retention of the substrate in question, pH and the type of bark texture. For development time, the five days (2, 6, 11, 21 and 40) on which moist chamber cultures were checked represented the resource states. Values of pH were subdivided into five classes (3.5-4.5, 4.5-5.5, 5.5-6.5, 6.5-7.5 and >7.5, whereas the resource states used for the other parameters were those described by Schnittler (2001).

To estimate the extent to which the survey was exhaustive in terms of recorded species, a bootstrap analysis, modified from the procedures described by Krebs (1999), was carried out (Schnittler and Stephenson, 2000; Schnittler, 2001). The corresponding plot of the mean cumulated number of species versus the number of samples was subjected to a regression analysis, using the saturation formula $y = Ax/(B + x)$, where x is the number of samples, y represents the number of species recorded, and the parameter A refers to the maximum number of species to be expected (Fig. 59).

The rank-abundance plot of all myxomycete species was used to test four species abundance models (geometric series, log series, log normal and MacArthur broken stick) according to the procedures described by Magurran (1988). The goodness of fit was compared with a chi-square test, using the deviations between the observed and expected number of species for classes (Table 3).

For analysis of myxomycete associations (i.e., in the sense of co-occurrence, as used herein), the Cole ($C_{1/2}$) and the Brave indices of interspecific association and its standard error were computed. These indices are based on a 2 x 2 contingency table for presence and absence of a pair of species in one moist chamber culture, ranging from -1 (the species never occur together in the same moist chamber) to 1 (the species always occur together in the same moist chamber). $Kb = \sqrt{\chi^2/N}$ and $C_{1/2} = (ad-bc)/(a+b)(b+d)$ accordingly, where $\chi^2 = (ad-bc)^2N/(a+b)(c+d)(a+c)(b+d)$, where N is the total number of moist chamber cultures (Cole, 1949).

Results and discussion

In the present study, with a total of 678 records of 44 species representing 18 genera were identified from moist chamber cultures (Table 2). The six most common species (*Comatricha laxa*, *Didymium anellus*, *Fuligo cinerea*,

Table 2. Abundance values and pH preferences of myxomycetes recorded from the Caspian Lowland. (Data are from moist chamber cultures prepared with substrates collected in 1998 during an expedition in the northwestern Caspian Lowland, Russia).

Species name	Acronym	Abundance rec[a]	Abundance sp[b]	PH m[c] (min-max)
Arcyria cinerea	ARCcin	14	1682	5.9 (3.8-7.4)
Arcyria minuta	ARCmin	11	1112	5.6 (3.8-7.5)
Arcyria pomiformis	ARCpom	7	272	5.6 (4.1-7.9)
Badhamia foliicola	BADfol	14	4003	5.6 (3.8-7.5)
**Comatricha ellae*	COMell	2	107	4.1
Comatricha laxa	COMlax	28	2316	5.4 (3.5-7.9)
Comatricha pulchella	COMpul	11	725	5.9 (4.6-6.9)
**Cribraria violacea*	CRIvio	1	52	6.9
Didymium anellus	DDYane	44	3435	6.4 (4.1-7.6)
**Didymium bahiense*	DDYbah	1	120	6.8
Didymium difforme	DDYdif	11	602	6.7 (5.9-7.5)
Didymium iridis	DDYiri	4	1129	6.7 (6.2-7.1)
Didymium squamulosum	DDYsqu	7	563	6.9 (6.5-7-1)
**Didymium trachysporum*	DDYtra	1	125	6.1
**Diderma cinereum*	DIDcin	1	8	7.0
Echinostelium arboreum	ECHarb	3	143	6.9 (5.4-7.8)
Echinostelium colliculosum	ECHcol	12	4374	6.9 (4.7-8.0)
Echinostelium minutum	ECHmin	15	1571	5.9 (4.1-7.6)
Fuligo cinerea	FULcin	26	3603	6.7 (5.7-7.8)
**Kelleromyxa fimicola*	KELfim	2	5027	7.5 (7.5-7-9)
Licea belmontiana	LICbel	12	7620	6.7 (5.9-7.8)
Licea denudescens	LICden	11	944	6.9 (6.2-7.9)
**Licea kleistobolus*	LICkle	1	10	6.5
**Licea nannengae*	LICnan	2	1050	6.5 (6.2-6.8)
**Licea parasitica*	LICpar	2	140	7.1 (6.4-7.8)
Macbrideola oblonga	MACobl	36	809	6.8 (5.8-8.0)
Perichaena chrysosperma	PERchr	4	269	6.5 (5.6-7.6)
Perichaena corticalis	PERcor	25	2378	6.6 (5.1-7.9)
Perichaena depressa	PERdep	55	6535	6.5 (5.7-7.8)
Perichaena liceoides	PERlic	36	11051	6.6 (4.1-7.6)
Perichaena luteola	PERlut	1	1300	7.5
**Perichaena quadrata*	PERqua	2	940	6.2 (5.8-6.7)
Perichaena vermicularis	PERver	43	1873	6.7 (5.7-8.0)
Physarum cinereum	PHYcin	13	3679	6.6 (5.5-7.7)
Physarum compressum	PHYcom	13	1432	6.6 (5.1-7.2)
Physarum decipiens	PHYdec	34	1872	6.7 (4.9-7.9)
Physarum didermoides	PHYdio	14	1508	6.8 (6.1-7.5)
**Physarum leucophaeum*	PHYleu	1	30	7.8
Physarum notabile	PHYnot	150	11682	6.6 (4.1-8.0)
Protophysarum phloiogenum	PPHphl	1	50	7.3

Table 2 continued. Abundance values and pH preferences of myxomycetes recorded from the Caspian Lowland. (Data are from moist chamber cultures prepared with substrates collected in 1998 during an expedition in the northwestern Caspian Lowland, Russia).

Species name	Acronym	Abundance rec[a]	Abundance sp[b]	PH m[c] (min-max)
**Stemonaria longa*	STAlon	1	90	5.2
Stemonitis fusca	STEfus	4	415	5.4 (4.5-6.9)
**Symphytocarpus flaccidus*	SYMfla	1	130	4.1
**Trichia brunnea*	TRIbru	1	45	7.9

[a]Number of records per substrate type. [b]Sum of sporocarps recorded from all moist chamber cultures with the respective species present. [c]Mean pH of all moist chamber cultures with the respective species present. *Rare species excluded from the ecological analysis.

