“Ecology and Biogeography of Myxomycetes”

Habilitationsschrift

zur Erlangung des akademischen Grades

doctor rerum naturalium habilitatus

(Dr. rer. nat. habil.)

vorgelegt dem Rat der Biologisch-Pharmazeutischen Fakultät

der Friedrich-Schiller-Universität Jena

von

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geboren am 13.04. 1963 in Ilmenau

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Erteilung der Lehrbefähigung am 15.10.2001

Preface

It may have been the medieval painter Hieronymus Bosch who was the first to draw a slime mould. At least some structures in his surrealistic paintings, in style centuries ahead of his time, can be interpreted that way. The great botanist Linné described a few species, mistaking them for tiny puffballs. But, only a few people have ever seen a slime mould in nature, since these hidden organisms go mainly unnoticed, doing neither good nor bad to humans. Not surprisingly, the myxomycetes (plasmodial slime moulds) are one of the least explored groups among macroscopically visible organisms, and even the ecology of many microbes is better known.

However, since the monographs of Arthur Lister, accompanied by excellent, hand-coloured lithographs of the fructifications, an increasing number of mycologists learned to enjoy the beauty of myxomycetes. Within the last decades, the group was given a steadily growing interest by taxonomists. It is the goal of this work to bring myxomycetes into the scope of researchers working on ecology and biodiversity and to demonstrate, that the methods used by these disciplines for many other groups of organisms will work for slime moulds as well. Hopefully, it will help to narrow down the knowledge gap between myxomycetes and other groups of cryptogams or micro-organisms.

More than ten years of intense field and laboratory work supplied the data presented herein, with the first half of this time needed mostly to come into the taxonomy of the group and gain experience where slime moulds can be found. Major parts were compiled during three years spent in North America, one year as a research fellow with Prof. Dr. T. Dickinson at the Royal Ontario Museum, Toronto, and two years of teaching and research with Prof. Dr. S.L. Stephenson at Fairmont State College, West Virginia.

It was the intention of this effort to elucidate the general trends in ecology, distribution and evolution of the myxomycetes. Therefore, the reader will not find descriptions of new species or taxonomic revisions, although undescribed taxa are mentioned occasionally. But, I am convinced that we need more and especially more precise knowledge about the ecology and distribution of already described species before we can be sure that new names will indeed reflect new biological entities.

After an introduction, summarizing the current knowledge about ecology and distribution of slime moulds, 13 selected papers follow. Six feature local surveys, six others focus on the ecology of myxomycetes in certain microhabitats or areas, and one is a first case study about the world distribution of a species. The two last chapters represent an effort to explain the evolution of the myxomycete fructification and to recognize the general pattern of myxomycete diversity on Earth.

Martin Schnittler, December 2000

Content and list of included papers

Chapter 1. Introduction - current situation in myxomycete research

The object of this thesis work are the plasmodial slime moulds (*Myxomycetes*); a small group of organisms, comprising ca. 1000 species world-wide. Although the first myxomycete species were already described by Linne (1753), it is one of the groups mostly neglected in modern research on taxonomy, biodiversity and ecology. The main reason for this neglect is the unique life history of myxomycetes, combining features of micro-organisms and fungi. Traditionally, micro-organisms are studied in isolated culture and in a laboratory environment. Fungi, especially those with macroscopically visible fructifications, can be studied using the methods of descriptive taxonomy and field ecology. Myxomycetes are difficult to grasp at the first approach, since most of the species do not complete their life cycle in axenic culture. Also the second approach is much more difficult to undertake than for most other organisms, since myxomycete fruitbodies are often tiny, very evanescent and often hard to find in the field. However, this group of organisms which connects the macroscopic and the microscopic world also affords an opportunity to bring ecological and biodiversity research into the world of micro-organisms. To establish myxomycetes as a group of organisms which can be treated successfully by these scientific disciplines is the goal of the present work.

Most of the ca. 3000 published papers dealing specifically with myxomycetes cover one of the following three topics: taxonomy, local surveys or myxomycetes as model organisms for cytological or biochemical research. However, only a limited number of comprehensive studies is available. The first monographic study was undertaken by Rostafinski (1875, 1876) but the real breakthrough in taxonomy came with the monographic studies of Arthur Lister (1894, 1911, 1925) which where greatly enhanced by the help and many additional papers of his daughter Gulielma. The most recent world monograph is the book of Martin & Alexopoulos (1969), comprising ca. 60% of all described taxa. Mitchell (1999, updated 2000) published a CD of all taxa described up to the present time, including names, citation of protologues, taxonomic descriptions and (for many taxa) digital images. Together with the additional synoptic keys, this is probably the most complete monographic treatment to date, complemented by a nomenclatural database of Lado & Hernandez (2000). Stephenson & Stempen (1994) provide an up-to-date introduction into general biology of myxomycetes. The filigreen fruitbodies are shown in beautiful colour photographs by Neubert, Nowotny & Baumann (1993, 1995, 2000). Many aspects of laboratory culture, physiology and biochemistry of myxomycetes are summarized by Gray & Alexopoulos (1968). Collins (1979) provides a review concerning the genetics of myxomycetes; these studies are continued in a series of papers by Clark (e.g., 1995).

The following sections of this chapter review the current knowledge about the group with particular emphasis on ecological and biogeographical problems.

Systematic position of the Myxomycetes.—After a period of more than 200 years in which myxomycetes were occasionally described and figured together with other organisms, often fungi, Link (1833) first perceived them as a distinct group, creating the name "Myxomycetes". De Bary (1858a, b, c, 1859, 1862, 1864) studied the life cycle and recognized myxomycetes as having close relationships with the protozoa. Consequently, he proposed the name "Mycetozoa" for the group. For more than a century these two names reflected the uncertainty about the systematic position of myxomycetes. The main character supporting their close relationship with protists are the amoeboid vegetative cells, shared by the related cellular slime moulds (Martin 1960). The first member of this group, also known as Dictyosteliales, was already discovered by Brefeld (1869). Today, ca. 60 dictyostelid species are known (J. Landolt, pers. comm.). In the sixties, the Protostelids, the sister group of the myxomycetes, were discovered and characterized in a series of papers by Olive & Stoianovitch (1969). Olive (1975) provides a comprehensive treatment of the 17 species of Protostelids described at this time (ca. 25 are currently known). These microscopic organisms produce very simple fruitbodies with a single spore. Forms such as the two-spored *Echinostelium bisporum* (Whitney et al. 1982, Spiegel & Feldman 1989) are considered to represent a link between Protostelids and myxomycetes. In both groups plasmodial stages can be found as one trophic stage in the life cycle. For this reason the name "Eumycetozoa" has been proposed to include both groups (Olive 1982, Spiegel & Feldman 1985, Spiegel 1991). Acrasids, also commonly referred as "slime moulds", appear to be unrelated to the Dictyosteliales, Protosteliales, and Myxomycetes, based on ultrastructural data (Olive 1975). Another character suggesting a close relationship of the three groups of myxomycete-like organisms with protists is the possession of flagella. Most, perhaps all, species of myxomycetes have the ability to form myxoflagellates characterized by one long and one short flagellum; the latter being almost invisible by light microscopy (Gottsberger 1967). These flagella are built according to the "9+2" pattern which is common among various groups of protists (Haskins & Guiness 1988). At the end of the 1960's, the position of the myxomycetes as a group of protists was widely accepted (Corliss 1984). An ultrastructural investigation suggests cercomonads as the closest relatives of myxomycetes among the protists (Karpov 1997). More often, the Plasmodiophorales, obligate phytoparasites, are classified within the protozoa and thought to be the group closest to the myxomycetes (Barr 1992). Kishnan et al. (1990) proposed a phylogeny of the protists (including myxomycetes) based on 5S rRNA sequences.

Even within the Protista, itself representing a very heterogenic taxon, the myxomycetes have a rather isolated position. This is confirmed by the latest study of Baldauf & Doolittle (1997) based on DNA-sequencing of the elongation factor-1α gene. Here, the myxomycete-like groups of dictyostelids, protostelids and myxomycetes form an own (monophyletic) clade within the "crown" group of the eucaryota. Surprisingly, this phylogenetic study, based on one sequence for a representative of each of

the three groups of myxomycete-like organisms, places the myxomycetes (yet as a distinct monophyletic group) among the multicellular eucaryotes, closer to animals and fungi than to protists. However, when judging these results it has to be noted that for the most species-rich of the three groups, the myxomycetes, DNA- or rRNA sequences were almost invariably derived from the few easily cultivable species (see below), all belonging to the order Physarales. Considering the remarkable morphological variability of myxomycete fructifications, it may be that the myxomycetes are not monophyletic as a group. This question can be solved only with a reliable methodology for the isolation of DNA from myxomycete spores and the development of primers specific for myxomycetes as a group.

For the purposes of this work, it is sufficient to adopt the view of Barr (1992), who proposes to treat the myxomycetes as members of the "union of fungi", a term used for members of different kingdoms traditionally studied by mycologists.

Laboratory culture.—Since myxomycetes live predatory on other micro-organisms such as bacteria, yeasts, algae, or true fungi, their cultivation is much more difficult than for other groups of micro-organisms. The first successful cultures of myxomycetes were achieved in the 1950's. Clark (1995) gives a list of the 98 species (about 10% of all described taxa) observed completing their life cycle in agar culture using bacteria as food organisms. Most of the easily cultured species are litter-inhabiting members of the order Physarales. Here, a number of species, with *Physarum polycephalum* as the most prominent example, can be cultured even without bacteria on artificial sources of nutrients, e.g., oatmeal. Species of the genera *Physarum* and *Didymium* are especially easy to culture and, for this reason, the overwhelming majority of our knowledge about physiology, histology, and reproductive systems in myxomycetes stems from these two genera.

Except for a single report concerning the cultivation of myxomycetes with green algae by Lazo (1961), no attempts to cultivate myxomycetes with food organisms other than bacteria have been made. But, as explained under "Ecology and nutrition", ecological guilds of myxomycetes exist also in microhabitats where other micro-organisms serve as the most likely food organisms. When myxomycetes are classified according to the substrata inhabited (compare chapter 15), only two of these ecological groups include species that are relatively easy to cultivate: myxomycetes inhabiting decaying plant litter (especially basic substrata), and coprophilous species developing on herbivore dung. Obligate corticolous myxomycetes have never completed their life cycle in culture. *Trichia persimilis* is the only species restricted to decaying wood that has been reported to grow in axenic culture (Rammeloo 1976). No attempt has yet been made to cultivate members of certain specialised ecological groups (e.g. myxomycetes that grow on rocks or decorticated wood covered with liverworts, cyanobacteria and unicellular algae, or the nivicolous species). An overview of methods

and cultivation media is given by Schinner & Aberham (1990) and Kalyanasundaram & Venkataramani (1974).

Myxomycete life cycle.—In spite of their relatively isolated position in the system of organisms, it is mycologists who traditionally deal with myxomycetes, because they form fruitbodies that resemble fungi. The life cycle (see Alexopoulos 1970, Madelin 1984) starts with haploid, unicellular myxoflagellates and myxamoebae hatching from spores. Usually by undergoing somatogamy, a diploid plasmodium is formed as the second trophic stage. This stage is unique among living organisms and consists of a multinuclear protoplasmic mass, surrounded only by a simple membrane and a slime sheath which moves by protoplasmic streaming. Three main types of plasmodia can be differentiated, ranging from microscopical protoplasmodia to phaneroplasmodia that can achieve macroscopic dimensions (Alexopoulos 1960, 1969). During fructification, almost the entire biomass of the plasmodium turns into fruitbodies. Undergoing meiosis, the spores are formed as very durable dispersal units.

In Nature, this life cycle seems to be much more variable than that figured in most textbooks. The following paragraphs focus on features of the life stages that are important for understanding the ecology. Fig. 1 gives an overview including all deviations from the "standard" life cycle known at the present time.

The spore is the usual dispersal unit of the myxomycetes. Typically, it is globose, between 5 and 15 µm in diameter and ornamented with warts, spines, or ridges. These ornaments are often arranged in a way that a complete or incomplete reticulum is formed. The spore wall is composed mainly from cellulose (Chapman et al. 1983), and pigments of various colours varying from red and yellow to brown and black. The darker pigmentation may act as a shield against ultraviolet radiation. Physarales and Stemonitales possess melanins as spore pigments. Although the spores of many, especially tropical, species loose their ability to germinate within weeks (J. Clark, pers. comm.), spores from some herbarium specimens of myxomycetes still germinated after 60 years (Erbisch 1964). The germination of spores is environmentally induced and may take from a few minutes to days. A considerable body of (mainly older) literature consists of observations on the conditions necessary for spore germination (e.g., Gilbert 1929). Germination seems to occur only under aerobic conditions (Braun 1971) and may be accelerated by a low osmotic pressure (Abe 1940). As it is known for myxobacteria, evidence also exists that, in myxomycetes, spores in mass germinate better than isolated ones (Dahlberg & Franke 1977).

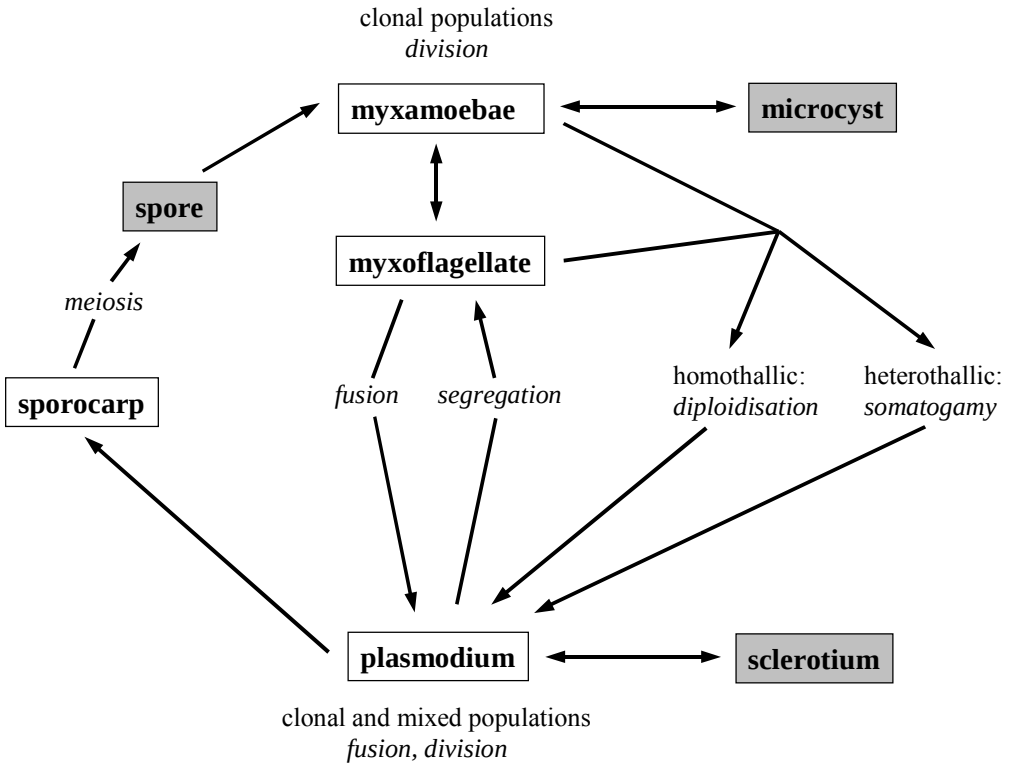

Fig. 1. Schematic representation of the possible conversions between the stages in the myxomycete life cycle. Boxes show the single stages, with the grey ones representing dormant stages. Very probably, substrate moisture determines if myxamoebae or myxoflagellates are formed. Both are capable to grow large, clonally structured populations but can eventually form plasmodia by somatogamy (heterothallic strains) or diploidisation of the nucleus (homothallic strains). Plasmodia can fissure or fuse (if genetically compatible) and thus establish populations as well. The separation of myxoflagellates from plasmodia has been shown. Consequently, diploid populations of myxamoebae or myxoflagellates are conceivable, which would be able to convert directly into plasmodia. In apomictic (homothallic) strains, the meiosis, usually occurring during spore cleavage, is apparently skipped, and the whole life cycle is completed in the diploid phase.

The spores may hatch with myxamoebae or myxoflagellates. The latter possess a long and a short flagellum. These unicellular micro-organisms, measuring usually between 5 and 10 µm, represent the first trophic stage of the myxomycetes. They can take up soluble nutrients or ingest other micro-organisms and even particles such as fungal spores (Gilbert 1928). Other micro-organisms serving as prey are actively recognized by chemotaxis, as observed for myxamoebae of *Didymium iridis* which were

attracted by bacteria over a distance of 600 µm (Konijn & Koevenig 1971). Myxamoebae and myxoflagellates multiply by division and are theoretically immortal (Clark 1992). As indicated by the quantitative studies of Feest (1987), their populations can reach considerable numbers. Although he could not identify myxomycete species, he detected numbers between 1000 and 10000 plasmodium-forming-units (trophic stages of myxomycete-like organisms) per gram of dry soil. Since myxamoebae inhabit all kinds of terrestrial decaying plant matter, they should be one of the most important regulators of bacterial density. It was shown that a single myxamoeba of *Physarum polycephalum* needs about 200 bacterial cells per division (Jacobson 1980). This may double a population of myxamoeabae in 3 to 15 hours, assuming an unlimited food supply. Myxamoebal populations may exist for long periods of time or may be the only life form of myxomycetes in certain habitats, as indicated by the observations of myxomycetes on microhabitats such as foliicolous liverworts (chapter 11). Under unfavourable conditions, microcysts occur as dormant stages. These are similar to spores but may not be so durable (Raper & Alexopoulos 1973). Microcysts are probably the most important dormant stage in arid regions which are only periodically moist (chapter 8). Myxamoebae or myxoflagellates are usually haploid, although diploid, non-heterothallic populations may well occur in Nature.

The unicellular stages form the plasmodium usually by somatogamy, which involves two or more myxamoebae or myxoflagellates (Wilson & Cadman 1928, Koevenig 1964). However, plasmodia can be formed by single myxamoebae through diploidisation, leading to polyploid strains (Clark & Mulleavy 1982). According to present knowledge, plasmodia are always at least diploid. Although plasmodia are principally immortal, in Nature they age and disintegrate if conditions are not suitable for fructification. A large number of papers has been published on the cytology (synchronous division of nuclei), biochemistry and physiology of plasmodia, almost all of which have been based on studies of plasmodia of the Physarales. However, this group represents only one of the three plasmodial types differentiated by Alexopoulos (1960). The most simple type, occurring in the Echinosteliales and many Liceales, is the protoplasmodium. It is small, about 100–300 µm in diameter and usually forms only a single fructification. If the number of nuclei exceeds a certain limit, these plasmodia divide (Haskins 1978). In contrast to other plasmodium types, even genetically compatible plasmodia do not fuse. The phaneroplasmodium is the most common type, occurring in most, if not all, Trichales and all Physarales. In Nature, these plasmodia may reach sizes of several centimetres, sometimes up to one meter, and can move actively over distances of several meters within days (Schnittler, unpubl. obs.). Theoretically, the growth of this plasmodium type is unlimited; it gives rise to large compound fructifications or extended colonies of thousands of separate sporocarps. The Stemonitales represent the third plasmodial type, called the aphanoplasmodium. Although of macroscopical size as well, these plasmodia are almost invisible, since their plasmodial strands are very thin. They are able to utilize hard substrata such as dead but still solid wood. It is probable that they can pass through the pores in sclerenchyma cells of woody substrates.