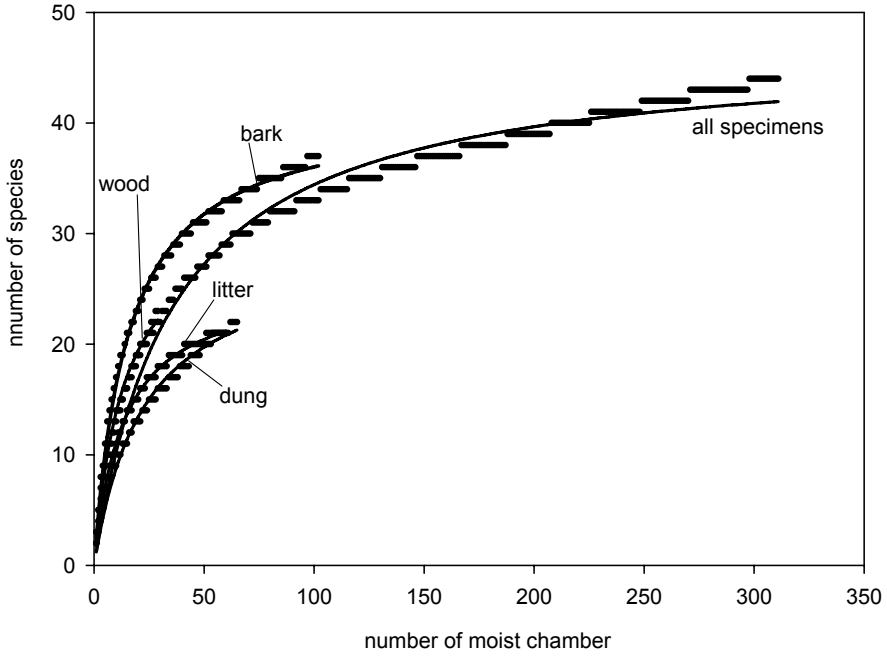


Fig. 59. Bootstrap analysis of the randomly permutated sequence of samples (moist chamber cultures) versus cumulated species numbers (black dotes). The presented values are the means of 100 runs. The solid lines show the results of regression analysis using a saturation function $y=Ax/(B + x)$, where A is the maximum number of species to be expected and B is the number of samples needed to reach half of the number of species to be expected.

Macbrideola oblonga, *Perichaena vermicularis* and *Physarum notabile*) represented 48% of the total number of specimens.

Completeness of survey

For a regression with a simple saturation function, an estimate of 32 species to be expected was obtained from the bootstrap analysis (Fig. 59). According to a fit with a saturation function extended by a linear term, 47 species would be expected to occur regularly. Comparing the actual numbers of species with estimations obtained by means of the bootstrap method (Table 3), the survey was complete to 88% for bark-inhabiting, 84% for litter-inhabiting, 76% for dung-inhabiting and 67% for wood-inhabiting species, respectively. As a result, it can be assumed that our sampling effort was sufficient for recovering all of the more common species in all types of substrates. In reality, of the 44 species recorded in total, 28 were represented by more than three records and included in our ecological analysis, whereas 16 rare species were excluded from the analysis (Table 2).

Myxomycete diversity

When considering results from this component of our study (Table 4) with data derived from all 1893 moist chamber cultures (Table 1), there is a close agreement. In both instances, species richness and diversity were significantly higher on bark than for other substrates. As can be observed from the rank-abundance plots of the myxomycete assemblages for the various substrates, the proportion of dominant species decreases progressively from bark to litter to dung to woody debris (Fig. 60). From the four rank-abundance models tested, the assemblages of bark-inhabiting and wood-inhabiting myxomycetes are described best by the log normal model series distribution (sum of chi squares = 0.92 and 0.35, correspondingly), the assemblage litter-inhabiting myxomycetes is described best by the geometric (4.75), and the assemblage of dung-inhabiting myxomycetes is described best by the logarithmic model with $P > 0.95$. The broken stick model did not fit any of the data sets (Table 5). Development time of sporocarps in moist chamber cultures is one of the most important characteristics defining ecological niches of particular species. As reported by Schnittler (2001), species of myxomycetes inhabiting arid areas demonstrate two life strategies that are clearly manifested in differences in development time of sporocarps in moist chamber cultures.

Table 3. Results of regression analysis for the dependence of the mean number of species and numbers of moist chamber cultures prepared with samples from the different substrates.

Substrate group	Bark	Litter	Dung	Wood	All specimens
Number of identified species	37	21	22	23	44
Number of moist chamber cultures	103	80	83	29	295
A	41.62	25.92	28.76	32.60	46.77
B	15.54	13.44	22.91	13.62	35.87
R	0.997	0.998	0.993	0.994	0.989
m	0.55	0.28	0.61	0.61	1.20

Note: A = is the maximum number of species to be expected, B = number of moist chambers to be need to get half of expected species, R = coefficient of regression, M = mistake of regression equation.

Table 4. Comparison of the assemblages of bark-, wood-, litter- and dung-inhabiting myxomycetes of the Caspian Lowland. (Data were obtained from the set of substrate samples collected in 1998.)

	Mc	PMc	R	S/Mc ± SE	S	G	S/G	H´
Bark	103	102	335	3.28 ± 0.17	37	14	2.8	3.02
Wood	29	29	92	3.17 ± 0.29	23	12	1.9	2.55
Litter	80	60	135	2.25 ± 0.17	21	11	1.9	2.54
Dung	83	65	116	1.78 ± 0.13	22	10	2.2	2.57
Total	295	256	678	2.65 ± 0.10	44	18	2.4	3.01

Note: Mc = number of moist chamber cultures prepared; PMc = number of positive moist chamber cultures; R = number of records; S/Mc = mean number species per culture ± SE; S = number of species; G = number of genera; S/G = species/genus ratio; H´ = Shannon's diversity index.

The data obtained in the present study provide additional evidence of this pattern (Fig. 61). Both groups of species were present in the desert of the Caspian lowland. Sporocarps of the first group of species appeared within 2 to 8 days after moist chamber cultures were prepared. This group is made up of species with small and rapidly developing sporocarps and either a proto- or aphanoplasmodium. This group consists largely of corticolous species in such genera as *Echinostelium*, *Comatricha* and *Macbrideola*. The absence of a peridium or its fast disappearance promotes rapid spore dissemination after rain showers in the desert. Sporocarps of the second group of species appear after 20 to 40 days of incubation. Two good examples are *Perichaena corticalis* and *P. depressa*. This pattern is typical for species with large sporocarps in which the spore mass is enclosed by a well formed and dense

Table 5. Empiric values of χ^2 for best model marked by bond font (k is number of classes for calculation of χ^2).

	Substrate group			
Distribution models	**Bark**	**Litter**	**Dung**	**Wood**
	k=7	k=6	k=6	k=6
Geometric	1.68	**4.75**	4.00	5.78
Logarithmic	2.66	8.43	**1.98**	0.40
MacArthur broken stick	4.64	6.88	7.72	7.00
Log-normal	**0.92**	6.53	3.10	**0.35**

peridium, often with incrustations of lime. The latter is the case for members of such genera as *Physarum*, *Didymium* and *Badhamia*). This second pattern prevails among coprophilous and litter-inhabiting myxomycetes.

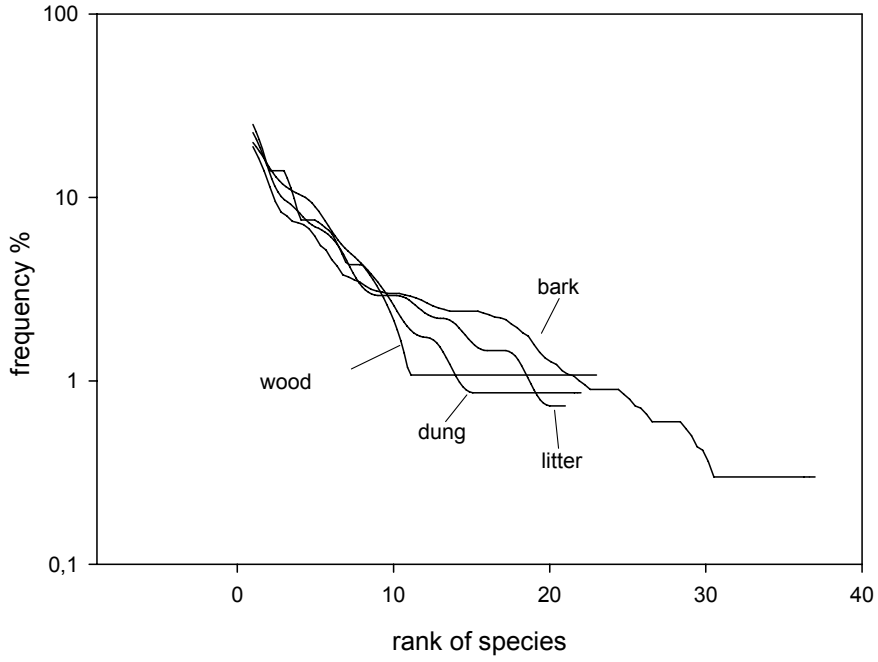


Fig. 60. Rank-abundance plot for species of myxomycetes recorded on the different substrates.

Environmental factors

One of the most important factors that determine the distribution of myxomycetes appears to be the pH of the substrate upon or within which they

occur. As reported for the Sonoran Desert (Blackwell and Gilberson, 1984), the Mahgyshlak Peninsula (Schnittler, 2001) and for the Colorado Plateau (Novozhilov *et al*., 2003), the pH of substrates in arid areas ranges from 6.0 to 10.4. For example, the pH of decomposing cactus debris usually varies between 7.0-10.0. In temperate humid and boreal regions, members of the families Trichiaceae and Cribrariaceae mostly occupy substrates, such as coniferous wood debris (Härkönen, 1977; Novozhilov *et al*., 1998), with a low pH (usually 3.5-5.5). In contrast, in the desert of the Caspian Lowland, all five species of *Perichaena* (Trichiaceae) occurred on substrates with a relatively higher (6.5-6.8) pH (Table 2). Most species of myxomycetes encountered on bark in the present study appear to have a relatively wide pH tolerance but show different pH optima (Table 2).

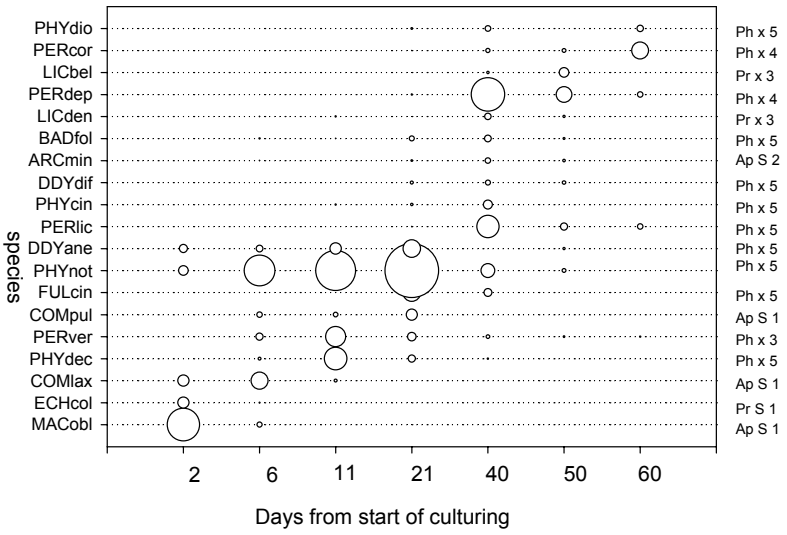


Fig. 61. Development times recorded for the 19 most common species. Circles represent the sum of the weighted abundances for all moist chambers with the respective species present on days 2, 6, 11, 21, 40, 50 and 60. Species names are abbreviated as explained in Table 2. Letter symbols preceding the species names indicate the plasmodium type (Pr = protoplasmodium, Ap = aphanoplasmodium, Ph = phaneroplasmodium) and the degree of stalk development (S = stalk longer than the sporotheca diam and x = sessile species). Numbers ranging from 1–5 classify the peridium type (1 = absent; 2 = fugacious but present in early developmental stages; 3 = thin, membranous and persistent; 4 = persistent, cartilaginous; 5 = persistent, covered with a dense crust of lime or amorphous material).