A few Stemonitales that form larger fructifications seem to inhabit exclusively solid wood, with *Amaurochaete atra* as the most prominent example (Eliasson 1977). Under favourable conditions, plasmodia are very mobile and can pass through very fine pores of the substratum. In *Didymium iridis*, plasmodia were able to pass through filters of 3 µm pore size, even though possessing nuclei with a diameter of 4 µm (Clark & Hakim 1980). If genetically compatible, plasmodia may coalesce (Haskins 1990), or segregate into myxamoebae or myxoflagellates (Indira 1964, Ross & Cummings 1967). Plasmodia, especially the large phaneroplasmodia, are capable to form sclerotia as a dormant stage, consisting of multinucleate macrocysts of 10–20 µm diameter.

The formation of the fructifications from plasmodia takes between several hours (corticolous myxomycetes) and one or two weeks (species from algae-covered rocks). The most commonly occurring type of myxomycete fructification is a globose spore case (sporotheca) raised on a slender stalk, reaching from 100 µm to several mm in height. A certain amount of biomass has to be allocated to supporting structures, which lift the spores over the substratum where they can dry out and so become airborne. Alternatively, sessile fructifications covered by thick peridia dry out with the substratum. The amount of biomass (and energy, respectively) used for the supporting structures varies with environmental conditions, as indicated by a comparison between fructifications from temperate and tropical zones (chapter 9). Beside solitary sporocarps, coalescent fructifications, called aethalia, occur in some species. Two types of sporocarp development, the subhypothallic and the epihypothallic, can be differentiated, the latter is thought to be limited to the Stemonitales (Ross 1973) but may also occur in some Echinosteliales (Schnittler et al. 2000).

Spores are dispersed most often by air movement, or by rainwater (Dixon 1963). Especially the species with massive aethalia have strongly hydrophobic spores which are released by rain drops hitting the fructifications. Arthropods that feed on the fructifications function as vectors (Blackwell 1984). Various other animal vectors are recorded: earthworms (Murray et al 1985), mites (Keller & Smith 1978), tardigrades (Kylin 1991), fruit flies of the genus *Drosophila* (in the case of *Badhamia gracilis*, D. Wrigley, pers. comm.), and even birds (Sutherland 1979). Very probably, beetles are the most common vectors (Lawrence and Newton 1980), with members of the Leiodidae (Wheeler 1984) and Lathrididae specialized to live on slime mould fructifications (Blackwell et al. 1982).

The unique feature in the life cycle of myxomycetes is the combination of single-cell stages living as true micro-organisms with fruiting bodies which achieve macroscopic dimensions in many species. Dried and boxed, they can be stored like other herbarium specimens.

Ecological implications of myxomycete reproductive systems.—A considerable number of papers have been published on the reproductive system of myxomycetes (Clark 2000). Although these papers are limited to the small number of species which can be grown in culture (mostly Physarales), they enable certain conclusions to be drawn for the group.

Like many protists, myxomycetes have no genders but compatibility alleles (mating types) which control the ability of myxamoebae or myxoflagellates to fuse and form plasmodia. This basic type of reproduction can be called heterothallic, since two non-identical mating types are necessary to ensure somatogamy, the sexual step in the myxomycete life cycle. However, in most of the species hitherto investigated, strains that skip this step have been discovered, which can be called apomictic or non-heterothallic. Apparently, in this case the whole life cycle can be completed in the diploid phase (Therrien & Yemma 1974). Such strains produce clones of identical myxamoebae or myxoflagellates, and consequently the morphological characters of the fructifications should be identical (except for modifications caused by different environmental conditions during development).

Clark (1995) gives an overview of the myxomycete species hitherto investigated for their reproductive systems. So far, data are available for 46 species; most of them are members of the Physarales. From 201 reported strains, 115 were non-heterothallic. On the species level, 28 species were found to reproduce non-heterothallic only, 8 include both heterothallic and non-heterothallic strains, and 10 only heterothallic ones. However, for the better-known species (at least five strains were investigated), this relationship is 2:8:2. This suggests, that the majority of the morphospecies known in myxomycetes reproduces both sexual and apomictic, with a possible bias towards the apomictic way of reproduction. Only a few species, such as *Echinostelium coelocephalum* (Haskins et al. 2000) or *E. minutum* (Clark & Haskins 1998) seem to consist exclusively of sexual strains. Very probably, apomictic forms can switch back to a heterothallic mode of reproduction (Collins 1980). This "switchback" reproductive system leads to a rather large number of clones, which occasionally undergo sexual recombination and form new clones. The ecological consequences are similar to those studied in vascular plants. Here, some genera like *Hieracium* or *Rubus*, which are successful invaders of heavily disturbed environments in man-made landscapes of Central Europe, show exactly this "switchback" reproductive system. It still allows the rapid creation of new traits by shuffling alleles via sexual recombination. When continuing to reproduce sexually, rare new traits would be subjected to genetic drift and face the risk of becoming extinct even if they provide increased fitness for the individual. However, a switchback to asexual reproduction allows the conservation of such traits. The resulting clones seem to be especially successful in heavily disturbed environments where there is a lower level of competition by other species (Schnittler 1993). According to a genetic model by Walsh (1995) only large populations can effort purely apomictic reproduction, since such species rely

entirely on mutations to produce new genes that increase fitness. The respective mutation rates are very low in more complex organisms, therefore large populations are necessary to ensure their realization in Nature. Seemingly, only tiny organisms (with a high density of individuals, and often a higher mutation rate due to their lower complexity) or organisms in competition-free environments can reach the necessary population sizes. This explains the rarity of apomictic reproduction among higher organisms. If both forms of reproduction are possible, their advantages can be combined.

Table 1. Comparison of reproductive systems and current taxonomic approaches in the myxomycete genus *Didymium* and in the flowering plant genera *Hieracium*, *Rubus*, and *Ranunculus auricomus* agg.

	Didymium	*Hieracium*	*Rubus*	*Ranunculus*
Described taxa:	67 taxa (world, Lado 2000)	ca. 750 main and intermediate taxa (world, Zahn 1987)	300–400 sexual, >1000 apomictic taxa (Weber 1995)	>650 taxa (Northern Europe, Ericcson 1992)
Repro-ductive system:	sexual and apomictic, conversion may occur	sexual and apo-mictic, conversion occurs regularly, interbreeding between clones	mainly apomictic, conversion and inbreeding can occur	exclusively asexual
Species concepts:	typologically based on morphology (Matsumoto & Deguchi 1999); biological concept proposed for the *D. iridis* complex (Clark & Mires 1999)	differentiation between main and intermediate (apomictic) species (Zahn 1987, Schuhwerk 1996)	only apomictic clones with a range exceeding 50 km considered as species (Weber 1973, 1996)	four species with apomictic sub-species (Marklund 1961, 1965); apo-mictic clones des-cribed as species (Ericsson 1992)
Traits: [a]	5–10	10–20	20–30	10–20
Dispersal:	airborne spores 9-12 µm diam.	wind dispersed achenes 0.5-1 mm diam.	bird dispersed drupelets 1-2 cm diam.	autochorous or ant dispersed fruits 0.5-2.5 mm diam.
Range size:	regional to whole continents; disjunct to continuous	local (isolated rock outcrops) to regional (100–500 km); disjunct to continuous	local to regional, mostly con-tinuous, some-times disjunct	local to regional, almost exclusivally continuous

[a] Approximate number of morphological traits used for species determination.

Indeed, as judged by the experience of the author from determining myxomycete fructifications, the existence of various local clones is very likely for many species of myxomycetes. Quite often, series of collections from one locality are morphologically identical to each other but show minor differences to series of collections from another locality which can be ascribed to the same species. As explained in chapter 1, these biotypes in the sense of Clark (2000) provide serious problems for the species concept in myxomycetes, which is based almost exclusively on morphological traits of the fructifications. Table 1, contributed by the author to the paper of Clark (2000) shows taxonomic approaches for myxomycetes in comparison with those for some apomictic groups of vascular plants.

Nutrition and habitat requirements.—Myxomycetes occur on all types of terrestrial decaying plant mass. Consequently, a broad spectrum of microbes can serve as food organisms. Bacteria are certainly the most common of these. Nothing is known about the preferences of single species, but the variety of microhabitats for myxomycetes suggests a similarly large variety of food organisms. Microhabitats rich in cyanobacteria and unicellular algae (Ing 1983, Schnittler & Novozhilov 1998) provide evidence for myxomycetes preying on these organisms; species such as *Badhamia gracilis* or *Didymium subreticulosporum* (Mosquera et al. 2000), specialized on decaying cacti infected by yeasts or the myxomycete assemblage on inflorescences (chapter 12) suggest yeasts as possible prey; and species such as *Badhamia utricularis* seem to be specialized for feeding on the fruitbodies of fleshy fungi (Howard & Currie 1932). As proven by Lazo (1961), myxomycete plasmodia can grow upon algae (although he used combinations of myxomycetes and algae which are unlikely to occur together in nature). In chapter 7 evidence for a naturally-occurring assemblage of myxomycetes feeding on algae is presented.

At least for some of the time, the relationship between myxomycetes and bacteria may be symbiotic, which may be one reason for the difficulties in the cultivation of many myxomycetes. Bacteria are incorporated into plasmodia and may stay alive for a certain time in this environment. Preferentially, this seems to be so in those strains with strong enzymes such as Pectinases (Schinner et al. 1990) or Amylases (Mubarak & Kalyanasundaram (1991).

Myxomycetes occur from the Arctic to tropical forests in a wide variety of habitats which have at least one feature in common: decaying plant tissue provides a microhabitat (defined here as a small piece of substratum with an uniform microclimate) suitable for the growth of food micro-organisms. Ing (1994) reviews the habitats where myxomycetes have been recorded world-wide. Although myxomycete distribution on Earth is undoubtedly limited by macroclimate and habitat requirement of the species, the papers presented in this thesis work provide strong evidence that microhabitat availability is the factor acting most strikingly on species' distribution. Chapter 15 provides a first

classification of the main microhabitat types upon which myxomycetes occur and gives estimations for numbers of species to be expected on these microhabitat types.

Ecological research in myxomycetes.—Most of the ca. 1200 papers reporting field-related research in myxomycetes are local species lists, often with only a few species mentioned in the frame of surveys focusing on various groups of fungi. The overwhelming majority of these reports do not mention the myxomycete substrata or give such data only for very rare species. About 100 papers present fairly complete regional surveys for myxomycetes and include studies with the moist chamber method. This technique is indispensable for the detection of species with minute fructifications, which account for almost one third of all the described taxa. Much higher proportions of minute taxa can be found among the corticolous myxomycetes (Gilbert & Martin 1933) and in species specialized for arid zones (Alexopoulos 1964, Blackwell & Gilbertson 1984).

A number of studies compare myxomycete assemblages in different forest types (Maimoni-Rodella & Gottsberger 1980, Eliasson 1981, Takahashi 1995, Ogata et al. 1996) or in regions with a different geology (Carr 1939). Drozdowicz (1992) studied the preferences of wood-inhabiting myxomycetes for wood of various stages of decay. The first comprehensive ecological study of a myxomycete assemblage was published by Stephenson (1988, 1989) from temperate upland forest of southwestern Virginia. For the first time data about the autecology of myxomycetes, e.g. niche breadths, were given and competition among species was investigated. Nevertheless, our knowledge about the ecological requirements of myxomycete species is still very fragmentary with only a few taxa studied (Sunhede 1973, Eliasson 1977).

Much more reliable in terms of completeness (but still very scattered in terms of geography) are studies of the ecology of dictyostelids, since a standard technique exists for the isolation of dictyostelids from soil, their primary microhabitat (Cavender & Raper 1965a, b). Even fewer studies exist for the Protostelids, a sister group of the myxomycetes, which can also be cultured more easily than myxomycetes (Moore & Spiegel 2000).

Present knowledge about geographical distribution.—Due to the limited number of regional surveys, no world distribution maps of myxomycetes have been compiled up to the present time. Many textbooks regard most of the species as cosmopolitan (in agreement with Martin & Alexopoulos (1969: 13). G.W. Martin made a first attempt to compile world distribution maps for some species, but his work was never published (S.L. Stephenson, pers. comm.).

Among experienced collectors it is well known that many myxomycete species are limited to tropical regions, whereas others seem to appear in temperate zones only. A first comparative study (Stephenson et al. 1993) revealed clear differences between tropical and temperate myxomycete assemblages, with only a minority of the species common in both regions. A distinct ecological group of myxomycetes, the nivicolous species, are associated with high snow cover in mountains. Myxomycetes are obviously capable of long-term dispersal via airborne spores, and propagules have been detected in a variety of materials ranging from pure rain water (Petterson 1940) to desert debris (Evenson, 1962). However, no reliable data exist about the probability of long-term dispersal in myxomycetes, or the proportion of spores which remain viable during this process.

About 115 checklists for countries or larger regions are published, but many of them do not include studies with the moist chamber method. Remarkable local monographs were published by Nannenga-Bremekamp (1974, 1991) focusing on the Netherlands; or Neubert, Nowotny & Baumann (1993, 1995, 2000) for Germany and Austria. The latter monograph is especially noteworthy by the excellent drawings and colour photographs of myxomycete fructifications. Novozhilov (1993) published a monographic treatment for Russia, likewise Yamamoto (1998) for Japan. One of the most complete treatments is the myxomycete flora for Great Britain (Ing 2000), followed by the Irish checklist (Ing & McHugh 1988). Other countries with a very well studied myxomycete flora are Finland (Härkönen 1979a, b, 1981, 1989, Härkönen et al. 1999), Germany (Schnittler et al. 1996), India (Lakhanpal & Mukerji 1981) and Spain (Lado 1993).

This chapter was intended to provide an overview of the current situation in myxomycete research. Chapter 2 focuses on problems in myxomycete taxonomy and reflects the increasing attention taxonomists have given to the group in recent years. Chapters 3 to 9 present the results of local surveys in different vegetation zones on Earth, aimed to reveal a complete species inventory of a chosen region as well as the abundance of each species. These surveys provide baseline data for comparing the diversity of myxomycetes within different vegetation zones. Chapter 3 shows an example of a myxomycete community found in the transition between taiga and tundra of the Taimyr Peninsula, Central Siberia. Chapter 4 summarizes the results of the few comprehensive surveys for myxomycetes carried out in the Arctic. Chapter 5 and 6 report surveys from the boreal zone in Russian Karelia, the latter focusing on a distinctive ecological group of myxomycetes, i.e. the snowline species inhabiting plant refuse near the melting snow in montane regions. Chapter 7 provides data about a myxomycete assemblage in a temperate montane forest of the Northern Ammergauer Alps, Germany. In spite of their harsh environmental conditions, arid regions have a surprisingly reach myxomycete biota. Chapter 8 shows a case study from a winter-cold desert in Kazakhstan. Chapter 9 adds a study from Andean cloud forests in Ecuador. Chapter 10 compares the myxomycete assemblages of different forest types in a

gradient from dry to wet forests in Costa Rica. Chapters 11 and 12 present two newly discovered tropical myxomycete assemblages from epiphyllic liverworts and from inflorescences of giant Zingiberales herbs; both form well-circumscribed micro-ecosystems which are convenient models for further studies of myxomycete ecology. Chapter 13 presents the first world distribution map of a myxomycete and demonstrates that spatial patterns of myxomycete distribution can be resolved even with the limited data available for this group of organisms. Chapter 14 is a quantitative analysis to characterize the autecology of the species, but also inter-species relationships, on the case of the community from the Kazakh desert. Whereas chapters 2 to 14 are original contributions to scientific journals, the last two chapters summarize the new results about myxomycete ecology and distribution. Chapter 15 presents conclusive data towards the evolution of the myxomycete fructification, derived from a biological database of all species hitherto described. Chapter 16 illustrates that these micro-organisms have distinctive distribution patterns which can be interpreted ecologically.

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Chapter 2. Species diversity in Myxomycetes based on the morphological species concept – a critical examination.

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Abstract: Using two databases, a world inventory of validly described taxa and a keyworded bibliography of myxomycete literature, research activities for myxomycetes from the year 1753 up to the present time have been documented by the authors. The numbers of described taxa and publications have both increased sharply during the last 30 years, reaching a total of 1012 described taxa of subgeneric rank, with about 1200 published papers presenting regional species lists and about 400 papers describing new taxa. An increasing number of recently described taxa appears to be very rare and is often known only from the type locality. With the well-known morphological plasticity of myxomycete fructifications caused by fluctuations in environmental conditions during development, it cannot be ruled out that aberrant fructifications have been described as new taxa under the current morphological species concept. On the other hand, many apomictic biotypes distinguished by only slight morphological differences may remain unrecognised. In this paper we propose a set of criteria to make descriptions of new taxa more comprehensive. Examples drawn from the authors' experiences illustrate the application of these criteria.

Key Words: database, myxomycetes, research history, species description, taxonomy

Introduction

Myxomycetes (plasmodial slime moulds) are phagotrophic eukaryotes that commonly occur in association with decaying plant material in terrestrial ecosystems. The myxomycete life cycle involves two morphologically distinct trophic stages, one consisting of uninucleate amoebae, with or without flagella, and the other consisting of a distinctive multinucleate structure, the plasmodium (Stephenson & Stempen 1994). Under favourable conditions, the plasmodium gives rise to one or more fruiting bodies containing spores. The spores complete the life cycle by germinating to produce the uninucleate amoeboflagellate cells. Two features, the production of fruiting bodies and dispersal by spores, cause myxomycetes to appear similar to fungi, therefore most of the research on this group

of organisms has been carried out by mycologists. The scientific careers of G.W. Martin and C.J. Alexopoulos illustrate this impressively (Lentz & Benjamin 1971, Blackwell 1988).

Due to both their cryptic life style and the almost complete absence of meaningful taxonomic plasmodial characters, field studies of myxomycetes have invariably focused on the reproductive, spore-producing, stage in the life cycle (Stephenson et al. 1993). Since plasmodia are often hidden within their substrates, fruiting bodies are usually the only readily observable indication of the presence of myxomycetes and can be stored as dry herbarium specimens. These features, as well as the difficulties to maintain most myxomycete species in culture, are the reason that the morphological species concept dominates myxomycete taxonomy.

Methods

Two databases were used to assess the world-wide species diversity in myxomycetes. The first database includes all original descriptions of myxomycetes, according to the current knowledge of the authors (Mitchell 2000). Names for taxa were cited according to Martin & Alexopoulos (1969) wherever possible. In all other cases a citation of the protologue and its reference is given. Due to the often very brief Latin diagnoses, the original authors' descriptions were translated into English, if necessary, and standardised using the terminology for myxomycete fructifications proposed by Lado & Pando (1997). For each taxon described as new from 1753-2000, the publication year of the respective basionym was recorded. Only validly published descriptions, according to the Code of Botanical Nomenclature (Greuter et al. 1994), were included. Based on a survey of the literature, our own collections and those of our colleagues, the known world-wide collections for each taxon were estimated. Taxa were classified into three groups: those known only from the type locality as one or more collections, those reported from 2 to 20 localities, and those reported from more than 20 localities.

A second database was compiled from all of the available literature relating to myxomycete taxonomy, ecology, reproductive system, floristics and distribution (Schnittler, in preparation). Whereas completeness was attempted in the topics mentioned above, papers dealing exclusively with biochemical or physiological aspects are certainly under-represented. Keywords were assigned to all references, allowing the main topics of a paper to be assessed, e.g. the description of a new species or a regional survey of myxomycetes. For regional species lists, all publications recording more than a small set of very conspicuous species and focusing at least partially on myxomycetes were considered. For taxonomic publications, only those papers describing new taxa were included. This excluded a small but important number of publications which dealt with the clarification of species concepts. To document the use of scanning electron microscopy (SEM), all publications containing SEM micrographs were recorded.