The most common corticolous species occurred on substrates with a pH between 5.0 and 7.0. Low substrate pH appears to be a limiting factor for growth and development of myxomycetes. The pH values (3.5-7.0, mean = 5.5 ± 1.0) recorded for the bark of *Tamarix* were the lowest for any substrate

sampled and were characterized by the poorest but the most distinctive assemblage of myxomycetes. Two of the more common species (*Comatricha laxa* and *C. pulchella*) displayed a preference for the acidic bark of *Tamarix*. Similar results were obtained in deserts of the Mangyshlak Peninsula (Schnittler and Novozhilov, 2000) and the Colorado Plateau (Novozhilov *et al*., 2003).

Ecological niche

Values calculated for niche breadth were lower for states describing microhabitat features (pH and substratum type) than for climatic parameters (light and wind exposition, Fig. 62). Small corticolous species such as *Arcyria*, *Echinostelium colliculosum*, *Comatricha laxa*, and *Macbrideola oblonga* tended to have smaller niche breadths than *Perichaena vermicularis*, *Physarum cinereum* and other litter-inhabiting species that usually have high values for niche breadth. For this reason, corticolous species seem to be more specialized than other ecological groups. Our results are consistent with data for myxomycetes in the Mangyshlak Peninsula (Schnittler, 2001) and show that the type of substrate and features of the microhabitat are more important factors for the distribution of corticolous myxomycetes than climatic factors. The results of a canonical correspondence analysis (CCA) presented in Fig. 63 support this statement. This pattern corresponds closely with the sets of data obtained from studies carried out on the Mangyshlak Peninsula (Schnittler, 2001) and the Colorado Plateau (Novozhilov *et al*., 2003).

Corticolous species

The 103 moist chamber cultures prepared with samples of bark yielded 37 species representing 14 genera of myxomycetes (Table 4). This microhabitat was characterized by the highest diversity (H' = 3.0, 335 collections) and species richness. The mean value for the number of species per moist chamber culture prepared with bark was 3.24 ± 0.16, with up to 8 taxa per culture. Ninety-nine percent of all bark moist chamber cultures were positive (i.e., displayed evidence of either plasmodia or sporocarps).

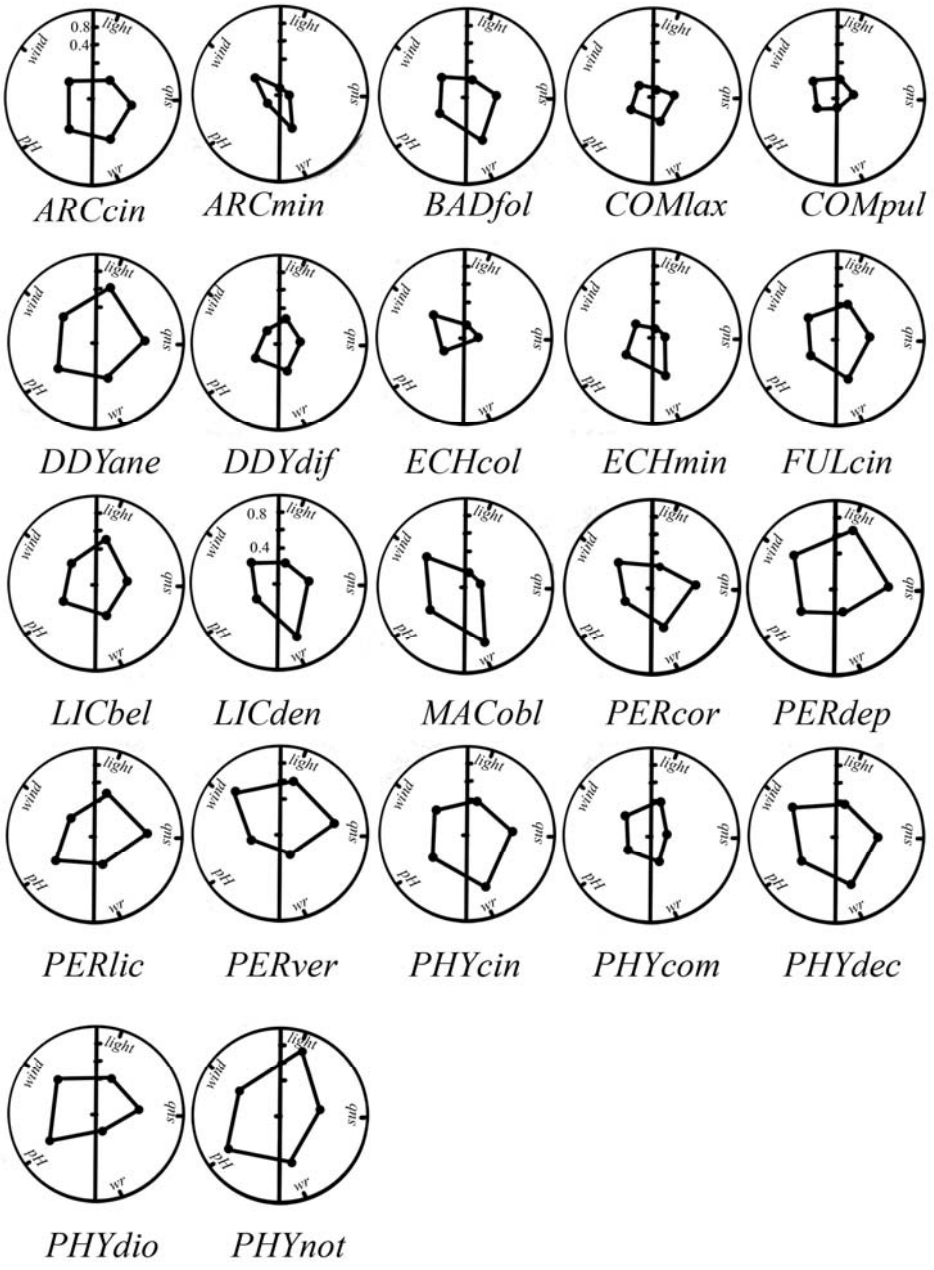


Fig. 62. Graphical visualization of niche breadths for five environmental parameters (light = light intensity, sub = substrate type, wr = water retention, pH, wind = wind exposure) for the 22 most common species (see Table 2 for abbreviations of species names).

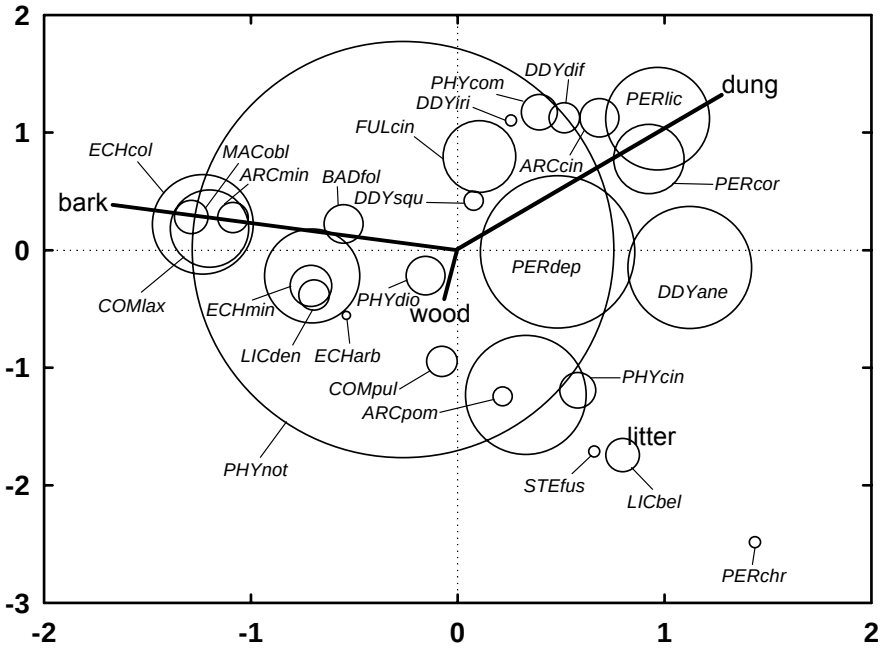


Fig. 63. Biplot for a CCA analysis of the occurrence of 28 species on different substrates. Size of each circles is proportional to the frequency of the species in question. For abbreviations of the species see Table 2. Eigenvalues for the first three axes are 0.374, 0.313 and 0.256.

This high percentage is easily explained by the high frequency of occurrence of some of the dominant species found in deserts. In comparison with results obtained from other arid regions, the percentage of positive recorded in the present study ranks as the highest. For example, 85% positive moist chambers were reported for the Mangyshlak Peninsula (Schnittler, 2001); 96% for the Plateau Colorado (Novozhilov *et al*., 2003); 48% in northern taiga in Finland (Härkönen, 1977); 59% (Peterson, 1952), 75% (Pendergrass, 1972) and 90% (Stephenson, 1989) in deciduous forests of eastern North America; 90% in deciduous forests in Austria (Nowotny, 1986); 80% in deciduous forests in Switzerland (Ing, 1994); and 81% in montane wet broadleaf forests in southern China (Härkönen *et al*., 2004). Species richness (calculated as the number species divided by the number of moist chamber cultures) obtained in the

Table 6. Comparison of the assemblages of bark-inhabiting myxomycetes on plants with different bark texture in the northwestern Caspian Lowland.

Bark texture[1]	Mc	PMc	R	Spr	S/Mc	S	G	S/G	H′
b2	10	9	20	2975	2.0 ± 0.2	8	6	1.3	1.8
b4	60	56	226	21421	4.0 ± 0.2	32	13	2.5	2.9
b5	41	37	89	10910	2.4 ± 0.2	26	10	2.6	2.6
Total	103	102	335	35306	3.28 ± 0.17	37	14	2.8	3.02

Note: [1]Bark texture groups (b2 = smooth but rupturing with age, b4 = furrowed, b5 = fibrous). Mc = number of moist chamber cultures prepared; PMc = number of positive moist chamber cultures; R = number of records; Spr = sum of sporocarps recorded in all moist chamber cultures with bark of the respective texture. S/Mc = mean number species per culture ± SE; S = number of species; G = number of genera; S/G = species/genus ratio; H′ = Shannon's diversity index.

study (0.1-0.2) were similar to those obtained for other arid regions (e.g., Novozhilov *et al*., 2003; Schnittler, 2001).

Bark texture appears to represent an important characteristic of this microhabitat as it relates to myxomycetes, both in terms of water retention and the possibility of the bark surface serving as a "trap" for myxomycete spores. As proposed by Schnittler (2001), the bark from living plants was classified into "texture groups" according to its physical features (Table 6). The texture groups used were (1) smooth bark that breaks into flakes, with these rolling outward in aging twigs, sometimes forming curls on dead twigs (b2) such as found on such plants as *Kraschenninnikovia* sp., *Halocnemum strobilaceum* (Pall.) Bieb., *Haloxylon aphyllum* (Minkw.); (2) solid and deeply furrowed bark (b4) like that characteristic of *Calligonum aphyllum* (Pall.) Guerke, *Elaeagnus angustifolia* L., *Morus nigra* L., *Populus alba* L., *P. nigra* L., *Salix alba* L., *Tamarix ramosissima* Ledeb., *Ulmus laevis* Pall., and *Ulmus pumila* L.; and (3) fibrous bark with a fur-like surface consisting of fine fibres (b5), characteristic of *Artemisia arenaria* DC., *A. abrotanum* L. (= *procera*), *A. lercheana* Web., *A. pauciflora* Web., and *A. scoparia* Waldst. et Kit. To reveal preferences of the myxomycetes for bark texture types, the CCA analysis included only those species recorded from bark.