Results and Discussion

According to our current data, 1012 subgeneric taxa of myxomycetes have been validly described as valid, including 866 of them at the species level. These figures are considerably higher than those published in standard floras for the group. Martin & Alexopoulos (1969) recognised 422 taxa, almost exclusively at the species level, in their world monograph. Nannenga-Bremekamp (1991) estimated that "about 600 named species" exist world-wide. Yamamoto (1998) listed 925 taxa of various rank (species, varieties, and forms) world-wide in his treatment of Japanese myxomycetes (mentioning all names recognised by him as valid).

Fig. 1 shows the increase in numbers of described sub-generic myxomycete taxa (species, varieties and forms) from the nomenclatural starting point. In contrast to almost all fungal groups the nomenclature of the myxomycetes begins with Linnaeus (1753). Persoon's initial work (1794) and supplements in subsequent years accounted for the first significant increase in the number of taxa, followed by Rostafinski's monograph (1874-1876) and the first edition of Lister's treatment (1894). The last world-wide monograph of the group by Martin & Alexopoulos (1969) marks the beginning of the modern era in myxomycete taxonomy, with an almost continuous and steep increase in the numbers of taxa described since its publication.

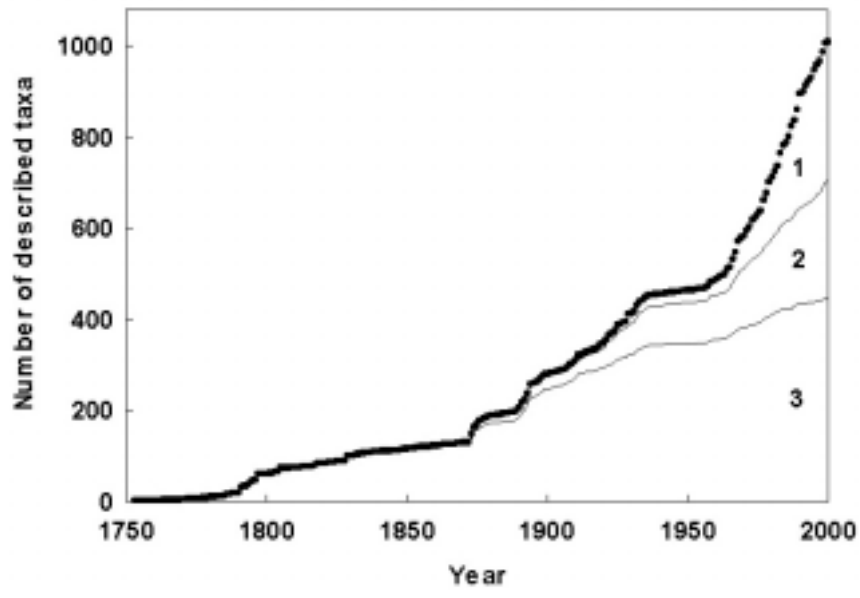

Fig. 1. Numbers of subgeneric myxomycete taxa described as new from the year 1753 (the nomenclatural starting point) up to the present time. The rarity status for all taxa was estimated, by assigning each taxon to one of the three classes, as explained under materials and methods. Numbers from one to three indicate the status of each group as: 1 – taxa known only from the type locality; 2 – taxa known from 2–20 collections; and 3 – more common taxa.

The number of published papers focusing on myxomycetes reflects the increasing interest in myxomycete taxonomy and ecology since the publication of the Martin & Alexopoulos monograph (Fig. 2). Up to the present time, about 3000 (or probably more, due to under-representation of publications on biochemical aspects) papers focusing on myxomycetes have been published (with 2796 currently recorded in the literature data base). About 1200 of these are local or regional species lists, and about 400 describe new taxa.

Even for a mycologist familiar with the myxomycetes, the number of described taxa for the group is surprisingly high, since regional species surveys seldom yield more than 150 taxa, and many species seem to be widely distributed, although often confined to special microhabitats. By comparison, only about 40 species of myxobacteria "can presently be distinguished more or less reliably" (Reichenbach 1993). Although being prokaryotic microorganisms, myxobacteria display a similar ecology (forming more or less elevated fructifications, preying on other, non-motile bacteria and dispersal by spore-like cells) and probably inhabit all substrata upon which myxomycetes occur. While myxobacteria have fewer morphological characters, they do have several taxonomic advantages over the myxomycetes since they are easier to culture and are already accessible to DNA-sequencing studies.

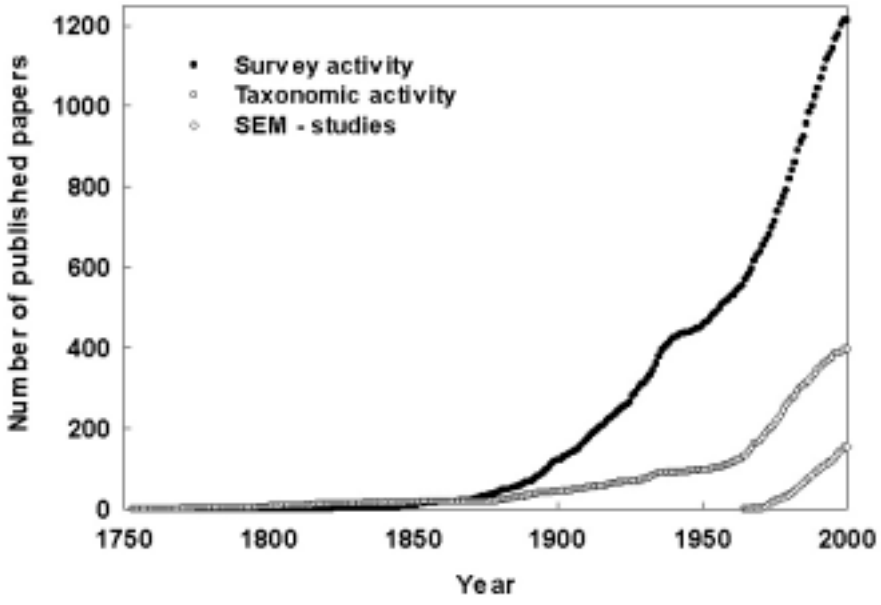

Fig. 2. Numbers of published regional species lists (filled circles – species lists), publications describing new taxa (open circles – taxonomic activity), and publications using scanning electron microscopy (open diamonds – SEM studies).

A closer look at the estimations for rarity or abundance of validly described myxomycete taxa may help to elucidate this situation (Fig. 1). From the 1012 taxa recorded in the taxonomic database, 446

were estimated to be at least fairly common (known from more than 20 collections and reported from several localities), 258 to be rare (known from 2–20 collections and more than one locality), and 305 reported only from the type locality (in one or a few collections). As it is impossible to achieve a complete overview of all myxomycete records, these estimations may overweight rarity. Furthermore, numerous taxa are not well documented and a better knowledge of their microhabitat requirements could easily produce many more records, as indicated by the ecology and distribution of *Barbeyella minutissima* Meyl. (Schnittler et al. 2000). Nevertheless, these estimations clearly reveal a rapidly increasing tendency towards the description of rare myxomycete taxa, often based on a single collection.

The use of SEM not only allows for more detailed species descriptions, but also greatly increases the resolution of taxonomic characters far beyond that of ordinary light microscopy. This has led to the description of taxa based entirely or largely on differences that are visible only by SEM. Prominent examples include *Hemitrichia serpula* var. *parviverrucospora* Lizárraga, Illana & Moreno (1999) and *Hemitrichia pseudoleiocarpa* Illana, Moreno, Lizárraga & Castillo (1999). The former deviates from the typical form of this very common species by the presence of small verrucae between the coarse network of ridges on the spores, whereas the latter is in habit looking "alike with *Arcyria leiocarpa*" (Cooke) G.W. Martin & Alexop., but differing by a less branched capillitium with more numerous free ends (which accounts for its position in *Arcyria*). However, the most notable differences between *H. pseudoleiocarpa* and *A. leiocarpa* are found in spore size (8–9 μm, versus 8–10 μm in the new species) and the presence of dendroid warts on the spore surface in the new species (versus simple warts in *A. leiocarpa*). This leaves the spore ornamentation as the only qualitative character distinguishing the two species.

Myxomycetes as a group have two contrasting features, which make their proper taxonomic treatment a challenge for the biologist. Due primarily to their cryptic vegetative stages and as a result of the paucity of taxonomic characters that these stages display, myxomycete taxonomy rests almost entirely on the morphology of the fruiting body. But, as every student of myxomycetes employing the moist chamber technique knows, the normal development of fruiting bodies is highly dependent upon environmental conditions; unsuitable conditions easily produce aberrant fructifications. Hence, environmental variability during the development of myxomycete fructifications is certainly a major source of variability in taxonomic characters, and the application of SEM provides a resolution well within this range of variability. Secondly, as shown by many experiments with the small percentage of species that are easy to cultivate, the occurrence of apomictic lineages (biotypes) in myxomycetes is a common phenomenon, which probably holds true for many of the species-rich genera. These

apomictic strands are probably produced by conversion of sexually reproducing forms (Collins et al. 1983). The consequences of this special reproductive behavior are explained in detail in this issue (Clark 2000). The main consequence of this phenomenon for taxonomy is that these apomictic biotypes are genetically isolated. As such, they can accumulate and conserve new characters inherited from their sexually reproducing parental forms or characters can be acquired by mutation. Instead of a continuum of characters, this process produces a set of character combinations deviating in minor features. With the sophisticated tools of modern taxonomy, such minor differences can be recognised. The taxonomic history of brambles (*Rubus*) in Germany can serve as an example for the taxonomic consequences of apomictic reproduction (Weber 1996, see Clark 2000). In this group of vascular plants, which possesses much more and better accessible morphological traits, two sexually reproducing parental species (*R. ulmifolius* and *R. canescens*) gave rise to an agamous complex with about 300 (Weber 1995) apomictic biotypes, which occasionally hybridise and form new biotypes.

As a consequence, myxomycete taxonomy must deal with the considerable morphological plasticity of the fructifications that results from environmental influence, adding a lot of "taxonomic noise" to the often minor differences that may result from genetically distinct (perhaps often apomictic) lineages in the group. With insufficient understanding of the causes of such variability, considerable caution is necessary in the description of new taxa. Thus, in this situation, the criteria for evaluating candidates for new taxa should be comprehensive. As a result of this thesis, we suggest the following five criteria.

1. When considering a taxon as being new to science, the body of world-wide published myxomycete literature should be checked to find any possible matching description.

Myxomycete distribution seems to depend much more on the available microhabitat than on geographic location. Two cases experienced by us may illustrate this point. *Lamproderma granulosum* Neubert, Nowotny & Schnittler (1990), described from several collections growing on liverwort mats on wet and well-sheltered sandstone rocks in eastern Germany, was found again in the same microhabitat in the Great Smoky Mountains, USA (Schnittler, unpubl. results). *Licea erecta* var. *erectoides* (Nann.-Bremek. & Y. Yamam.) Y. Yamam. (Yamamoto 1999) was recently found as five perfectly matured sporocarps in a Costa Rican rainforest. Considered at the species level, four collections of this myxomycete are now known: India, Darjeeling, on decaying bamboo twigs (typus of *L. erecta*, Thind & Dhillon 1967); Japan, Kochi Pref., two collections differing somewhat from each other on decaying aerial twigs and on tree bark (originally described as *L. erectoides*, Nannenga-Bremekamp & Yamamoto 1983); and Costa Rica, cloud forest at Monteverde, from decaying leaf sheaths of a living *Chamaedorea* palm (perfectly matching the description of *L. erectoides*, Schnittler, unpub. results). Although these localities span the globe, the microhabitat and vegetation type appear to be similar.

2. To exclude the possibility of describing an aberrant form that has resulted from development under adverse conditions, a new taxon should be represented by several specimens from more than one locality.

While checking the Costa Rican myxomycete collections at the University of San Jose herbarium, one specimen was found that did not conform to any known species description. It consisted of one, perfectly mature collection of at least 1000 sporocarps from a high-elevation cloud forest of the Cerra de la Muerte (leg. A. Jiminez). The sporocarps occur gregariously, but not crowded, and display the general habit of a large *Cribraria* with a well developed stalk and a network of perforations in the upper half of the peridium. However, the spore size and ornamentation are identical to those of *Tubifera ferruginosa* which, although predominantly temperate in distribution, is known to occur at high elevations in Costa Rica. Even though the description of a new taxon would be formally correct and acceptable, since the material is more than sufficient for a type collection, it is certainly possible that this specimen represents an aberrant form of *T. ferruginosa*. However, the possibility that it represents a new taxon cannot be ruled out at this stage.

3. Since there are often only minor morphological differences in the characters separating apomictic species groups, taxonomic descriptions should be as exact as possible. Therefore, photographs made by light microscopy as well as SEM images of all relevant parts of a fructification should be mandatory for an original description. Colours, especially for the dry spore-mass, should be referred to a colour chart, and the variability of characters for the specimens investigated should be given. Spore-to-spore cultures should be attempted to ascertain the constancy of the main characters upon which the diagnosis of the new taxon is based.

The description of *Didymium annulisporum* Keller & Schoknecht (1989) provides an excellent example, since it included SEM and LM photographs as well as culture work.

4. The characters distinguishing the new taxon from its closest relatives should be critically evaluated for their constancy, and the new taxon should deviate from the others in more than one character, to exclude cases where a single gene mutation could have altered the species' appearance.

A possible character that may be affected by mutations in a single gene is that of clustered versus free spores. Evidence for this assumption can be derived from the fact that a number of synsporous taxa have been described throughout many genera of myxomycetes. Except for the genus *Badhamia*, with at least seven taxa having firmly clustered spores, all other species with conglobate spores are unique for their genus and are often very rare (Table 1). Therefore, the possibility cannot be ruled out that clustered spores occur easily but rarely as a mutation in numerous myxomycete species. It is conceivable that this condition is mostly not of evolutionary advantage, due to the reduced probability that the spores become airborne for efficient dispersal.

5. To facilitate the repeated discovery of a suspected new species, not only its localities, but also the habitat of all known specimens of a new taxon should be described. This includes a figure for the elevation, at least a brief description of the vegetation type, and all possible details of the microhabitat.

A case in point is that of the recent discovery of a new corticolous species of *Licea* by the second author which was at first considered to be an aberrant form that lacked peridial pigments. The taxon was originally found as a single sporocarp in a culture of the bark of living Elder (*Sambucus nigra*). Further moist chamber cultures of bark of the same phorophyte yielded identical material from numerous localities in the Weald, south-east England. The same taxon later appeared on *Sambucus pubens* bark from the Great Smoky Mountains National Park, USA and on *Quercus ilex* bark from Madrid, Spain. In all cases the species was associated with algae, primarily on bark with a high water-capacity. Many field collections were also made and the taxon was eventually described as *Licea sambucina* D.W. Mitchell (Mitchell & McHugh 2000).

Obviously, the application of these criteria would not only help prevent the accumulation of doubtful species in myxomycetes and the resulting taxonomic confusion, but they would also lead to an accumulation of “candidate specimens” (which do not yet meet these criteria) in the collections of myxomycetologists. This is not a very satisfactory situation. A possible solution could be an Internet site, where descriptions of such candidates could be posted to be evaluated for their taxonomic value by the scientific community. As an additional effect, this would greatly enhance the possibility that another investigator might find more specimens of the putative new taxon, thereby accumulating further evidence that it represents a true biological entity.

Hopefully, in the near future, myxomycete fructifications will be accessible to DNA sequencing, providing an useful additional tool to support or improve the current morphological species concept, as is already the case for many other groups of organisms.

Acknowledgements

For helpful suggestions and proof reading of the manuscript we are indebted to Drs. J. Clark and S.L. Stephenson. We also owe thanks to W. Nowotny for providing the opportunity to present this paper in Stapfia.

Table 1. Described myxomycete taxa with clustered (conglobate) spores. For the rarity status, 1 refers to a taxon known from the type locality only, 2 stands for rare taxa known from 2–20 collections, and 3 for more common taxa. The column headed 'Spore clusters' denotes the number of spores per cluster. In the last column a common and similar species of the same genus is mentioned, which differs mainly by having free spores.

Species name[a]	Rarity status	Spore clusters	Possible counterpart species
Badhamia bispora Whitney	2	2	*B. nitens* Berk. (see below)
Badhamia calcaripes Gottsb.	1	6–20	—
Badhamia capsulifera (Bull.) Berk.	2	6–20	—
Badhamia crassipella Whitney & H.W. Keller	3	4–40	—
Badhamia dubia Nann.-Bremek.	2	7–12	—
Badhamia nitens Berk.	3	6–12	—
Badhamia papaveracea Berk. & Rav.	3	6–20	—
Badhamia populina Lister & G. Lister	2	10–20	—
Badhamia versicolor Lister	3	10–40	—
Calomyxa synspora M.L. Farr & Kowalski	1	5–30	*C. metallica* (Berk.) Nieuwl.
Diachea koazei Y. Yamam.	2	10–20	*D. leucopodia* (Bull.) Rostaf.
Diacheopsis synspora Nann.-Bremek. & Y. Yamam.	1	4–8	*D. metallica* Meyl.
Dianema corticatum Lister	3	2–6	—
Didymium synsporon T.E. Brooks & H.W. Keller	2	4–25	*D. difforme* (Pers.) S.F. Gray
Enerthenema berkeleyanum Rostaf.	2	4–12	*E. papillatum* (Pers.) Rostaf.
Licea synsporos Nann.-Bremek.	2	ca. 14	*L. tenera* Jahn
Leocarpus bisporus Nann.-Bremek. & D.W. Mitchell	2	2	*L. fragilis* (Dicks.) Rostaf.
Macbrideola synsporus (Alexop.) Alexop.	3	7–15	*M. oblonga* Pando & Lado
Minakatella longifila G. Lister	2	8–14	—
Perichaena syncarpon T.E. Brooks	2	4–16	*P. depressa* Libert
Physarum bitunicatum S. Carter & Nann.-Bremek.	1	4–12	*P. rubiginosum* Fr. ?
Physarum lakhanpalii Nann.-Bremek. & Y. Yamam.	2	4–6	*P. decipiens* Curtis
Physarum miniatum Nann.-Bremek.	1	2–6	*P. nasuense* Emoto
Physarum synsporum Stephenson & Nann.-Bremek.	1	3–8	*P. decipiens* Curtis ?
Reticularia olivacea (Ehrenb.) Fr.	3	1–20	spores free or clustered
Trichia conglobata M.L. Farr	1	2–12	*T. lutescens* (Lister) Lister
Trichia synsporum Kowalski & McNichols	1	2–3	*T. varia* (Pers.) Pers.
Symphytocarpus syncarpus (Yamashiro) Y. Yamam.	1	5–8	*S. confluens* (Cooke & Ellis) Ing & Nann.-Bremek.

[a] For the following species not mentioned in Martin & Alexopoulos (1969) a citation of the protologue is given: *Badhamia bispora* Whitney Mycologia **70**:672.1978; *B. calcaripes* Gottsb. Nova Hedwigia **22**:491.1972; *B. crassipella* Whitney & H.W. Keller Mycologia **74**:620.1982; *B. dubia* Nann.-Bremek. Proc. K. Ned. Akad. Wet. C **71**: 49.1968; *Calomyxa synspora* M.L. Farr & Kowalski Mycologia **66**:886.1974; *Diachea koazei* Y. Yamam. J. Jap. Bot. **62**:346.1987 (syn: *D. synspora* H.Z. Li Acta Mycol. Sinica **7**:99.1988); *Diacheopsis synspora* Nann.-Bremek. & Y. Yamam. Proc. K. Ned. Akad. Wet. C **89**:223.1986; *Didymium synsporon* T.E. Brooks & H.W. Keller Mycologia **65**:287.1973; *Licea synsporos* Nann.-Bremek. Proc. K. Ned. Akad. Wet. C **71**:42.1968; *Leocarpus bisporus* Nann.-Bremek. & D.W. Mitchell, in Nann.-Bremek. Proc. K. Ned. Akad. Wet. C **92**:512.1989; *Macbrideola oblonga* Pando & Lado Mycotaxon **31**: 302. 1988; *Physarum bitunicatum* S. Carter & Nann.-Bremek. Proc. K. Ned. Akad. Wet. C **75**:328.1972; *P. synsporum* Stephenson & Nann.-Bremek. Proc. K. Ned. Akad. Wet. C **93**:193.1990; *Trichia conglobata* M.L. Farr Mycologia **66**:882.1974; *Trichia synspora* Kowalski & McNichols Mycologia **66**:372.1974; *Symphytocarpus syncarpus* (Yamashiro) Y. Yamam. J. Jap. Bot. **59**:256.1984.