Dominance decreased but evenness increased over the range of bark textures from b2 to b5 and b4 (Fig. 64). Smooth bark that ruptures with age bark (b2) appears to be unfavourable for myxomycete colonization. For example, the most common and large shrub (*Haloxylon aphyllum*) in the desert with this type of bark forms a significant mass of wood and litter in the desert b but has the lowest myxomycete diversity. Only 20 records were recorded from plants with the bark of type b2 (Table 6), and 8 of these were of the ubiquitous species *Physarum notabile*.

Maximum of alpha-diversity myxomycete biota was registered on

deeply furrowed bark (b4, Table 6). This bark is characterized a smoother curve for the rank-abundance plot, and this coordinates with the highest value for evenness of diversity. Obviously, numerous microhabitats can be found on such a bark, making it the most favourable for different species of myxomycetes. This type of bark has the maximum surface per unit of surface area and better retains water and propagules than bark of other textures, thus presenting favourable conditions for a plasmodium, especially in the harsh and extremely dry conditions characteristic of deserts. The number species recorded from this type of bark (as many as 8) would seem to confirm this. It should emphasized that in other vegetation types, such as in the mountain forests of south China (Härkönen *et al*., 2004), rough bark (e.g., bark of *Metasequoia glyptostroboides* and *Sassafras tzumu*) also displayed maximum myxomycete diversity.

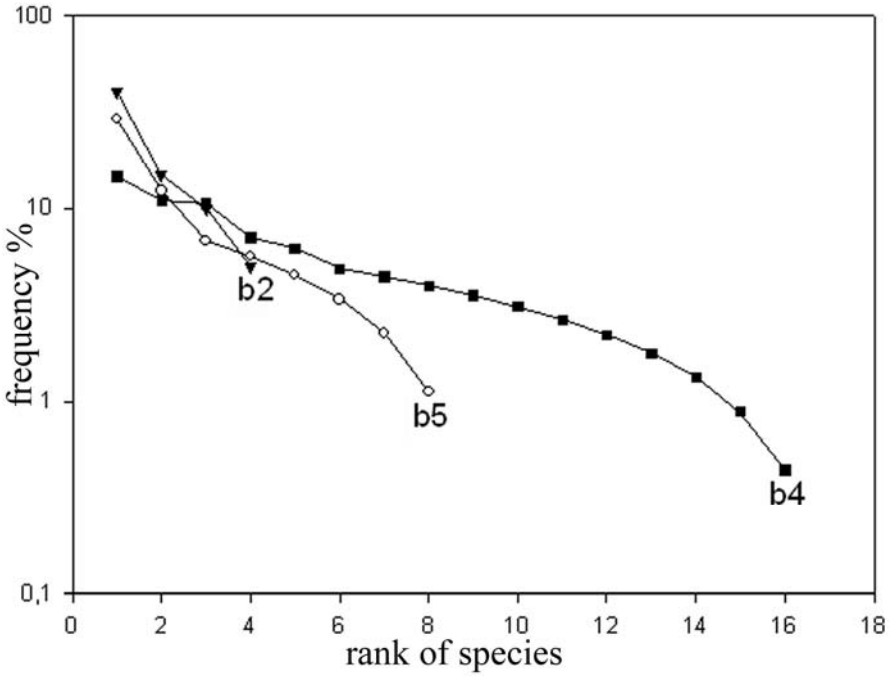


Fig. 64. Rank-abundance plot for the observed myxomycetes on barks with different texture.

However, high myxomycete diversity on a particular plant is not always positively correlated with either the abundance of that plant in the community being considered or the bark texture of the plant in question. Myxomycete diversity can be reduced dramatically as the result of the influence of a single unfavourable environmental factor. For example, in spite of the fact that the

bark of *Tamarix* has a favourable texture (b4), the low pH of the bark hinders colonization of this shrub by corticolous myxomycetes. This appears to be the primary reason why *Tamarix*, one of the largest and most widely distributed shrubs in deserts, is characterized by so few corticolous myxomycetes.

As can be observed from the biplot of CCA (Fig. 65), bark b4 and b5 give two clear species clusters. The first cluster includes species associated with large trees in tree lines and in riparian habitats and on *Calligonum aphyllum* in sand dunes. Myxomycete diversity on the bark of this shrub was the highest in the general study area (45 records, 17 species); other plants with similar bark texture also demonstrate a high level of myxomycete diversity.

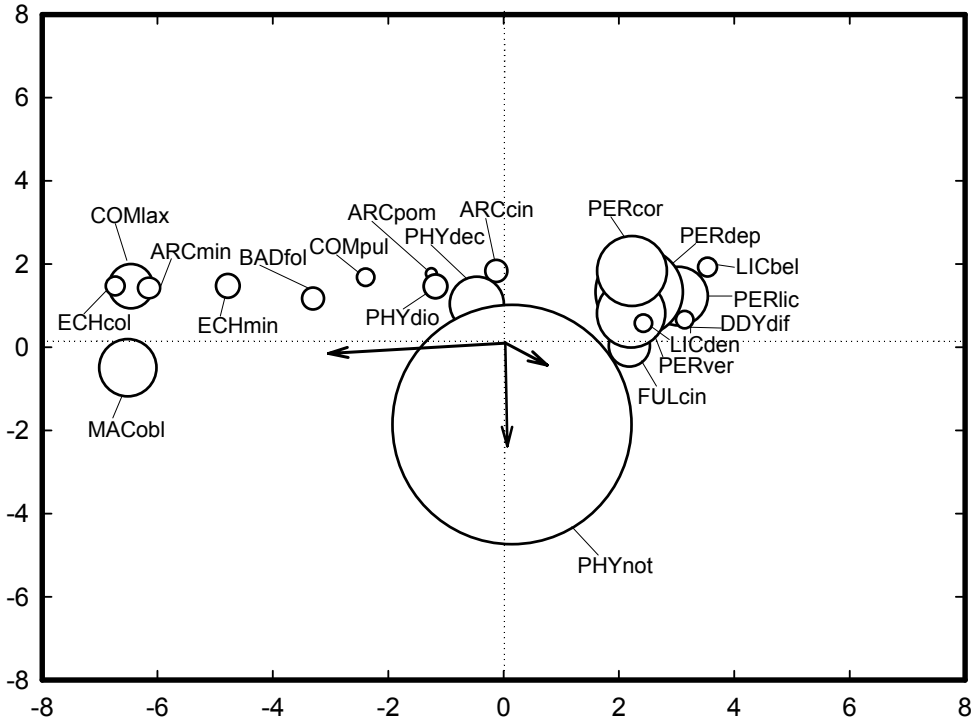


Fig. 65. Biplot of a canonical correspondence analysis (CCA) of the occurrences of the 20 most common species of corticolous myxomycetes on different substrates. The size of each circle is proportional to the frequency of the species in question. For abbreviations of the species see Table 2.