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Karstenia 39: *77-97, 1999*

Myxomycetes of the Taimyr Peninsula (North-Central Siberia)

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NOVOZHILOV, Y. K., SCHNITTLER, M. & STEPHENSON, S. L., 1999: Myxomycetes of the Taimyr Peninsula (north-central Siberia). – Karstenia 39:77-97. Helsinki. ISSN 0435-3402.

Fifty-six species of myxomycetes representing twenty-six genera were identified from 371 collections that originated almost exclusively from 270 moist chamber cultures prepared with samples of decaying plant material collected on the Taimyr Peninsula (Russia, north-central Siberia) and in the adjacent Putorana Plateau. Species numbers progressively decrease from northern taiga and forest-tundra over southern tundra to the typical tundra subzone. Forty species in 18 genera were recorded in the northern taiga subzone, 40 species in 19 genera in forest-tundra, and 25 species in 17 genera in the tundra subzones. A taxonomic specificity or community endemism of myxomycete assemblages in tundra as compared to those of northern taiga communities was not found. In general, the myxomycete flora of the tundra zone of the Taimyr Peninsula can be considered as an impoverished flora of the northern taiga subzone. Ten ubiquitous species were recorded from at least one half of all studied localities. The average number of species per genus (2.1) calculated in our study indicates a rather low species diversity for high latitudes, contrary to the floras of temperate and tropical zones where this ratio ranges from 2.2 to 4.6. Values for the coefficient of community, calculated for all pairwise combinations of different study areas in the Arctic, range from 0.45 to 0.63, thus indicating fairly high levels of similarity among arctic and subarctic myxomycete floras.

Key words: myxomycetes, biodiversity, ecology, Arctic, Russia, Taimyr Peninsula

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Introduction

Myxomycetes (plasmodial slime moulds) are common inhabitants of decaying plant material in boreal forests of the taiga zone, as shown by several studies in Alaska (Stephenson & Laursen 1990, 1998), Scandinavia (Eliasson & Strid 1976; Härkönen 1978, 1979a, b; Johannesen 1984; Schinner 1983), and north-western Russia (Novozhilov 1985, Schnittler & Novozhilov 1996). Probably some species common in the taiga can move farther north to the zone of forest-tundra and tundra, invading new and unusual microhabitats. At present, myxomycete communities of open forest-tundra, tundra, and herb-rich grassland ecosystems of high-latitude regions of the Arctic and Subarctic have received relatively little study (Ing 1994). Major surveys have been carried out in certain regions of the Subarctic and Arctic, including: Iceland (GØtzsche 1984, 1990), Greenland (GØtzsche 1989), Alaska (Stephenson & Laursen 1990, 1993, 1998; Stephenson et al. 1994), and the northern biological province Inarin Lappi in Finland (Härkönen 1979b). Available information for the myxomycetes of the Russian Arctic is fragmentary and rather meagre (Novozhilov et al. 1998a, 1998b). Only a few papers with species lists for some areas

such as the Khibine Mountains in the Kola Peninsula (Novozhilov & Schnittler 1997), the Chukchi Peninsula (Novozhilov 1986, Stephenson et al. 1994), and the Taimyr Peninsula (Novozhilov & Schnittler 1996) have been published previously. The primary objective of the research reported herein was to obtain data on the distribution and ecology of myxomycetes in tundra, forest-tundra, and northern taiga forest ecosystems of the Taimyr Peninsula of north-central Siberia and adjacent areas of the Putorana Plateau.

Materials and Methods

The main sources of information used in the present study were specimens obtained from moist chamber cultures of various substrata, especially those on which corticolous and fimicolous species are known to occur, and to a lesser extent field collections of myxomycetes. For each vegetation unit, an effort was made to examine all types of microhabitats upon which sporocarps of myxomycetes might be expected. These included the bark surface of living trees and shrubs, litter of shrubs and trees as well as from various herbaceous plants, and the dung of herbivorous animals. Two hundred seventy moist chamber cultures were prepared as described by Härkönen (1977, 1981a) and Stephenson (1985, 1989) and maintained for up to 2.5 months. Herein, a 'collection' is defined 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 is considered as one collection. For each moist chamber, pH values were determined using a Orion 610 pH meter.

Myxomycete communities were compared using the Sorenson - Czekanowski coefficient of community (Roberts 1986). This index ranges from 0 (no species in common) to 1 (all species are members of both communities). Species diversity indices were calculated for myxomycete communities in different microhabitats using Shannon's formula (Shannon & Weaver, 1963); species diversity (H′) = $-\sum P_i \log P_i$, where P_i is the relative abundance of a particular species (the proportion of the total number of individuals represented by species i). Maximum values for this diversity index are usually observed when there are many species with equal abundances. Values decrease with both a reduction in the number of species and an increase in abundance of a very few species.

Nomenclature used herein follows Martin & Alexopoulos (1969) for myxomycetes, with a few exceptions indicated by taxonomic references, and Czerepanov (1995) for vascular plants. For determination, sporocarps were often preserved as permanent slides in polyvinyl lactophenol and/or glycerol gelatine, to distinguish between limeless and lime-containing structures. Colour descriptions in taxonomical comments are given according to Petersen (1996). In several cases, sporocarp structures were studied with a JEOL 35c scanning electron microscope (SEM) at St. Petersburg. Specimens are deposited in 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 stored at the herbarium Haussknecht, Jena, Germany (JE).

Study Area

The Taimyr Peninsula and the adjacent Putorana Plateau is one of the harshest landscapes of north-central Siberia. The highly continental climate is characterised by winter temperatures that drop as low as -45 °C. Average January and July temperatures are -30.6 and +11.4 °C, respectively. In summer, the temperature rises rapidly, exceeding +10 °C at the end of June. Maximum air temperatures in July can be very high in the tundra and may reach 20 °C. The annual precipitation in the region ranges between 300 and 350 mm, with approximately one-third falling as rain in July-August (Chernov & Matveyeva 1997; Romanova 1971).

Study sites included all typical plant communities in the tundra, forest-tundra and northern taiga vegetation zones. These three vegetation zones intergrade frequently within relatively small distances, often resulting in a vegetation mosaic. Therefore, an exact geographical delimitation is almost impossible (Alexandrova 1977, Kozhevnikov 1996, Sirois 1983, Tikhomirov 1970). On the Taimyr Peninsula, the tundra belt extends 600-700 km from south to north, with a southern border at about 72 °N (Fig. 1). In the south, it borders the forest-tundra and in the north the polar desert (Fig. 2). As an ecotone, the forest-tundra zone connects the two contrasting types of landscape (Chernov & Matveyeva 1997).

Myxomycete and substratum samples were collected from mid-June to mid-July during the

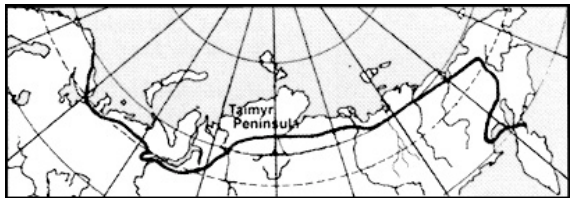

Fig 1. Geographical location of the Taimyr Peninsula within Russia. A solid line indicates the northern limit of boreal forests according to Tolmachev (1960).

1995-96 field seasons at 10 localities (Figs. 1, 2). These are listed below.

1. Putorana Plateau, slopes of hills called "Krasnyi Kamen′", ca. 80 km N of the city of Norilsk, 69°29' N, 88°32' E;
2. Taimyr Peninsula, Kaiak settlement, the watershed of the Kotui River, 71°30' N, 103°00' E;
3. Kheta settlement, the watershed of the Kheta River, 71°31' N, 99°24' E;

4. Khatanga city, the shore of the Kazach'ia River, 72°00' N, 102°38' E;
5. Zhdanikha settlement, the watershed of the Khatanga River, the Nuzhdina Golf, 72°17' N, 103°22' E;
6. Pekas-Khory Island, the watershed of the Khatanga River, 72°27' N, 103°30' E;
7. The watershed of the Khatanga River on the Oboynaya gulf, 72°28' N, 104°15' E;
8. Starorybnoe settlement at the northern bank of the Khatanga River, 72°45' N, 104°50' E;
9. Severnyi Promontory in the region of the watershed of the Khatanga River, 72°46' N, 105°14' E;
10. The Kosmatyi Promontory on the watershed of the Khatanga River, 73°39' N, 109°42' E.

Elevations of the sites on the Putorana Plateau (loc. 1) varies between at 100 and 200 m above sea level, resulting in the presence of all vegetation zones from northern taiga, to montane polar desert (Kozhevnikov 1996). The Taimyr Peninsula is a lowland, all investigated localities (2-10) are below 50 m. A transsect, ranging from the northern taiga on the Kotui River (loc. 2) and on the Kheta River (3) to the forest-tundra (4-7), southern tundra (6-8), and typical tundra (9-10) in the watershed of the Khatanga River was studied.

Five vegetation subzones were differentiated and consecutively numbered by Roman numerals (Fig. 2):

I. Northern taiga (loc. 1-3). The timberline (boundary of zonal woodlands) delimiting this subzone northwards is formed mainly by pure larch (*Larix gmelinii*) forests. As considered herein, northern taiga is regarded as light, open-crowned forest with less than 60% canopy coverage. Fallen trees are mainly exposed to

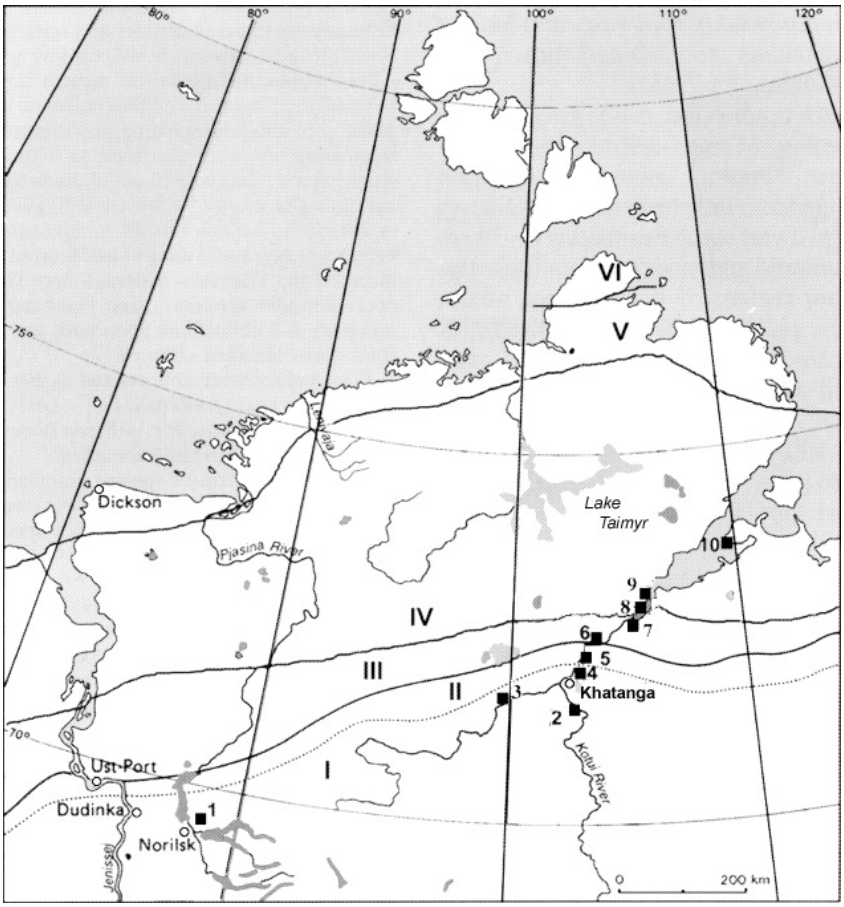

Fig. 2. Map of the Taimyr Peninsula showing the location of the ten sample sites (black rectangles). Numbers refer to the sites listed in the text. A dotted line shows the northern boundary of the light larch taiga, whereas solid black lines indicate the boundaries of the tundra subzones: I - northern taiga; II - forest-tundra; III - southern tundra; IV - typical tundra; V - arctic tundra; VI - polar desert. Map compiled from Chernov & Matveyeva (1997).

direct sunlight, which slows down their decay, thus probably excluding numerous wood-inhabiting myxomycetes. In the Putorana Plateau, spruce (*Picea obovata*) is intermixed in the larch stands. On wet depressions, rich herbfields of tall perennials such as *Cirsium helenioides* or *Heracleum sibiricum* can be found in the understorey.

II. Forest tundra (loc. 1, 3, 4, 5). Here, closed larch woodlands appear only locally under favourable conditions (e.g., in stream valleys or on south-facing slopes), with small, widely separated trees up to 10 m in height. Logs up to 40 cm thickness may occur. To the north, but also in the natural meadows of the stream valleys, shrub thickets (*Duschekia fruticosa* and *Salix* spp.) intermixed with single, small larch trees dominate. In the Putorana Plateau, tall and large thickets of willows, alder (*Duschekia fruticosa*), and juniper (*Juniperus communis* ssp. *sibirica*) form a subalpine forest-tundra on hillsides.

III. Southern tundra (loc. 6-8). The absolute northern boundary of trees delimits the tundra. As used here, "tundra" includes vegetation types that range from tall shrub communities up to 1.5 m high to dwarf shrub heathlands (5-20 cm high) and graminoid and moss communities. The most important feature of the southern tundra subzone is the presence of shrubs (*Duschekia fruticosa*, *Salix* spp.) growing up to 1.5 m tall, which can form large patches, providing still medium-sized wood debris. These tall and closed shrub thickets are typical for "intrazonal" biotopes, such as river valleys, rivulets, and lake depressions and can provide medium-sized pieces of coarse woody debris.

IV. Typical tundra (loc. 9, 10). Low shrubs such as dwarf birch (*Betula nana*) up to 50 cm, and various dwarf willows prevail in the typical tundra. On the ground of these very dense thickets still leafy litter accumulates, sheltered from the strong winds. Woody debris is present usually as twigs of a 1-3 cm (rarely up to 10 cm) in diameter.

V. Arctic tundra (locality 1). This subzone was investigated as mountain tundra in the Putorana Plateau only. At elevations higher than 200 m, arctic mountain tundra with dwarf birch and various prostate ericaceous shrubs prevails. Locally, shrub thickets of >10 cm in height occur, but grass- or lichen-rich communities dominate. Small accumulations of litter still exist, and coarse woody debris can be found as small twigs and trunks mostly <2 cm diameter. Wind exposed sites are already free of vegetation.

VI. Polar desert (not investigated). In this subzone, mosses and lichens dominate, and shrubs grow only with subterranean twigs (e.g. *Salix polaris*). The vegetation present forms no closed cover.

Annotated species list

The following annotated list includes all recorded species in alphabetical order. Species names are followed by the collections numbers of the first author (numbers of five or six digits) and/or the second author (numbers of four digits). The string "..." indicates common species for which not all collection numbers were listed. Determinations considered as doubtful are given with the note "cf." (confer). The total numbers of records for field and moist chamber collections (symbols fc and mc) are provided in brackets, followed by the locality numbers as given in Fig. 2, with the number of records for each locality given in parentheses. Next, the distribution of species in different vegetation subzones and microhabitats is listed. The vegetation subzone is indicated by a Roman numeral After a colon, the number of records is given, separated by a hyphen from the abbreviation of the plant's name providing the substratum. Substratum types (listed in parentheses) were classified as following: w - decayed coarse wood debris (>10 cm in diameter); b - bark of living trees and shrubs; l - litter, including leaves, branchlets, or *Duschekia* catkins as well as remnants of various herbaceous plants; and d - dung of herbivorous animals, such as the lemming (*Lemmus lemmus*), hare (*Lepus* sp.), reindeer (*Rangifer tarandus*), and polar partridge (*Lagopus lagopus*). All collections upon bark and litter originated from moist chamber cultures.

Plant names were abbreviated as: *Bet.* - *Betula nana*, *Dus.* - *Duschekia fruticosa*, *Lar.* - *Larix gmelinii*, *Jun.* - *Juniperus communis*, *Pic.* - *Picea obovata*, *Sal.* - *Salix* spp., and *Sor.* - *Sorbus aucuparia*.

For an estimation of species abundance, the percentage scale of Stephenson et al. 1993 was adapted. This is based on the proportion of a species on the total number of records: R - rare (<0.5%, recorded once or twice), O - occasional (0.5-1.5%, 3-6 records), C - common (1.5-3%, 7-11 records), A - abundant (> 3%, more than 11 records). Since our field survey took place in June, many species of xylophilous myxomycetes that sporulate later in the year may be underrepresented. Consequently, this scale was applied to moist chamber collections only.

In the list, abbreviations used for distribution of myxomycetes in subarctic and arctic regions were IC - Iceland (GØtzsche 1984, 1990), FL - northern biological province Inarin Lappi in Finland (Härkönen 1979b), KP - Kola Peninsula (Novozhilov & Schnittler 1997), PU - Polar Ural, YP - Yamal Peninsula (Novozhilov et al. 1998a), CP - northern-eastern part of the Chukchi

Peninsula (Novozhilov 1986, Stephenson et al. 1994), AL - Alaska (Stephenson & Laursen 1990, 1993, 1998; Stephenson et al. 1994), and GR - Greenland (GØtzsche 1989).

A *Arcyria cinerea* (Bull.) Pers. 48959...; [fc – 1; mc – 42]. Loc. 1 (20), 2 (9), 4 (1), 5 (7), 6(1), 7 (5). **I**: 2 – *Dus.* (w), 4 – *Lar.* (w), 2 – *Pic.* (w), 1 – *Sal.* (w), 2 – *Jun.* (b), 1 – *Pic.* (b), 2 – *Sal.* (b), 1 – *Dus.* (l). **II**: 1 – *Dus.* (w), 5 – *Lar.* (w), 1 – *Dus.* (b), 1 – *Sal.* (b), 3 – *Dus.* (l). **III**: 5 – *Dus.* (w), 1 – *Lar.* (w), 1 – *Dus.* (b), 1 – *Sal.* (b), 3 – *Jun.* (b), 2 – *Dus.* (l), 2 – hare (d). **V**: 2 – *Sal.* (b). Appearing regularly in moist chamber cultures of decaying wood but also inhabiting bark of living trees and shrubs, rarely on litter and dung. One of the most common and abundant myxomycetes in the Taimyr Peninsula, recorded also from numerous localities in the Subarctic and Arctic. – IC, FL, KP, PU, YP, CP, AL, GR.

R *Arcyria denudata* (L.) Wettst. 49161, 49229; [mc – 2]. Loc. 1 (1), 2 (1). **I**: 1 – *Pic.* (w), 1 – *Lar.* (w). Widely distributed in boreal forests but seemingly less common than the previous species in the arctic area. On the Taimyr Peninsula recorded from the northern taiga zone only, also collected from Inarin Lappi (Finland). As a typically wood–inhabiting species, it is clearly underrepresented in our study.

A *Arcyria incarnata* (Pers.) Pers. 48964...; [fc – 1; mc – 14]. Loc. 1(6), 2 (7), 5 (1), 6 (1). **I**: 2 – *Pic.* (w), 4 – *Lar.* (w), 2 – *Sal.* (w), 1 – *Sal.* (b). **II**: 3 – *Lar.* (w). **III**: 3 – *Dus.* (w). – IC, FL, PU, CP, AL, GR.

R *Arcyria obvelata* (Oeder) Onsberg 48970, 49242; [fc – 1, mc – 1]. Locality: 1 (2). **I**: 2 – *Pic.* (w). Apparently rare in the subarctic and arctic area (FL, KP), as a wood-inhabiting species probably underrepresented in this survey.

O *Arcyria pomiformis* (Leers) Rost. 49136...; [mc – 3]. Loc. 1 (1), 2 (1), 4(1). **I**: 2 – *Lar.* (w). **II**: 1 – *Lar.* (w). – FL, KP, CP, AL, GR.

R *Arcyodes incarnata* (Alb. & Schw.) Cooke 49179 [mc]. Locality: 2. **II**: 1 – *Sal.* (w). – KP, CP.

R *Calomyxa metallica* (Berk.) Nieuwl. 7131 [mc – 1]. Locality: 2 (1). **I**: 1 – *Lar.* (w). – IC, PU, YP, CP, AL, GR.

O *Ceratiomyxa fruticulosa* (Müll.) Macbr. 48965...; [fc – 3, mc – 3]. Loc. 1 (5), 2 (1). **I**: 1 – *Dus.* (w), 2 – *Pic.* (w), 1 – *Lar.* (w). **II**: 1 – *Lar.* (w). **III**: 1 – *Dus.* (w). Seemingly restricted to woody debris, whose availability limits its distribution northwards. – IC, FL, KP, PU, CP, AL, GR.

R *Comatricha laxa* Rost. 49182 [mc]. Locality: 1. **I**: 1 – *Pic.* (w). Probably common in the boreal zone (Schnittler & Novozhilov 1996) but rare in the Arctic. – IC, PU, CP, AL, GR.

A *Comatricha nigra* (Pers. ex J.F. Gmelin) Schroet. 48919...; [fc – 5, mc – 42]. Loc. 1 (11), 2 (14), 4 (2), 5 (10), 6 (1), 7 (9). **I**: 2 – *Dus.* (w), 2 – *Lar.* (w), 1 – *Pic.* (w), 1 – *Sal.* (w), 7 – *Lar.* (b), 3 – *Pic.* (b). **II**: 1 – *Dus.* (w), 3 – *Lar.* (w), 1 – *Sal.* (w), 14 – *Lar.* (b), 1 –*Dus.* (l). **III**: 3 – *Dus.* (w), 1 – *Lar.* (w), 6 – *Lar.* (b), 1 – *Dus.* (b). Common in the arctic area in all typical plant communities in the tundra, forest-tundra, and northern taiga. – IC, FL, KP, PU, CP, AL, GR.

R *Comatricha pulchella* (Bab. & Berk.) Rost. 7375 [mc]. Locality: 2 (1). **I**: 1 – *Lar.* (w). Apparently rare in the Arctic.

R *Craterium leucocephalum* (Pers.) Ditmar 204185 [mc]. Locality: 9 (1). **IV**: *Sal.* (w). One record on small *Salix* twigs from the litter layer. Probably a species requiring higher temperatures for development and therefore rare in the Arctic. – IC, PU, AL.

R *Cribraria* cf. *atrofusca* Martin et Lovejoy 49237 [mc]. Locality: 2 (1). **I**: *Lar.* (w). In the arctic area, so far known only from the Taimyr Peninsula.

With its long stalks and small capitula, this form approaches in habit *C. languescens*. Deviating characters are the large spores (9.6–)10.2–11.4(–13.2) µm in diameter and the strongly thickened, pillow–shaped knots of the peridial network.

O *Cribraria microcarpa* (Schrad.) Pers. 7112, 7211, 7216, 7327; [mc – 4]. Loc. 2 (2), 4 (1), 5 (1). **I**: 2 – *Lar.* (w). **II**: 2 – *Lar.* (w). In the Arctic known only from the Taimyr Peninsula. A widely distributed species often occurring in moist chambers. In the present survey found on decorticated, thick *Larix* logs.

O *Cribraria violacea* Rex 49156, 49199, 49241, 7342; [mc – 4]. Locality: 2 (4). **I**: 1 – *Lar.* (w), 1 – *Sal.* (w). 1 – *Sal.* (b). **II**: 1 – *Sal.* (b). A mostly tropical species with probably higher temperature requirements than provided by typical conditions in the Arctic. Our records and additional ones from Alaska, both arctic regions with a continental climate and comparatively high summer temperatures, seem to confirm this.

R *Cribraria vulgaris* Schrad. 49157 [mc]. Locality: 2. **II**: 1 – *Lar.* (w). Widely distributed within the temperate zone but very rare in the Arctic, where it is known from the Taimyr Peninsula only.

– *Diderma radiatum* (L.) Morgan 48944 [fc]. Locality: 5. **II**: 1 – *Lar.* (w). – FL, CP, AL.

R *Didymium difforme* (Pers.) S.F.Gray 49109 [mc]. Locality: 5. **II**: 1 – polar partridge (d). In contrast to other coprophilous species it can utilise also acidic dung (in our case a pH of 5.9 was measured). Widely distributed over all continents, also common in the Arctic where it has been found on litter and dung of herbivorous animals (Eliasson & Lundqvist 1979). Also common on cultivated grain (Härkönen & Koponen 1978). – KP, YP, CP, AL, GR.

O *Didymium dubium* Rost. 48947...; [fc – 4, mc – 3]. Loc. 1 (4), 9 (2). **I**: 1– *Lar.* (b), 3 – grasses (l). **IV**: 2 – *Sal.* (w), 1 – on grass litter collected by lemming for their dens (l). – KP, YP, AL, GR.

R *Didymium melanospermum* (Pers.) Macbr. 49247 [mc]. Locality: 4. **II**: 1 – *Dus.* (w). In contrast to other *Didymium* species with a preference for litter and dung, this species typically occurs on mossy coarse woody debris, more rarely on litter. – FL, PU, CP, AL.

R *Didymium squamulosum* (Alb. & Schw.) Fr. 49100, 49246; [mc – 2]. Loc. 4 (1), 7 (1). **II**: 1 – *Dus.* (l). **III**: 1 – *Sal.* (l). – FL, YP, CP, AL, GR.

C *Echinostelium brooksii* Whitney (Fig. 5 E – F) 49256...; [mc – 8]. Loc. 1 (1), 2 (4), 4 (1), 5 (1), 7 (1). **I**: 2 – *Lar.* (w), 1 – *Lar.* (b), 1 – *Sal.* (b). **II**: 1 – *Lar.* (w), 1 – *Lar.* (b), 1 – *Sal.* (b). **III**: 1 – *Lar.* (w). – IC.

All specimens fit the description given by Whitney (1980) except that the spores rarely show a thinner area in the wall. The columella is lenticular, borne on a short cylindrical projection of the stipe reaching 4–8 µm in diameter and 2–4 µm in height. The spores are minutely spinulose (Fig. 5, F), and 10–12 µm in diameter. This species, regarded as rare, was found surprisingly often in moist chambers, preferentially on the acidic bark of *Larix* (pH 3.8–5.5; mean 4.3 ± 0.7).

A *Echinostelium minutum* de Bary 49116...; [mc – 60]. Loc. 1 (15), 2 (15), 3 (1), 4 (3), 5 (10), 7 (13), 8 (1), 9 (2). **I**: 1 – *Bet.* (w), 2 – *Dus.* (w), 3 – *Lar.* (w), 2 – *Pic.* (w), 3 – *Sal.* (w), 3 – *Sal.* (b), 1 – *Dus.* (l). **II**: 8 – *Lar.* (w), 2 – *Dus.* (w), 1 – *Sal.* (w), 1 – *Dus.* (b), 2 – *Lar.* (b), 1 – *Sal.* (b), 5 – *Dus.* (l), 1 – lemming (d). **III**: 9 – *Dus.* (w), 3 – *Lar.* (w), 1 – *Sal.* (w), 1 – *Dus.* (b), 2 – *Lar.* (b), 2 – *Sal.* (b), 3 – *Dus.* (l). **IV**: 2 – *Sal.* (w). **V**: 1 – *Sal.* (b). On the Taimyr Peninsula this was the most common corticolous species (pH 3.3–6.1, mean 4.5 ± 0.8). Together with the previous species, these seem to be the only two species of the genus with a preference for acidic substrata. – IC, KP, PU, YP, CP, AL, GR.

This very common and easily recognised species occurs in Taimyr collections in white or cream forms only. The pink form often reported by other workers was not observed.

O *Enerthenema papillatum* (Pers.) Rost. 48925...; [fc – 1, mc – 5]. Loc. 1 (1), 2 (4), 7 (1). **I**: 1 – *Pic.* (w), 1 – *Lar.* (w), 2 – *Lar.* (b). **II**: 1 – *Lar.* (w). **III**: 1 – *Lar.* (w). A rather common species on moderately to strongly decayed coniferous wood, more rarely on bark of living *Larix*. – IC, FL, PU, CP, AL, GR.

– *Enteridium splendens* var. *juranum* (Meylan) Härkönen 48952, 48963, 48967; [fc – 3]. Locality: 1 (3). **I**: 2 – *Dus.* (w). **III**: 1 – *Lar.* (w). All fruitings were from relatively dry but larger logs and branches; this is one of the first wood–inhabiting species to appear in the year. – IC, GR.

R *Hemitrichia abietina* (Wigand) G. Lister 48934, 49226; [fc – 1, mc – 1]. Loc. 2 (1), 5 (1). **II**: 2 – *Lar.* (w). Previously not known from the Arctic.

Sporocarps short–stalked, subglobose or turbinate, 0.5–0.9 mm in diameter, shining, yellow to orange. Peridium thin, membranous, iridescent. Spores bright yellow in mass, light yellow by transmitted light, verrucose, 10–12 µm. This species approaches *Trichia lutescens* in habit but exhibits a capillitium structure typical for *Hemitrichia*.

– *Lamproderma sauteri* Rost. 48951, 48955, 48958; [fc – 3]. Locality: 1 (3). **I**: 1 – grasses (l). **III**: 1 – *Dus.* (w), 1 – grasses (l). Found at south–exposed slopes on litter of *Duschekia.* A common and variable nivicolous species, abundant in the temperate and boreal zone, but still with only a few reports from Scandinavia (Fries 1912) and southern and central Finland (Härkönen 1979b). Often found in nivicolous situations (Novozhilov & Schnittler 1997); among the snow-bank myxomycetes it may be one of the northernmost species. Our records were all weathered and must have developed in spring, indicating a nivicolous situation during growth. – IC, KP, GR.

R *Leocarpus fragilis* Dicks. 49187 [mc]. Locality: 5. **II**: 1 – *Dus.* (l). – IC, KP, PU, CP, AL, GR.

C *Licea belmontiana* Nann.–Brem. (Fig. 3 A – D) 49127...; [mc – 10]. Loc. 1 (4), 2 (1), 4 (1), 5 (1), 7 (2), 8 (1). **I**: 1 – *Lar.* (b). **II**: 1 – *Lar.* (w), 1 – *Lar.* (b). **III**: 1 – *Dus.* (w), 2 – *Lar.* (w), 1 – *Jun.* (b), 3 – *Dus.* (l). New for the Arctic.

The distinguishing characteristics of this species are the smooth peridium without

tubercles, the apical plate acting as a lid with the basal plates forming petaloid lobes, and the dark brown spore–mass with spores rosy to brown under transmitted light, reaching only 10–13 µm in diameter. The characters of our specimens match the type specimen of *L. belmontiana* (NEB 5879). D. Mitchell (pers. comm.) questioned the identity of our specimens but stated that they fit in *L. belmontiana* better than in any other species. Colour, size, and ornamentation of the spores and the ornamentation of the inner surface of the peridium are similar to *L. denudescens* Keller & Brooks. However, *L. denudescens* differs from our specimens in a thicker outer layer of the peridium that is gelatinous in consistency when moist, finally weathering away by exposure to rain over a period of time. In this species, the moist sporangium has the appearance of a shiny golden brown ball in a drop of clear gelatine (Keller & Brooks 1977). In additional, the peridium of *L. denudescens* dehisces irregularly, lacking distinct ridges and platelets (Fig. 3 E – H). Our specimens of *L. belmontiana* differ from other species of *Licea* with petaloid dehiscence and smooth spores (e.g., *L. tuberculata*, *L. castanea*, *L. nigromarginata*) by having a thin but double–layered peridium, deep olive to light olive brown coloration under transmitted light, and the absence of tubercles (pegs) and warts along the edges of platelets, and larger spores. *Licea castanea* and *L. nigromarginata* have both platelet margins with pronounced tubercles, whereas *L. tuberculata* has a black, strongly tuberculous peridium, a yellow-brown spore mass, and spores 9–11 µm in diameter.

O *Licea kleistobolus* Martin 49110...; [mc – 6]. Loc. 2 (3), 5 (2), 7 (1). **I**: 1 – *Lar.* (w), 1 – *Lar.* (b). **II**: 2 – *Lar.* (w), 1 – *Dus.* (l). **III**: 1 – *Lar.* (w). The species as a whole is almost cosmopolitan and rather common in the boreal zone (Schnittler & Novozhilov 1996), but evidently rare in the Arctic. – PU, CP, AL.

Collections 7123 and 7357 differ from the typical appearance of this species by amber–coloured fructifications and very small spores (6.6–)7.0–7.5(–8.0) µm. In this form, the sporocarps are tiny, (0.08–)0.1–0.12(–0.15) mm in diameter, sessile on a broad base, globose–depressed, and always completely round in shape. This very inconspicuous form was found twice on decorticated, moderately decaying *Larix* logs.

A *Licea minima* Fr. (Fig. 4 A – D) 49103...; [mc – 19]. Loc. 1 (4), 2 (9), 4 (1), 5 (2), 7 (2), 10 (1). **I**: 1 – *Dus.* (w), 7 – *Lar.* (w), 1 – *Pic.* (w), 1 – *Sal.* (w), 1 – *Jun.* (b), 1 – *Lar.* (b). **II**: 2 – *Lar.* (w), 1 – *Sal.* (w), 1 – *Lar.* (b). **III**: 1 – *Sal.* (b), 1 – hare (d). **IV**: 1 – *Sal.* (l). One of the most common and abundant species in the Arctic, inhabiting woody, mostly acidic debris (pH measured in four moist chambers: 3.6 – 3.9, mean 3.7 ± 0.1). – IC, FL, KP, YP, CP, AL, GR.

Our specimens have the typical characters of this species. The firm and brittle peridium consists of 2–3 closely adherent layers and appears red–brown in transmitted light. The outer membraneous layer is dark or dull due to the presence of inclusions, the dense and homogeneous middle layer is up to 2 µm thick and more or less smooth in texture, whereas a third, inner layer with a shining surface is ornamented with tiny warts, globules and tubercles near the dehiscence line. The spores are red-brown in mass, concolorous by transmitted light, thick-walled with a paler area, verruculose, and 10–13 µm in diameter.

A *Licea testudinacea* Nann.–Bremek. (Fig. 4 E – H) 49095...; [mc – 18]. Loc. 1(5), 2 (5), 5 (4), 7 (3), 9 (1). **I**: 2 – *Lar.* (w), 1 – *Pic.* (w), 2 – *Sal.* (w), 1 – *Sal.* (b). **II**: 2 – *Dus.* (w), 1 – *Sal.*(w), 1 – *Sal.* (b), 1 – *Dus.* (l). **III**: 1 – *Dus.* (w), 1 – *Lar.* (w), 1 – *Sal.* (w), 1 – *Sor.* (w), 1 – *Sal.* (b), 1 – *Dus.* (l). **IV**: 1 – *Sal.* (w).

Our records are the first for arctic regions, but this species may be more widespread. Since it strongly resembles *L. minima*, it may be confused with this species. *Licea testudinacea* was reported from Iceland, but Gøtzsche's (1990) comments on the Icelandic specimens strongly indicate that it may represent *L. minima*.

Our material is quite typical except for the spores, which are somewhat smaller than usually described for the species (11–15 µm). *Licea testudinacea* appears to be most closely related to *L. minima* and *L. chelonoides*. It is distinguished from *L. minima* by the darker, more olive and not rusty-coloured spore mass. In the latter species the spores are always reddish brown by transmitted light and the peridium has two or three layers. *L. chelonoides* differs by dull black sporocarps not shining when dry, platelet margins with 5 or more rows of tubercles, and spores measuring 15–18 µm in diameter.

– *Lycogala epidendrum* (L.) Fr. 48941, 48954, 48975, 48984; [fc – 4]. Loc. 1(2), 2 (1), 5 (1). **I**: 1 – *Lar.* (w), 1 – *Lar.* (w). **II**: 1 – *Lar.* (w), 1 – *Pic.* (w). Widely distributed but uncommon in the Arctic. Seemingly, the availability of coarse woody debris probably limits the northern distribution of this species. The Spitsbergen record was on the remnants of a log house

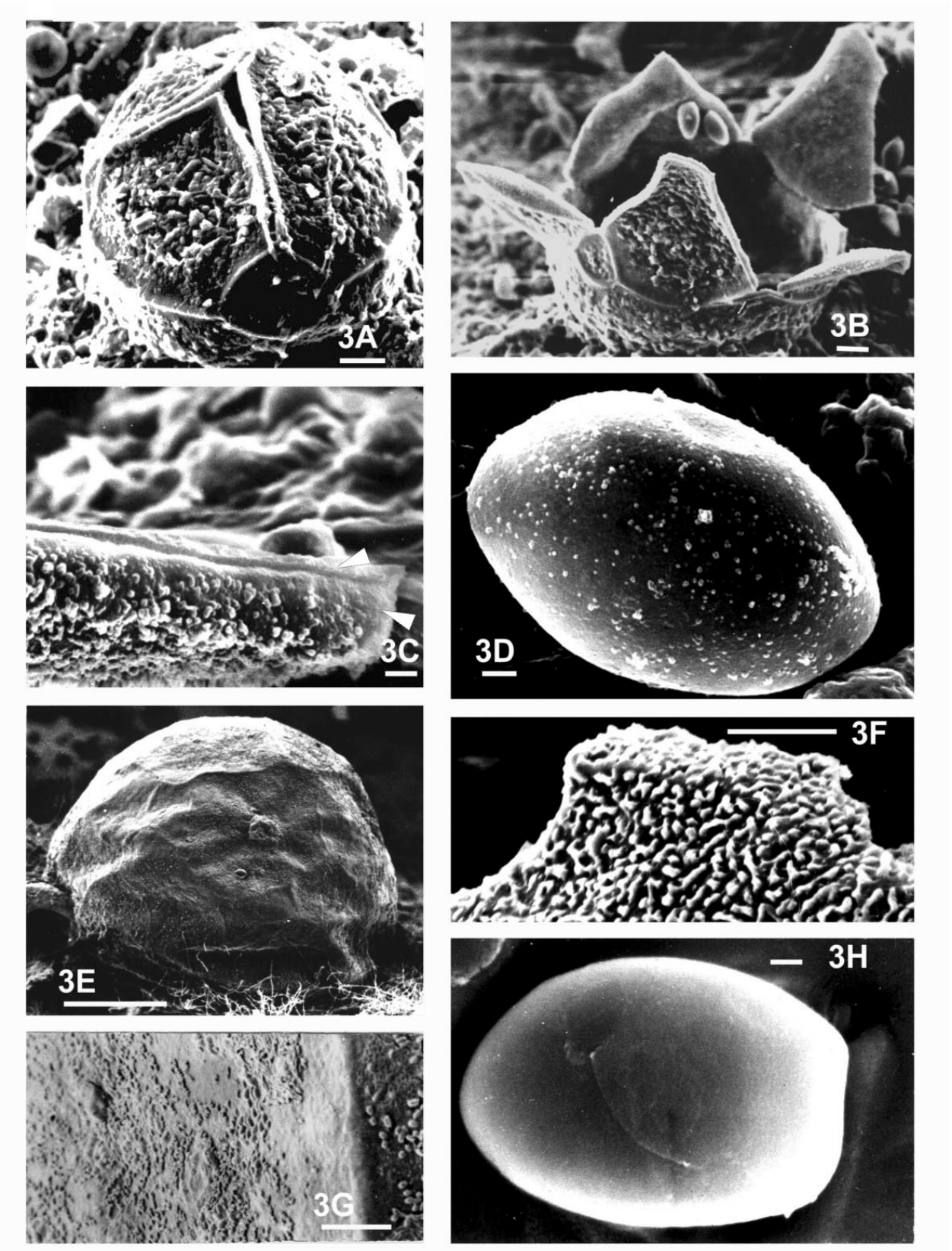

Fig. 3. SEM-photos of *Licea belmontiana* (LE 49175), A – D, and *L. denudescens* (Keller, HWK 2754), E – H. A) Closed sporocarp of *L. belmontiana*. Bar = 10 µm. B) Opened sporocarp. Bar = 10 µm. C) Double-layered peridium and its ornamentation of the inner side near the preformed line of dehiscence, (peridium layers are shown by arrows). Bar = 1 µm. D) Spore. Bar = 1 µm. E) Closed sporocarp of *L. denudescens*. Bar = 10 µm. F) Ornamentation of the inner side of peridium. Bar = 1 µm. G) Ornamentation of the outer side of peridium. Bar = 10 µm. H) Spore. Bar = 1 µm.