Examples are *Populus alba* and *P. nigra* (37 records, 16 species), *Salix alba* (31 records, 13 species), *Elaeagnus angustifolia* (30 records, 12 species), and *Ulmus pumila* and *U. laevis* (16 records, 10 species). The second more distant cluster on the biplot (Fig. 65) is correlated with the fibrous bark (b5) of

sagebrush (89 records, 26 species). The assemblage of myxomycetes associated with the bark of sagebrush contains fewer species that seem specifically limited to this microhabitat. Instead, the bark of sagebrush is a suitable microhabitat not only for obligate corticolous species but also for litter-inhabiting species. It seems likely that the relatively low height of such shrubs as *Artemisia* would allow the migration of a plasmodium from soil and litter to bark. In addition, the propagules of litter- and soil-inhabiting species could be introduced to the bark along with drops of water and soil during heavy showers in summer. *Didymium difforme*, *Licea denudescens*, *L. belmontiana*, *Fuligo cinerea*, *Perichaena corticalis*, *P. depressa*, *P. liceoides* and *P. vermicularis* were associated with bark of *Artemisia lercheana*, but only *L. denudescens* member of this group that exhibits a clear preference (more than 50% of all records) for the bark of this plant. *Licea belmontiana* prefers the litter of sagebrush (more than 50% of all records), and the other species also occurred on litter and dung. *Physarum notabile*, the most common species in the desert, had the widest niche breath (Fig. 62). This would have been expected for a ubiquitous species that was found to be associated with many different substrates, avoiding only the acidic bark of *Tamarix*.

Some corticolous species demonstrate a high degree of conjugacy. Prominent examples are *Comatricha laxa – C. pulchella* (Kb = 0.28, $C_{1/2}$ = 0.18, χ^2_{01} = 23.89, standard χ^2_{01} = 6.64), *Macbrideola oblonga – Physarum decipiens* (Kb = 0.25, $C_{1/2}$ = 0.25, χ^2_{01} = 19.12), and *Echinostelium colliculosum – Macbrideola oblonga* (Kb = 0.36, $C_{1/2}$ = 0.19, χ^2_{01} = 39.06). These same species also a show high degree of conjugacy in other arid areas such as the deserts of the Mangyshlak Peninsula (Schnittler, 2001) and the Colorado Plateau (Novozhilov *et al*., 2003), where they were recorded on the same types of substrates. Therefore, it seems likely that these species are members of a distinct ecological assemblage of corticolous myxomycetes that is consistently associated with plants in arid areas of different regions of the world.

When comparing our data for bark-inhabiting and litter-inhabiting myxomycetes of northwestern Caspian Lowland with similar sets of data from tropical forests in Costa Rica (Schnittler and Stephenson, 2000), tropical forests in Thailand (Tran *et al*., 2006) and temperate upland forests in Virginia in the United States (Stephenson, 1988, 1989), deserts would seem to be characterized by the highest proportion of corticolous species, whereas litter-inhabiting species appear to be most diverse in tropical forests.

Table 7. Results of statistical analyses for bark- and litter-inhabiting myxomycetes from the desert of the Caspian Lowland (CL), tropical forests of Costa Rica (CR) and temperate upland forests of Virginia (VA).

	CL		CR		VA	
	B	**L**	**B**	**L**	**B**	**L**
Number of species	37	21	25	43	47	34
Number of records	335	135	103	405	1107	398
Number of cultures	103	80	171	305	632	507
Mean records per culture	3.28	2.25	0.60	1.33	1.75	0.78
Number of species to expect with the Bootstrap method	41.6[a]	25.9	35.6	50.7	51.9	42.5

[a]Expressed as the correlation coefficient between the ordered rank of the species and the logarithm of their frequency.

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References

Blackwell, M.M. and Gilbertson, R.L. (1980). Sonoran desert Myxomycetes. Mycotaxon 11: 139-149.

Blackwell, M.M. and Gilbertson, R.L. (1984) Distribution and sporulation phenology of myxomycetes in the Sonoran desert of Arizona. Microbial Ecology 10: 369-377.

Czerepanov, S.K. (1995*). Vascular plants of Russia and adjacent states (the former USSR).* Cambridge: Cambridge University Press.

Dobrovol'skaya, T.G., Chernov, I.Y. and Zvyagintsev, D.G. (1997). Characterizing the structure of bacterial communities. Microbiologia 66: 408-414 [in Russian].

Evenson, A.E. (1961). A preliminary report of the myxomycetes of Southern Arizona. Mycologia 53: 137-144.

Faurel, L.G., Feldmann, J. and Schotter, G. (1965). Catalogue des Myxomycetes de l' Afrique du Nord. Bulletin de la Société d'Histoire Naturelle de l' Afrique du Nord. 55: 9-35.

Feinsinger, P., Spears, E.E.and Poole, R.W. (1981). A simple measure of niche breadth. Ecology 62: 27-32.

Gams, W. (2005). Report of the Committee for Fungi: 13. Taxon 54: 828-830.

Härkönen, M. (1977). Corticolous Myxomycetes in three different habitats in southern Finland. Karstenia 17: 19-32.

Härkönen, M. (1981). Myxomycetes developed on litter of common Finnish trees in moist chamber cultures. Nordic Journal of Botany 1: 791-794.