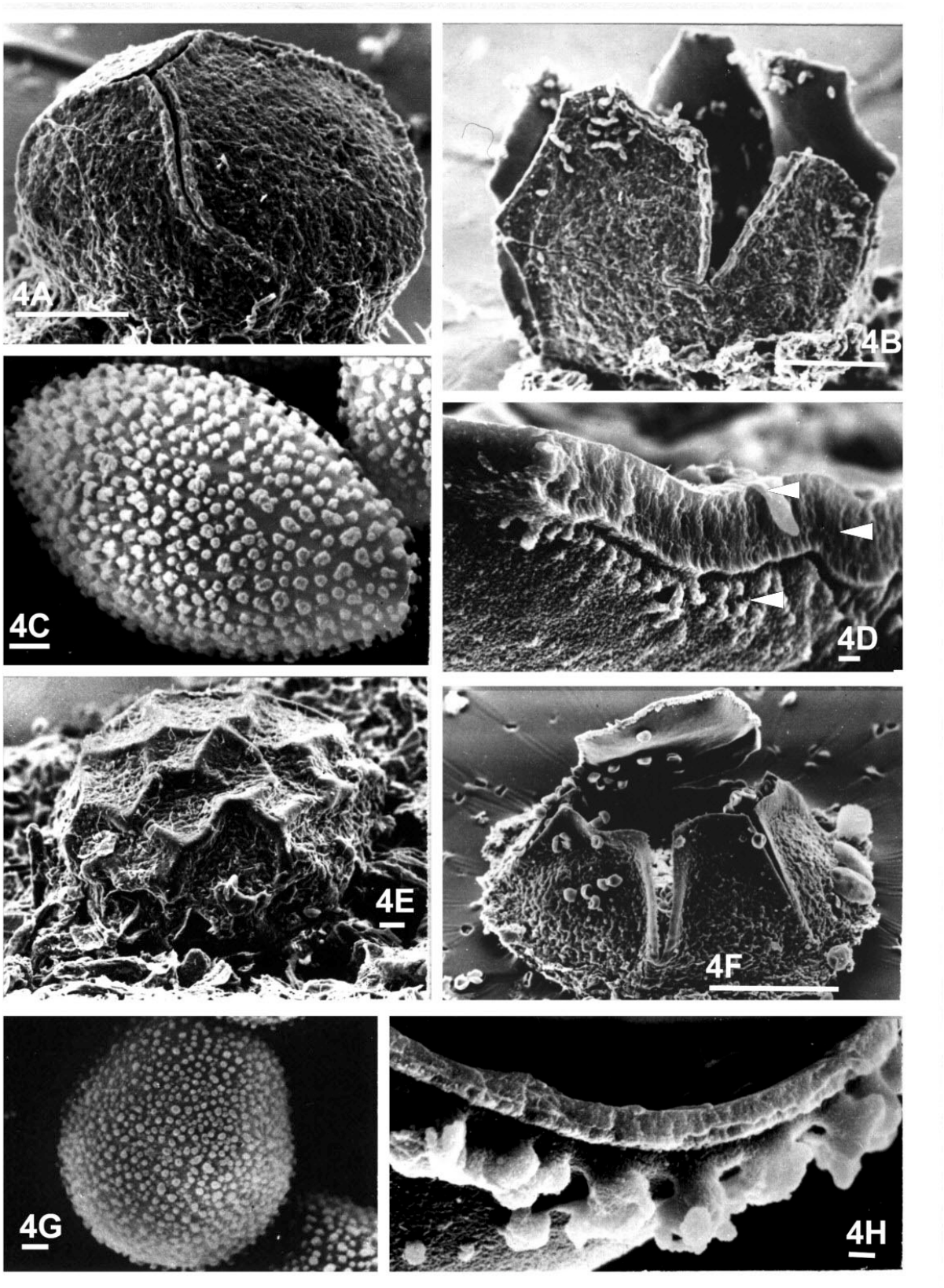

Fig. 4. SEM-photos of *Licea minima* (LE 49124), A – D, and *L. testudinacea* (LE 49132), E – H. A) Closed sporocarp of *L. minima*. Bar = 100 µm. B) Opened sporocarp. Bar = 100 µm. C) Spore. Bar = 1 µm. D) Three-layered peridium and its ornamentation of the inner side near the preformed line of dehiscence (peridium layers are shown by arrows). Bar = 1 µm. E) Closed sporocarp of *L. testudinacea*. Bar = 10 µm. F) Opened sporocarp. Bar = 100 µm. G) Spore. Bar = 1 µm. H) One-layered peridium and its ornamentation of the inner side near the preformed line of dehiscence. Bar = 1 µm.

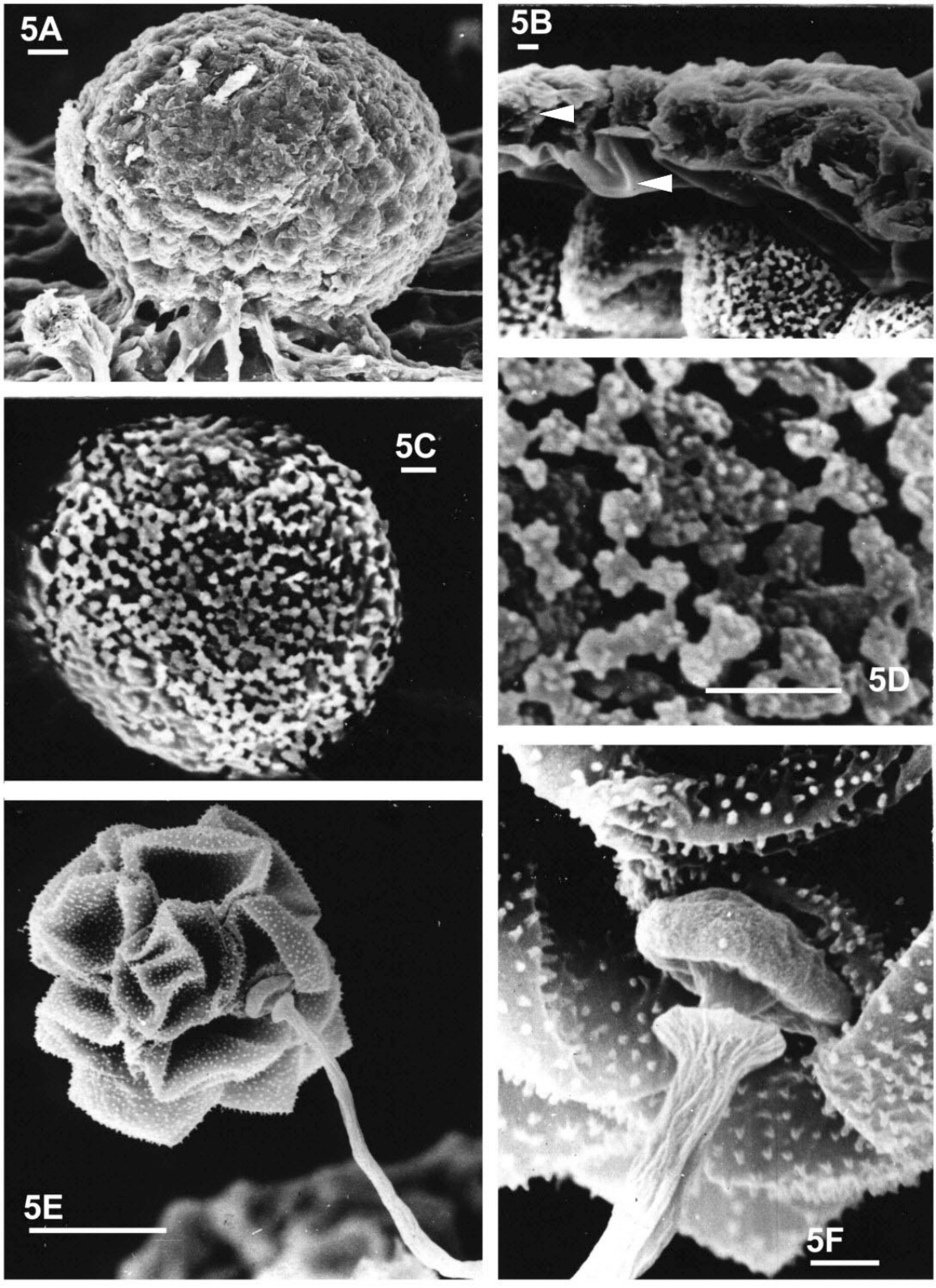

Fig 5. SEM-photos of *Perichaena* spec. (LE 204007), A – D, and *Echinostelium brooksii* (sc 7314), E – F. A) Sporocarp with numerous large tubercules. Bar = 10 µm. B) Double-layered peridium. The outer layer of peridium is closely adherent to the membranous inner layer (peridium layers are shown by arrows). Bar = 1 µm. C) Spore. Bar = 1 µm. D) Spore ornamentation. Bar = 1 µm. E) Whole sporocarp of *E. brooksii*. Bar = 10 µm. F) Lenticular columella with adjacent collapsed and minutely spinulose spores. Bar = 1µm.

(Elvebakk et al. 1996). – IC, Spitsbergen, FL, KP, PU, CP, AL, GR.

O *Macbrideola cornea* (G. Lister & Cran) Alexop. 49111, 7349, 7358; [mc – 3]. Loc. 2 (1), 5 (1), 7 (1). **II**: 1 – *Sal.* (b), 1 – polar partridge (d). **III**: 1 – *Sal.* (l). – PU, GR. Fruiting typically on bark of living trees and shrubs, our record from dung is unusual although not the only one for this species from this substratum (Eliasson & Keller 1999).

– *Mucilago crustacea* F.H. Wigg. 48946 [fc]. Locality: 5. **II**: 1 – grasses (l). Our record comes from a moss- and grass-rich, open patch of the forest–tundra. Probably a soil myxomycete, in temperate zones fruiting in meadows and herbfields. Apparently not restricted to wood or litter, it may be one of the few species inhabiting typical tundra, as indicated also by findings from Alaska (Stephenson & Laursen 1993). – IC, FL, PU, CP, AL, GR.

R *Paradiacheopsis* cf. *cribrata* Nann.–Bremek. 49163, 7197; [mc – 2]. Loc. 2 (1), 5 (1). **I**: 1 – *Lar.* (w). **II**: 1 – *Lar.* (b). – IC.

This is an extremely variable species. As reported by Härkönen (1977), the complex consisting of small, *Comatricha*–like species is very difficult to resolve taxonomically. Our collections differ slightly from each other in the development of the surface net, but are separated from the very common *Comatricha nigra* by duller spore colour, smaller size, shorter stalks and a rigid capillitium anastomosing to an incomplete surface net.

A *Paradiacheopsis fimbriata* (G. Lister & Cran) Hertel 49134...; [mc – 20]. Loc. 2 (11), 3 (1), 4 (4), 5 (4). **I**: 4 – *Lar.* (w), 3 – *Lar.* (b). **II**: 6 – *Lar.* (w), 7 – *Lar.* (b). Found always on living and coarse wood debris of *Larix*; with a clear preference for its acidic bark (pH from 11 moist chambers: 3.4–5.7, mean 3.9 ± 0.7). – FL, PU, CP.

C *Perichaena chrysosperma* (Currey) A. Lister 49099...; [mc – 6]. Loc. 1 (1), 2 (5). **I**: 1 – *Lar.* (w), 1 – *Sal.* (w), 1 – *Sal.* (b). **II**: 1 – *Sal.* (b), 1 – *Dus.* (l). **III**: 1 – *Sor.* (w), 1 – *Sal.* (b). This species develops in the litter layer on even tiny wood fragments such as the dead branchlets of shrubs. A widespread corticolous species. – IC, PU, CP, AL, GR.

R *Perichaena depressa* Libert 49218, 49233; [mc – 2]. Loc. 4 (1), 5 (1). **II**: 2 – Polar partridge (d). Dung as a second microhabitat seemingly allows this species to extend its range further northwards. Almost cosmopolitan in distribution, but in the Arctic recorded only from the Chukchi Peninsula and Alaska.

R *Perichaena* sp. (Fig. 5 A – D) 204007, 204181; [mc – 2]. Locality: 3 (2). **II**: 2 – reindeer (d).

Sporocarps crowded, gregarious or scattered, globose to subglobose, pulvinate to elongate, 0.2–0.7 mm in diameter. Sessile on a constricted base, not iridescent but glossy and shining, buff-yellow, orange-yellow to apricot-orange, dehiscing more or less irregularly. Peridium persistent, double; outer layer closely adherent to the membranous inner layer, rough, bearing numerous large tubercles, more or less cartilaginous, brittle, fairly evenly thick, probably without lime, yellow brown in transmitted light, shining, opaque with granular deposits. Inner layer membranous, rather elastic, thin, delicate, translucent in transmitted light, limeless. Hypothallus inconspicuous, scanty. Capillitium absent. Spores orange-yellow, yellowish brown, honey yellow, or orange-golden in mass, bright to buff yellow in transmitted light, globose, wall of uniform thickness and colour, neither areolate nor with a germination pore, minutely roughened (asperulate) under an oil immersion lens, or verruculose (delicately warted), complete and evenly ornamented, 14.0–15.0 µm in diameter. The epispore belongs to the pilate type (Rammeloo 1974). Verrucae consist of small pila, which are more or less evenly distributed on the spore surface; the capita of pila are separate or sometimes connected to one another, relatively large, 0.1–0.4 µm wide, with 3–6 small tubercles.

Our specimens differ strongly from all other coprophilous species of *Licea* and *Perichaena* with golden-yellow spore mass. In habit and sporocarp size they resemble *Perichaena corticalis* var. *liceoides* and *L. tenera* Jahn. The main differences between these species and the Taimyr specimens are spore size and ornamentation. *Perichaena corticalis* var. *liceoides* has spores 9.2–10 µm in diameter, evenly covered with prominent spines (Gilert 1990, Ukkola et al. 1996). According to the original description (Jahn 1918), *L. tenera* has smooth to faintly spinulose spores, 10–12 (–13) µm in diameter with a thinner-walled area on one side. Our specimens approach some *Licea* species not only in general habit but also in the absence of a capillitium. However, the presence or absence of a capillitium as a taxonomically important character has been questioned (Alexopoulos 1976, Eliasson 1977, Keller &

Brooks 1971). We assume, that the Taimyr specimens represent another intermediate taxon between *Perichaena* and *Licea*. It can be tentatively placed within the facultatively fimicolous group of species within the genus *Perichaena* that includes *P. chrysosperma*, *P. depressa*, *P. minor*, *P. pedata*, *P. quadrata*, and *P. corticalis* var. *liceoides* (Eliasson & Keller 1999, Keller & Eliasson 1992).

O *Perichaena vermicularis* (Schw.) Rost. 7208, 7209, 7377, 7367, 48957; [fc – 1, mc – 4]. Loc. 1 (1), 2 (2), 4 (1), 5 (1). **I**: 1 – grasses (l), 1 – *Sal.* (w). **II**: 1 – *Dus.* (w), 1 – *Lar.* (w), 1 – *Sal.* (b). Cosmopolitan, but apparently less common than *P. chrysosperma* in the Arctic. – AL, GR.

Our collections consist of two ecological forms. All specimens on decayed wood and bark of living trees and shrubs are typical for the corticolous form of this species, having a rather thick, dark brown peridium, and a scanty capillitium. In contrast, the field collection from grassy litter shows a membranous, thin peridium and numerous elastic capillitial threads consisting of filaments 2.0–3.0 µm in diameter, densely ornamented with warts and short spines. The primary ornamentation of the inner surface of the peridium consists of rather sparse warts of irregular form, up to 0.5 µm wide.

C *Physarum bivalve* Pers. 49118...; [mc – 7]. Loc. 1 (1), 2 (4), 7 (2). **I**: 2 – *Dus.* (l), 1 – hare (d). **II**: 1 – *Sal.* (l). **III**: 3 – *Dus.* (l). One of the few almost ubiquitous litter species, widely distributed in the boreal zone and the Arctic on leaf litter and dung of herbivorous animals. – KP, CP, AL.

– *Physarum cinereum* (Batsch) Pers. 48973 [fc]. Locality: 1 (1). **I**: 1 – grasses (l), the typical form not intermediate to *P. vernum*. Widely distributed in the Arctic but less abundant than the previous species, mainly on living plants and different types of litter substrata. – IC, KP, CP, AL, GR.

O *Physarum* cf. *nudum* Macbr. 49164, 49192, 7138, 7205, 7220; [mc – 5]. Loc. 1 (1), 2 (1), 5 (1), 7 (2). **I**: 2 – *Lar.* (b). **II**: 1 – *Lar.* (b). **III**: 2 – *Lar.* (b). For the Arctic, up to now found only on the Taimyr Peninsula.

Three collections are immature, but two (7138, 49192) are mature, consisting of numerous, crowded but not heaped sporocarps, very seldom short plasmodiocarps which are 0.3–0.5 mm wide and globose in cross-section, sessile with a restricted base on an inconspicuous hypothallus. Capillitium a dense, three-dimensional network of translucent, colourless and often flattened threads 2–3(–10) µm in diameter, with numerous elongated but very inconspicuous and not sharply separated, ash-grey nodes of granular lime 20–50 µm in length. Spores in mass violaceous–brown, globose, very pale violaceous grey under transmitted light, ornamented with slightly irregularly distributed, very fine warts of less than 0.15 µm in height but visible clearly under an oil immersion lens, (8.1–) 8.5–9.7–(–10.5) µm in diameter. 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 found in a different microhabitat (litter).

O *Physarum nutans* Pers. 48910...; [fc – 2, mc – 3]. Loc. 1(1), 2 (3), 5 (1). **I**: 1 – *Pic.* (w), 1 – *Lar.* (b). **II**: 2 – *Lar.* (w), 1 – *Pic.* (w). – FL, PU, CP, GR.

R *Physarum oblatum* Macbr. 49193, 7130; [mc – 2]. Locality: 2 (2). **I**: 2 – *Sal.* (w). Rather rare in in the Arctic. – AL, CP.

R *Physarum viride* (Bull.) Pers. 49124 [mc]. Locality: 5. **II**: 1 – *Lar.* (w). Rarely recorded from moist chambers and perhaps underrepresented in our survey, which was carried out in June. – FL, PU, KP, CP.

O *Prototrichia metallica* (Berk.) Massee 49117, 49122, 49123, 49185; [mc – 4]. Loc. 2 (1), 5 (2), 7 (1). **I**: 1 – *Lar.* (w). **II**: 2 – *Lar.* (w). **III**: 1 – *Lar.* (w). – CP, GR.

One of the northernmost records for this species.

– *Stemonitis axifera* (Bull.) Macbr. 48962, 48968; [fc – 2]. Locality: 1 (2). **I**: 1 – *Pic.* (w). **III**: 1 – grasses (l). – PU, KP, CP, AL.

– *Stemonitis smithii* Macbr. 48969 [fc]. Locality: 1. **II**: 1 – *Pic.* (w). – KP, AL.

R *Stemonitopsis subcaespitosa* (Peck) Nann.–Brem. 7191, 7364; [mc – 2]. Locality: 1 (2). **III**: 2 – *Dus.* (w). In the Arctic so far known only from the Taimyr Peninsula.

Characteristic features of this species are the small but cylindrical, reddish brown sporocarps 2–2.5 mm in height, and a surface net consisting of sinuous threads with meshes (10–)15–35 µm wide. Comparison with authentic material collected by Hagelstein in eastern North America revealed similarity for all characters except the slightly smaller spores (7.0–)–7.5–7.8(–8.0) µm in diameter.

R *Trichia botrytis* (J.F.Gmel.) Pers. 49130, 49183; [mc – 2]. Loc. 2 (1), 5 (1). **I**: 1 – *Lar.* (w). **II**: 1 – *Dus.* (w). Widely distributed in boreal and arctic zones. – IC, PU, KP, CP.

R *Trichia decipiens* (Pers.) Macbr. 49194 [mc]. Locality: 4. **II**: 1 – *Dus.* (l). One of the most common and abundant species in the boreal zone, perhaps underrepresented in our survey.– IC, FL, KP, CP, AL, GR.

R *Trichia lutescens* (Lister) Lister 49101, 7366; [mc – 2]. Locality: 5 (2). **II**: 1 – *Dus.* (b), 1 – *Dus.* (l). Widely distributed but uncommon in the boreal and arctic zones. – IC, FL, PU, CP, AL, GR.

O *Trichia munda* (A. Lister) Meylan 49113...; [mc – 5]. Loc. 1 (1), 2 (2), 4 (1), 7 (1). **I**: 1 – *Lar.* (w), 1 – *Dus.* (l). **II**: 1 – *Dus.* (l). **III**: 1 – *Bet.* (l). **V**: 1 – *Sal.* (b). Typically, the first sporocarps appear in moist chamber culture only after one or two months on very wet litter, often directly under a thin water film. Rare elsewhere, it is surprisingly often recorded in arctic regions, always on leafy litter. – IC, PU, YP, CP, AL, GR.

This species resembles *T. botrytis*, to which it is probably most closely related. Our material agrees well with the description of specimens from Iceland and Greenland (GØtzsche 1989, 1990).

O *Trichia varia* (Pers.) Pers. 48901...;[fc – 4, mc – 1]. Loc. 1 (1), 2 (3), 5 (1). **I**: 1 – *Lar.* (w), 1 – *Pic.* (w). **II**: 2 – *Lar.* (w), 1 – *Dus.* (l). Widely distributed and abundant in boreal and arctic regions on decayed wood. – IC, FL, PU, YP, CP, AL, GR.

Results and discussion

Our survey is the first systematic study of myxomycetes of North Central Siberia carried out with the moist chamber technique. Data on the frequency of myxomycetes on various substrata are given in Table 1. Substrata were classified as follows: coarse woody debris (decaying logs, branches, and twigs more than 2.5 cm in diameter, hereafter referred to as "wood"), litter of various types (leaves, grasses, dead stems of herbaceous plants), and dung of herbivorous animals. From the 270 moist chamber cultures prepared, 331 collections and 48 species were obtained in 145 (54 %) cultures positive for myxomycetes (Table 2).

The mean value for the number of species per moist chamber culture was calculated as 1.22 ± 0.09. The most productive substrate was wood, preferentially logs, trunks and snags of trees and larger shrubs. Sixty-four (66 %) (samples) from a total of 97 moist chamber cultures were positive for myxomycetes. From 80 cultures prepared with bark of living trees and shrubs 51 (64 %) were positive for myxomycetes. Various types of litter samples were used to prepare 63 moist chamber cultures, 23 (37 %) of these yielded myxomycetes. From 30 moist chamber cultures prepared with animal droppings, only 7 (23 %) were positive.

Transportation opportunities confined our survey time to June and July of the years 1995 and 1996, which is definitely earlier than the fructification peak of most wood-inhabiting myxomycetes. Only 39 field collections representing 19 species were obtained and 8 of these species were found exclusively in the field. As such, our total of 56 species in 26 genera represents only a preliminary account of the myxomycete biota of the region, which undoubtedly could be supplemented by records of numerous wood-inhabiting species.

Myxomycete habitats

Very often, arctic and subarctic regions are perceived as a monotone landscape with a limited number of vascular plants and a dominance of cryptogams. But even the few taller plants present provide numerous microhabitats with different conditions of soil, mesoclimate, microclimate, and microrelief. As a result, thus, the microhabitat diversity in arctic landscapes is almost comparable to that of boreal regions (Chernov & Matveyeva 1997). However, most substrata, especially woody ones, are present at a much lower density. In spite of the scarcity of trees, the forest-tundra as well as the northern taiga provides all microhabitats typically found in boreal forests, but most of the substrata are less sheltered from wind, rain, and direct sunlight. The quantity and quality of microhabitats suitable for myxomycete growth and development decrease considerably northwards to the southern and typical tundra. The most striking difference is the reduction in coarse woody debris, including logs, trunks and snags north of the timberline. The southern tundra is characterised by tall shrub communities in sheltered places, on the Taimyr Peninsula consisting mainly in *Duschekia fruticosa* and different species of willows having trunks up to 10 cm thick. But shrub thickets with trunks up to 3 cm thick may occur even in typical tundra.

Table 1. Occurrence of myxomycetes on various types of substrata collected from all vegetation subzones of the Taimyr Peninsula. Data from southern tundra, typical tundra, arctic tundra and mountain tundra were combined in one set. Single numbers or numbers before slash indicate records from moist chamber cultures, those after a slash represent collections made in the field. Abbreviations used for the substrata are: w - coarse wood debris, l - litter, b - bark of living trees and shrubs, d - dung of herbivorous animals.

Species	Taiga				Forest tundra				Tundra				Total
	w	l	b	d	w	l	b	d	w	l	b	d	
Arcyria cinerea	9	1	5		6	3	2		5/1	2	7	2	43
Arcyria denudata	2												2
Arcyria incarnata	7/1		1		3				3				15
Arcyria obvelata	1/1												2
Arcyria pomiformis	2				1								3
Arcyodes incarnata					1								1
Calomyxa metallica	1												1
Ceratiomyxa fruticulosa	2/2				1				1				6
Comatricha laxa	1												1
Comatricha nigra	3/3		10		4/1	1	14		3/1		7		47
Comatricha pulchella	1												1
Craterium leucocephalum									1				1
Cribraria cf. *atrofusca*	1												1
Cribraria microcarpa	2				2								4
Cribraria violacea	2		1				1						4
Cribraria vulgaris					1								1
Diderma radiatum					1								1
Didymium difforme								1					1
Didymium dubium		3	1						-/2	1			7
Didymium melanospermum					1								1
Didymium squamulosum						1				1			2
Echinostelium brooksii	2		2		1		2		1				8
Echinostelium minutum	11	1	3		11	5	4	1	15	3	6		60
Enerthenema papillatum	2		2		-/1				1				6
Enteridium splendens var. *juranum*	-/2								-/1				3
Hemitrichia abietina					1/1								2
Lamproderma sauteri		-/1							-/1	-/1			3
Leocarpus fragilis						1							1
Licea belmontiana			1		1		1		3	3	1		10
Licea kleistobolus	1		1		2	1			1				6
Licea minima	10		2		3		1			1	1	1	19
Licea testudinacea	5		1		3	1	1		5	1	1		18
Lycogala epidendrum	-/2				-/2								4
Macbrideola cornea							1	1		1			3
Mucilago crustacea						-/1							1
Paradiacheopsis cf. *cribrata*	1						1						2
Paradiacheopsis fimbriata	4		3		6		7						20
Perichaena chrysosperma	2		1			1	1		1				6
Perichaena depressa								2					2
Perichaena sp.								2					2
Perichaena vermicularis	1	-/1			2		1						5
Physarum cinereum		-/1											1
Physarum bivalve		2		1		1				3			7
Physarum cf. *nudum*			2				1				2		5
Physarum nutans	1		1		1/2								5
Physarum oblatum	2												2
Physarum viride					1								1
Prototrichia metallica	1				2				1				4
Stemonitis axifera	-/1									-/1			2
Stemonitis smithii	-/1												1
Stemonitopsis subcaespitosa									2				2
Trichia botrytis	1				1								2
Trichia decipiens						1							1
Trichia lutescens						1	1						2
Trichia munda	1	1				1				1	1		5
Trichia varia	-/2				-/2	1							5

Table 2. Results obtained from moist chamber cultures prepared with substratum samples collected in the vegetation subzones of the Taimyr Peninsula. Roman numbers written in bold refer to the vegetation subszones as explained in the text.

Vegetation subzones	Number of moist chamber cultures	Positive moist chamber cultures (% of total)	Number of collections	Number of species	Average yield (species per moist chamber) Mean ± SE	Shannon diversity index (H´)
I Taiga	55	45 (82)	122	32	2.19 ± 0.26	1.31
Wood (w)	24	21 (88)	79	28	3.54 ± 0.48	1.26
Litter (l)	7	3 (43)	5	4	0.71 ± 0.40	0.58
Bark (b)	21	18 (86)	37	16	1.76 ± 0.23	1.06
Dung (d)	3	1 (33)	1	1	0.33 ± 0.33	0
II Forest tundra	110	54 (49)	119	36	1.08 ± 0.12	1.28
Wood (w)	34	21 (62)	54	22	1.66 ± 0.27	1.24
Bark (b)	34	19 (56)	39	15	1.15 ± 0.21	0.94
Litter (l)	25	8 (32)	19	13	0.76 ± 0.28	1.01
Dung (d)	17	4 (24)	7	5	0.41 ± 0.15	0.67
III-IV Tundra	105	51 (49)	90	22	0.84 ± 0.10	0.99
Wood (w)	39	22 (56)	45	15	1.13 ± 0.21	0.98
Bark (b)	25	14 (56)	26	8	1.04 ± 0.20	0.76
Litter (l)	31	12 (39)	16	9	0.52 ± 0.14	0.90
Dung (d)	10	2 (20)	3	2	0.30 ± 0.21	0.28
All subzones	270	145 (54)	331	48	1.22 ± 0.09	1.32
Wood (w)	97	64 (66)	178	37	1.82 ± 0.19	1.29
Bark (b)	80	51 (64)	102	21	1.27 ± 0.13	1.03
Litter (l)	63	23 (37)	40	16	0.63 ± 0.13	1.05
Dung (d)	30	7 (23)	11	8	0.32 ± 0.11	0.88

On the other hand, patches of tundra-like vegetation can occur already in the northern taiga on exposed sites. In the lowlands of the Taimyr Peninsula, all subzones differentiated herein on the basis of vegetation structure form a mosaic pattern over wide areas.

Moist chamber cultures prepared with samples of wood yielded 37 species representing 16 genera of myxomycetes. This microhabitat showed the highest diversity (H' = 1.29, 178 collections) and species richness. The mean value for number of species per moist chamber culture prepared with wood was 1.82 ± 0.19, with up to 10 taxa per culture (Table 2).

Wood has a wide range of chemical and physical characteristics (Stephenson 1988, Samuelsson et al. 1994). As a result, it can be seen that considerable variation exists among the various species with respect to patterns of substratum relationships. The most common species were *Echinostelium minutum* (37 collections), *Arcyria cinerea* (20), *Licea minima* (13), *L. testudinacea* (13), *Arcyria incarnata* (13), *Paradiacheopsis fimbriata* (10), and *Comatricha nigra* (10). Wood-inhabiting species were found surprisingly often on even tiny branchlets. A good example is *C. nigra*, which was often collected on small, decorticated branchlets of *Duschekia* or *Salix*. *Echinostelium minutum*, *Licea* spp., and *Perichaena* spp. were found on small decaying twigs (sometimes only 5 mm in diameter) or under the exfoliating bark of branchlets lying in-between leafy litter in dense shrub thickets. Thus, the timberline is not an absolute biogeographic "barrier" for wood-inhabiting myxomycetes. Some usually wood-inhabiting species occur far into the tundra, using different types of microhabitats such as litter, twigs, bark of living shrubs, and dung of animals. *Arcyria cinerea*, *Echinostelium minutum*, and *Perichaena depressa* were found sporadically on animal dung. Here, dung as a second microhabitat seemingly allows the species to extend its range further northwards. Wood-inhabiting myxomycetes were found to be the largest ecological group (44 taxa) in spite of the fact that species not regularly occurring in moist chambers are certainly underrepresented in our survey. The species of *Trichia* illustrate this, all species except *T. varia* were recorded only sporadically from moist chambers but not as field collections.

Twenty-one species in 12 genera were collected on bark of living trees and shrubs from 80 moist chamber cultures (H' = 1.03, 102 collections). Both a low number of species (21)

and a few exceedingly abundant species (e.g. *Comatricha nigra*: 31 collections) explain the relatively low diversity index value. An average species number of 1.27 ± 0.13 per culture, with a maximum of 5 taxa in one moist chamber, was recorded (Table 2).

Larix gmelinii, the most common tree forming the timberline, has a bark pH of 2.6–4.7 (mean from 46 collections: 3.7 ± 0.1), followed by *Salix* spp. with 3.5–5.9 (mean from 14 collections: 4.8 ± 0.2), and *Duschekia fruticosa* 4.7–6.4 (mean from 9 collections: 5.6 ± 0.2). The two conifers (*L. gmelinii* and *Picea obovata*) have a scaly and fissured bark, but species diversity (H' = 0.85, 81 collections) was similar to that found for the smooth bark of deciduous shrubs (*Duschekia fruticosa*, *Salix* spp., H' = 0.84, 32 collections). However, the species per culture ratio was lower for coniferous bark (mean from 53 cultures: 1.2 ± 0.2) than for deciduous shrubs (1.6 ± 0.3). From the 21 species found on bark, only *Comatricha nigra* (31 records), *Echinostelium minutum* (13), *Arcyria cinerea* (11), and *Paradiacheopsis fimbriata* (10) are predominantly corticolous. Both average yield of moist chambers as well as Shannon diversity indexes are slightly higher than those reported for the acidic bark of coniferous trees (*Picea rubens*, *Tsuga canadensis*) in the temperate forests of south-western Virginia of the United States (Stephenson 1989). Most of the species of myxomycetes encountered in the present study appear to have a relatively wide pH tolerance but show different pH optima. As a general observation, corticolous species seem to have more narrow pH amplitudes than wood-inhabiting species. *Comatricha nigra* was collected 30 times on the bark of living *Larix* and *Picea* but only once on the bark of *Duschekia fruticosa; Paradiacheopsis fimbriata* was found only on *Larix* (10 times on bark of living *Larix* and 10 records from *Larix* logs); and *Physarum* cf. *nudum* appeared exclusively on the bark of *Larix*. The most probable reason is the low pH of the bark of all common coniferous substrata samples in the present study.

Sixteen species in 8 genera were collected on litter from 63 moist chamber cultures (H´ = 1.05, 40 collections, mean 0.63 ± 0.13 species per culture). Especially in the tundra, litter plays an important role as a microhabitat, accumulating in deep shade in the southern tundra under dense thickets of *Duschekia* and *Salix* up to 1.5 m tall. But even the wind-sheltering effects of the dwarf shrubs prevailing in the typical and northern tundra is enormous.

Measurements of microclimate conditions associated with the arctic-alpine dwarf shrub *Loiseleuria procumbens* in the Austrian Alps revealed a reduction of wind velocity from 16 m/s at 3 cm height to almost 0 m/s on the ground, a minimum air moisture of still 80 % even on dry and sunny days, and a pronounced heating effect, enhancing temperatures from 12 °C on the shrub canopy (3 cm high) to more than 45 °C on ground (Chernusca 1976). Similar effects can be assumed for the Taimyr Peninsula with its continental climate. Such shrub thickets work as natural moist chambers, especially for litter myxomycetes, allowing them to develop as far north as shrubs occur. Species such as *Arcyria cinerea* (6 collections), *Echinostelium minutum* (9), *Physarum bivalve* (6), and *Trichia munda* (3) were most abundant in litter cultures. But, except *Physarum bivalve*, all these species also grow on other substratum types like wood and bark. One explanation for this phenomenon could be the similar low average pH of litter (5.85 ± 0.12, 45 samples). However, only the probably nivicole *Lamproderma sauteri* (2 collections) and *Physarum bivalve* (6) revealed a clear preference for litter. With only 20 species recorded, the survey for litter-inhabiting myxomycetes is probably incomplete. Detailed investigations of herbfields occurring in wet depressions and along streams in the northern taiga and forest-tundra might well reveal a whole assemblage of litter-inhabiting species. Such communities were seen at the foot of the " Krasnyi Kamen′ " hills (locality 1), where a dense cover of herbaceous plants (e.g., *Cirsium helenioides* and various umbellifers) up to 1 m tall provides large amounts of soft, decaying plant detritus, often with the hollow stems lying in the dense shade under the new shoots.

Dung-inhabiting myxomycetes are widely distributed within the Arctic (Cox 1981, GØtzsche 1989, Eliasson & Keller 1999,), but this microhabitat was not very productive in the present study (H' = 0.88, 11 collections, mean 0.32 ± 0.11 species per culture). With only six species recorded from 25 substratum samples, the dung of herbivorous animals was significantly less productive than in arid zones of the world (Blackwell & Gilbertson 1980, Novozhilov & Golubeva 1986). The main reason might again be the relative acidity of dung in our study (4.6–7.3, mean 5.94 ± 0.1). Presumably, all other conditions should be sufficient for myxomycete growth and development. The dung of partridge was often encountered in dense shrub thickets, where the birds can find shelter. Besides *Didymium difforme*, *Perichaena depressa*, and the apparently new species of *Perichaena* no myxomycetes were found exclusively on this substratum.

Noteworthy are the three weathered specimens of *Lamproderma sauteri* collected from a steep, south-exposed hillslope. According to our experience, this is a species found in nivicolous situations. As such, these specimens would represent the northernmost known records of a nivicolous myxomycete.