Härkönen, M., Rikkinen, J., Ukkola, T., Enroth, J., Virtanen, V., Jääskeläinen, K., Rinne, E., Hiltunen, L., Piippo, S. and He X. (2004). Corticolous myxomycetes and other epiphytic cryptogams on seven native tree species in Hunan Province, China. Syst. Geogr. Plant. 74: 189-198.

Hernández-Crespo, J.C. and C. Lado. (2005). An on-line nomenclatural information system of Eumycetozoa. http://www.nomen.eumycetozoa.com (24-X-2005).

Ing, B. (1994). The phytosociology of myxomycetes. New Phytologist 126: 175-201.

Keller, H.W. and Brooks, T.E. (1977). Corticolous Myxomycetes VII: Contribution toward a monograph of *Licea*, five new species. Mycologia 69: 667-684.

Kirk, P.M. and Ansell, A.E. (1992). *Authors of fungal names. A list of authors of scientific names of fungi, with recommended standard forms of their names, including abbreviations*. Index of Fungi supplement. CAB International. Plymouth: Latimer Trend & Co. Ltd.

Krebs, C.J. (1999). *Ecological Methodology*. Menlo Park: Eddison-Welsey Educ Publ.

Lado, C. (2001). A nomenclatural taxabase of Myxomycetes. Madrid: CSIC.

Lado, C., Eliasson, U., Stephenson, S. L., Estrada-Torres, A. and Schnittler, M. (2005). (1688-1691) Proposals to conserve the names *Amaurochaete* against *Lachnobolus*, *Ceratiomyxa* against *Famintzinia*, *Cribraria* Pers. against *Cribraria* Schrad. ex J. F. Gmel. And *Hemitrichia* against *Hyporhamma* (Myxomycetes). Taxon 54: 543-545.

Lado, C., Estrada-Torres, A., Ramirez, M. and Conde, E. (2002). A study of the succulenticolous Myxomycetes from arid zones of Mexico. Scripta Botanica Belgica 22: 58.

Martin, G.W. and Alexopoulos, C.J. (1969). *The Myxomycetes*. University of Iowa Press: Iowa City.

Magurran, A.E. (1988). *Ecological Diversity and its Measurement*. London: Princeton University Press.

Moreno, G., Castillo, A.M., Illana, C. and Lizárraga, M. (1996). Two new species of *Didymium* of Spain. In: *Abstracts of the second International Congress on Systematics and Ecology of Myxomycetes.* Real Jardin Botanico, CSIC: Madrid, Spain: 57.

Novozhilov, Yu.K. and Golubeva, O.G. (1986). Epiphytic myxomycetes from the Mongolian Altai and the Gobi desert. Micologia i fitopatologia 20: 368-374 [in Russian].

Novozhilov, Yu.K., Schnittler, M. and Stephenson, S.L. (1998). The myxomycetes of Russian subarctic and arctic areas // Micologia i fitopatologia 32: 18-29.

Novozhilov, Yu.K., Mitchell, D.W. and Schnittler, M. (2003). Myxomycete biodiversity of the Colorado Plateau. Mycological Progress 2: 243-258.

Nowotny, W. (1986). Myxomyceten auf der Rinde lebender Baume aus Oberoesterreich. Beiträge zur Kenntnis der Pilze Mitteleuropas. 2: 235-238.

Pendergrass, L. (1972). Myxomycetes from bark of living trees in Panola Mountain State Park. [Thesis of the degree of Master of Science]. Atlanta: Atlanta University.

Petersen, J.H. (1996). The Danish Mycological Society's Colour-chart, Greve.

Peterson, J.E. (1952). Myxomycetes developed on bark of living trees in moist chamber culture. [Thesis for the degree of Master of Science]. East Lansing: Michigan State College.

Ramon, E. (1968). Myxomycetes of Israel. Israel Journal of Botany 17: 207-211.

Safronova, I.N. (2002). On the Caspian subprovince of the Saharo-Gobian desert region. Botanicheskiy zhurnal 87: 57-62. [in Russian].

Schnittler, M. (2001). Ecology of Myxomycetes of a winter-cold desert in western Kazakhstan.

Mycologia 93: 653-669.
Schnittler, M. and Novozhilov, Yu.K. (2000). Myxomycetes of the winter-cold desert in western Kazakhstan. Mycotaxon 74: 267-286.
Schnittler, M. and Stephenson, S.L. (2000). Myxomycete biodiversity in four different forest types in Costa Rica. Mycologia 92: 626-637.
Schnittler, M., Lado, C. and Stephenson, S.L. (2002). Rapid biodiversity assessment of a tropical myxomycete assemblage—Maquipucuna Cloud Forest Reserve, Ecuador. Fungal Diversity 9: 135-167.
Shannon, C.E., Weaver, W. (1963). The mathematical theory of communication. Urbana: Univ. Illinois Press.
Stephenson, S.L. (1988). Distribution and ecology of myxomycetes in temperate forests. I. Patterns of occurrence in the upland forests of southwestern Virginia. Canadian Journal of Botany 66: 2187-2207.
Stephenson, S.L. (1989). Distribution and ecology of myxomycetes in temperate forests. II. Patterns of occurrence on bark surface of living trees, leaf litter, and dung. Mycologia 81: 608-621.
Stephenson, S.L., Kalyanasundaram, I. and Lakhanpal, T.N. (1993). A comparative biogeographical study of myxomycetes in the mid-Appalachians of eastern North America and two regions of India. Journal of Biogeography 20: 645-657.
Ter Braak, C.J.F. (1986). Canonical correspondence analysis: a new eigenvector technique for multivariate analysis. Ecology 67: 1167-1179.
Ter Braak, C.J.F. (1987). The analysis of vegetation-environment relationships by canonical correspondence analysis. Vegetatio 69: 69-77.
Tran, H.T.M., Stephenson, S.L., Hyde, K.D. and Mongkolporn, O. (2006). Distribution and occurrence of myxomycetes in tropical forests of northern Thailand. Fungal Diversity 22: 227-242.
Whittaker, R.H., Levin S.A. and Root, R.B. (1973). Niche, habitat, and ecotope. American Naturalist 107: 321-338.
Wrigley De Basanta, D. and Lado, C. (2005). A taxonomic evaluation of the stipitate *Licea* species. Fungal Diversity 20: 261-314.

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