Distribution patterns of myxomycetes in the vegetation subzones of the Taimyr Peninsula

Results of moist chamber cultures obtained for all substrate types in the different vegetation subzones are presented in Table 2. Due to the patchy nature of the vegetation, collections from one geographical locality may be assigned to more than one subzone. In general, the species richness of myxomycetes decreases northwards. The Shannon diversity index for the taiga (H' = 1.31) is slightly higher than the value for the forest-tundra (H' = 1.28), whereas the value is much lower for the tundra (H' = 0.99). However, this pattern differs among particular ecological groups. For example, the mean value of the number of wood-inhabiting species per moist chamber culture decreases from 3.54 in the taiga to 1.66 and 1.13 in the forest-tundra and tundra, respectively. This correlates with a decrease in species richness and diversity (Table 2). Corticolous myxomycetes exhibit similar patterns. In contrast, litter-inhabiting myxomycetes show a higher diversity index in forest-tundra (H' = 1.01) and tundra (H' = 0.90) than in the taiga (H '= 0.58). Myxomycetes cultured from dung in the taiga subzone occurred too sporadically to indicate any distribution trends.

In the tundra, myxomycetes are represented mainly by multizonal and even cosmopolitan species. Many boreal species are widely distributed within the northern taiga and can be found also in forest-tundra and tundra vegetation. As noted above, some multizonal species show high population density in the southern tundra. However, only *Echinostelium minutum* (2 collections), *Didymium dubium* (2), *Craterium leucocephalum* (1), *Licea minima* (1), and *L. testudinacea* (1) were recorded for the typical tundra (localities 9, 10). In addition, *Arcyria cinerea* (2 collections) and *Trichia munda* (1) were recorded in areas with mountain tundra on the Putorana Plateau and may also occur in the typical lowland tundra of the Taimyr Peninsula. Presumably, differences among myxomycete assemblages in taiga, forest-tundra, and tundra are more the result of differences in the abundance of shared species than actual differences in species composition. Only one species (*Licea belmontiana*) was recorded mainly in the southern tundra zone (7 collections, 70 % of all collections). When the coefficient of community indices were used as measure to compare vegetation subzones, values between 0.53 and 0.66 were calculated (Table 3).

Table 3. Comparison of myxomycete assemblages in the vegetation subzones of the Taimyr Peninsula. Both the community coefficient value (upper right) and the number of species shared by the territories (lower left) are given. Field collections were omitted for this analysis.

	Northern taiga	Forest tundra	Tundra
Northern taiga	***	0.66	0.65
Forest tundra	22	***	0.53
Tundra	17	15	***
Number of species	32	36	21
Number of genera	14	15	15
Number of families	8	7	7
Species per family	4	5.1	1.5
Species per genus	2.3	2.4	1.4

Although myxomycetes were represented in the tundra with almost the same number of families and genera than in forest-taiga and taiga, species numbers in the tundra were much lower (Table 3). Among myxomycete families, members of the Trichiaceae (represented by 88 collections, 17 species, and 6 genera) and Stemonitaceae (76 collections, 8 species, and 5 genera) were found to be most abundant in the Taimyr Peninsula. Both families contain many species able to endure a low substratum pH. This trend was observed also in other areas of arctic and subarctic regions (Novozhilov et al. 1998b). In general, the species per genus (S/R) ratio, ranging from 1.4 to 2.4 within the three vegetation zones is low compared with values obtained for temperate or tropical regions, where the S/R ratio ranges from 2.2 to 4.6 (Novozhilov 1985, Stephenson et al. 1993).

As shown in Table 4, the myxomycete biota of the Taimyr Peninsula is similar to those of other arctic and subarctic regions. Expressed as coefficient of community index (CC), Russian northern Karelia has the most similar myxomycete biota (CC = 0.51). Values for the northern taiga (Finland, Russian Karelia) range from 0.35 to 0.51, whereas the data sets for

temperate, tropical, mediterranean, and desert vegetation extend from 0.20 to 0.36. As might be expected, CC values for the desert zone reveal the least degree of similarity (0.20). Even when comparing with the data set from the most similar vegetation zone (Russian Karelia), the CC value is surprisingly low. An obvious reason is that many species not appearing in moist chambers are underrepresented in this survey.

Table 4. Comparison of the results of the present study with various regional myxomycete floras from different climate zones. Note: CC – coefficient of community; T – total number of registered species in the region; S – species recorded only in the Taimyr Peninsula; C - number of species in common.

Regions	CC	T	S	C
RK	0.51	92	18	37
Am1	0.36	56	37	18
FL	0.35	171	15	40
TR	0.35	41	38	17
Am2	0.33	113	27	28
ISR	0.33	86	32	23
CR	0.31	108	30	25
SI	0.26	101	35	20
PR	0.24	79	39	16
Da	0.20	64	43	12

Notes. Boreal zone, coniferous forest (taiga): Russian northern Karelia (RK) – (Schnittler & Novozhilov 1996); Finland (FL) – (Härkönen 1978, 1979a, b, 1981a, b, 1989). Temperate zone: two areas of the north–eastern United States: Cheat Mountain, coniferous forest (Am1), and Mountain Lake, mainly deciduous forest (Am2) – (Stephenson et al., 1993). Tropical zone: Southern India (SI) – (Stephenson et al. 1993); Costa Rica (CR) – (Alexopoulos & Saenz 1975, Schnittler, person. comm.); Puerto Rico (PR) – (Hagelstein 1927, 1944, Martin & Alexopoulos 1969, Farr 1976, Novozhilov & Rollins, pers. comm.). Mediteranean zone: Israel (ISR) – (Ramon 1968, Binyamini 1986, 1987, 1991, Lado 1994); Turkey (TR) – (Härkönen & Uotila 1983, Härkönen 1988). Desert areas (Da): Arizona (Evenson 1961, Ranzoni 1968); Sonora desert (Blackwell & Gilbertson 1980); Mongolia, Gobi desert (Novozhilov & Golubeva 1986); Kazakhstan, Mangyshlak Peninsula (Schnittler, pers. comm.).

On the other hand, in comparison to surveys from the northern taiga that included results from many moist chamber cultures (Finland, Russian Karelia), the number of species recorded only in the present study was surprisingly high. Although most of these species are rare, our data point towards a certain degree of distinctiveness for the Taimyr myxomycete flora. On the other hand, it must be stated that many species (e.g., *Echinostelium minutum*, *Comatricha nigra*, and *Arcyria cinerea* as the three most abundant species) commonly recorded from the Taimyr Peninsula are widely distributed throughout the world, having rather wide ecological amplitudes. Of the 56 species listed herein, only 28 were found more than twice (Table 1). At present, from surveys carried out in high-latitude regions of the northern hemisphere (the range of latitudes represented by the various study areas extends from 59° to 77° N), 150 myxomycete species from about 1800 collections are known (S.L. Stephenson, pers. comm.), compared with 275 species from eastern North America (Martin & Alexopoulos 1969) and 300 from India (Venkataramani & Kalyanasundaram 1986).

What are the distribution limits for myxomycetes in arctic regions?

Obviously, the main factors for the decrease in the number of myxomycete species in arctic regions are unfavourable temperature conditions and the reduced range and extent of available microhabitats. Along with the surveys from Alaska (Stephenson & Laursen 1993, 1998) and Greenland (GØtzsche 1989), our survey is the northernmost one carried out so far. With a high degree of continentality and extremely low winter temperatures, the climate of the Taimyr Peninsula is definitely very harsh, but the 56 myxomycete species recorded indicate that winter temperature is certainly not a limiting factor for myxomycete distribution.

A more important factor seems to be the mean July temperature. In the Taimyr Peninsula at 70° N, the mean July temperature usually varies between 10 and 12° C (Chernov & Matveyeva 1997, Romanova 1971), which is a relatively high value for this latitude. In the southern tundra and the forest-tundra, daily air temperatures of 25°C can prevail for more than a week. Presumably for this reason a species like *Cribraria violacea* with a mainly tropical distribution and a short development cycle can grow successfully, whereas numerous litter species of *Didymium* and *Physarum* (often common in temperate regions) with longer development times are seemingly absent.

For many cryptogams, fungi, insects or small animals, a lack of coarse woody debris is

certainly a factor limiting their northern distribution (Samuelsson et al. 1994). Many myxomycetes were found also on tiny branchlets, although others with large fructifications, like *Lycogala epidendrum*, seem to be confined to thicker logs. This may explain the only record of this species from Spitsbergen (Elvebakk et al. 1996), collected from the remnants of a wooden loghouse. Also *Enteridium splendens* var. *juranum*, was found exclusively on logs with a diameter >20 cm. In contrast, litter is available as a substrate even far north in the typical tundra, and species of myxomycetes specialised for this substratum type may be more limited by macroclimate. In addition, the low levels of nutrients (especially nitrogen) in arctic soils may be a limiting factor, as possibly indicated by the virtual absence of the elsewhere common *Didymium difforme*, usually associated with nitrogen-rich substrata. In the north, this species may switch to dung. In Russian Karelia it was found twice on litter, and once on dung (Schnittler & Novozhilov 1996), and in the Kola Peninsula (Novozhilov & Schnittler 1997) once on dung.

The low pH values recorded for most substrata constitute very probably another limiting factor for myxomycete occurrence in the north, especially for many members of the Physarales, and certainly for bark-inhabit species. All sampled substrata were rather acidic, especially bark (mean 4.16 ± 0.10, 83 samples measured), followed by wood (4.90 ± 0.12, 51 samples), litter (5.85 ± 0.12, 45 samples), and dung (5.94 ± 0.14, 25 samples). In summary, there is a strong evidence that at least on the Taimyr Peninsula with its higher summer temperatures the northern limits of myxomycete distribution are much more determined by microhabitat availability than by macroclimatic conditions.

Acknowledgments. We acknowledge logistical support provided by Dr. D. Bolsheianov of the Arctic and Antarctic Research Institute, St. Petersburg, Russia. Appreciation is extended to Dr. I. Yu. Kirtsideli for collecting substrate samples for moist chambers in some areas of the Taimyr Peninsula. We also wish to express our thanks to L.A. Karzeva, St. Petersburg, for technical assistance during the SEM-investigations. We wish to thank D.W. Mitchell, United Kingdom, for his valuable comments relating to the collection of *Licea belmontiana* reported herein, Prof. J. Rammeloo (National Botanical Garden, Belgium),and Prof. U. H. Eliasson (Göteborg University, Sweden) for the loan of specimens of *Licea belmontiana* and *L. denudescens.* This work was supported in part by grants (N 96-04-48209, N 95-04-11790a, 98-07-90346) from the Russian Foundation for Basic Research [RFBR].

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Received on 1 June 1999

Distribution and ecology of myxomycetes in high-latitude regions of the Northern Hemisphere

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Abstract

Aim The objective of this study was to analyze the data represented by 1,976 specimens of myxomycetes collected in high-latitude regions of the Northern Hemisphere to obtain information on the biogeographical relationships and patterns of occurrence of these organisms. The question of what factors limit myxomycete distribution in high-latitude and cold-dominated regions was also addressed.

Location Specimens of myxomycetes considered herein were collected from twelve study areas in Iceland, northern Russia and Alaska, and Greenland. The vast majority of specimens were collected during the period of 1989 to 1998.

Methods Nine hundred and thirty-three specimens were recorded as field collections. In addition, 1,043 specimens originated from moist chamber cultures prepared with 1,453 substratum samples collected in the various study areas. From a database recording the type of substratum (wood, bark of living trees, litter, or dung) for each specimen, patterns of substratum occurrence for particular species of myxomycetes in high-latitude regions were determined.

Results From the 150 species recorded for the twelve study areas, thirty-three were found to be widely distributed (recorded from at least five study areas), and only forty-one had a frequency of occurrence higher than 1 % either in moist chambers or as field collections. These data were examined in an effort to identify possible factors limiting the distribution of myxomycetes in high-latitude regions.

Main conclusions Upon first inspection, the arctic and subarctic myxomycete biota seems to be a depauperate version of that of temperate and boreal regions. However, a few species elsewhere recorded as rare but found to be fairly common in this study indicate that a certain degree of distinctiveness exists in arctic and subarctic myxomycetes.

Keywords
Alaska, Arctic, biogeography, forest-tundra, myxomycetes, Russia, subArctic, tundra.

INTRODUCTION

Myxomycetes (plasmodial slime moulds) are primitive, phagotrophic eukaryotes that commonly occur in association with decaying plant material in terrestrial ecosystems. The myxomycete life cycle involves two morphologically distinct trophic stages, one consisting of uninucleate amoebae, with or without flagella, and the other consisting of a distinctive multinucleate structure, the plasmodium (Martin et al., 1983).

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Under favourable conditions, the plasmodium gives rise to one or more fruiting bodies containing spores. The spores complete the life cycle by germinating to produce the uninucleate amoeboflagellate cells. Field studies of myxomycetes have invariably focused on the reproductive, or spore-producing, stage in the life cycle. The reason for this is that myxomycetes are very seldom evident in nature except at this one point in their life cycle (Stephenson et al., 1993). Although their exact evolutionary affinities are still debated, the myxomycetes constitute a well-defined and homogeneous group of approximately 900 species. Some are probably cosmopolitan in distribution, but a number of species appear to be confined to the tropics or subtropics and some others have been collected only in temperate regions (Alexopoulos, 1963; Farr, 1976; Martin et al., 1983).

Most of what is known about the assemblages of myxomycetes associated with particular types of terrestrial ecosystems has been derived from studies carried out in temperate regions of the world. Although myxomycetes are known to occur in the arctic and subarctic, the species associated with these high-latitude regions of the world have received very little study. Stephenson and Laursen (1993) recorded 17 species from arctic and subarctic alpine tundra in Alaska, whereas Götzsche (1984, 1989, 1990) reported 48 species from Iceland and 54 species from various localities in Greenland. More recently, Stephenson and Laursen (1998) recorded a total of 90 species for all of Alaska, but this figure included numerous records from areas that fall within the boreal forest zone. A study from boreal Russian Karelia listed 150 species (Schnittler & Novozhilov, 1996). The totals reported for several of the Scandinavian countries, including Finland (Härkönen, 1979, 1981, 1989), Norway (Johannesen, 1982, 1984) and Sweden (Santesson, 1964; Eliasson, 1981), are considerably higher (>150 species for each country). However, much of this region of western Europe is characterised by a relatively milder climate (and thus a greater diversity of vegetation types) than most other areas of the Northern Hemisphere located as far north. As such, a higher species richness of myxomycetes might be expected, based on studies carried out in temperate regions of the world (e.g. Stephenson et al., 1993). Although overall species richness of myxomycetes appears to be relatively low in high-latitude and cold-dominated regions of the world, these organisms have been reported as not uncommon in certain types of microhabitats (Stephenson & Laursen, 1993; Stephenson et. al., 1994).

Temperature and moisture are generally considered as the most important factors influencing the distribution and occurrence of myxomycetes in nature (Martin et al., 1983; Stephenson & Stempen, 1994). The availability of at least some moisture in a given microhabitat is an absolute prerequisite for myxomycete growth and development, but even when moisture is abundant, few fruiting bodies are produced under low temperature conditions (Maimoni-Rodella & Gottsberger, 1980; Venkataramani & Kalyanasundaram, 1986). The climate of high-latitude regions of the Northern Hemisphere varies widely from subtemperate (with cool summers and often abundant annual precipitation) in some of the more southern coastal regions, to continental (with moderately warm summers and long, cold winters) throughout most of northern North America, Europe and Asia, and arctic (with short, cool summers and extremely severe winters) at the very highest latitudes considered in the present study (Larsen, 1980; Slaughter & Viereck, 1986; Stonehouse, 1989). Most of the plant communities from which specimens were collected are in areas underlain by permafrost, and the mean daily temperatures are below 0 °C for more than six months of the year. Extreme winter temperatures below -50 °C are not uncommon in some areas. Presumably, such climatic regimes would not be favourable to the growth of most species of myxomycetes.

The primary objective of the present study was to assemble taxonomic, ecological, and distributional data on all of the species of myxomycetes reported from and/or represented by specimens collected in high-latitude regions of the Northern Hemisphere. In addition, the following specific questions were addressed: (1) What species of myxomycetes actually occur in these high-latitude regions? (2) Are there any species that seem to be predominantly arctic/subarctic in their distributions? (3) Which factors might limit the distributions of myxomycetes at high latitudes?

MATERIALS AND METHODS

Myxomycetes were collected in Alaska (Stephenson) on various occasions during the 1989 to 1998 field seasons and in Russia (Novozhilov & Schnittler) during the period of 1990 to 1996. In addition, data from specimens collected in Greenland and Iceland (Götzsche, 1984, 1989, 1990) also were included. On each collecting trip to one of the study areas, an effort was made to examine all types of substrata upon which fruiting bodies of myxomycetes might be expected to occur, and all of the specimens encountered were collected and/or recorded. For the purpose of this study, a 'specimen' was defined as one or more fruiting bodies (sporangia, aethalia, pseudoaethalia or plasmodiocarps) considered to have originated from a single plasmodium (Stephenson, 1989). In virtually all cases, this could be determined without difficulty. The method used in collecting a specimen involved removing most of the fruiting bodies along with a portion of the substratum upon which they occurred. Notes were made on any unusual fruiting position or substrata.

Collections of myxomycetes were not limited to just those species represented by specimens that had fruited in the field under natural conditions. The moist chamber culture technique as it applies to myxomycetes (Gilbert & Martin, 1933; Stephenson, 1985) provides a convenient and often very productive method of supplementing field collections, and moist chambers were used with considerable success in the present study. Samples of organic material (e.g. leaf litter, bark, dead herbaceous plant parts, and dung) were collected from the study areas, air-dried, and returned to the laboratory. Whereas bark samples from living trees were collected between 1.0 and 1.7 m height, to ensure that only species with bark as the trophic substratum were recovered, all other substrata were gathered from the ground. Moist chamber cultures were prepared in the manner described by Härkönen (1977, 1981) and Stephenson (1985, 1989). The moist chambers used consisted generally of disposable plastic Petri dishes (10 cm diameter) lined with filter paper. Samples were moistened with distilled water. After approximately 24 h, excess water in each dish was poured off. Cultures were kept at room temperature (22-25 °C) in diffuse daylight and examined at regular intervals for periods up to six months.

All specimens of myxomycetes collected in the field or from moist chamber cultures were dried at room temperature and then glued in small boxes for permanent storage. Vouchers are deposited in the herbaria of Fairmont State College (FWVA), the V.L. Komarov Botanical Institute

Table 1 Occurrence of myxomycetes in the twelve study areas. A number before a slash indicates the total of all specimens collected in the field, whereas a number after a slash indicates the total of all specimens obtained from moist chambers. Abbreviations used for the study areas are: IC = Iceland, KM = Khibine Mountains, PU = Polar Ural, YP = Yamal Peninsula, PP = Plateau Putorana, TP = Taimyr Peninsula, MG = Magadan region, CH = Chukchi Peninsula, SP = Seward Peninsula, CA = Central Alaska, NA = Northern Alaska, and GR = Greenland. Species are arranged in groups according to their distribution among study areas. Species represented by records from nivicolous situations are indicated with an asterisk (*).

Species [a]	IC	KM	PU	YP	PP	TP	MG	CH	SP	CA	NA	GR
Echinostelium minutum	-/39	-/5	-/10	-/3	-/15	-/45	-/2	-/21	-/10	-/2	-/2	-/24
Arcyria cinerea	12/18	1/5	-/13	-/2	1/19	-/23	-/7	2/12	1/18	1/4		5/1
Comatricha nigra	18/2	2/1	2/3		4/7	1/35	2/3	2/10	-/13	3/-	-/2	16/-
Lycogala epidendrum	31/-	1/-	2/-		2/-	2/-	5/-	4/-	2/-	8/-	3/-	14/-
Ceratiomyxa fruticulosa	2/-	3/-	-/1		2/3	1/-	3/-	3/-	2/-	3/-		8/-
Leocarpus fragilis	1/-	1/-	2/-			-/1	6/-	3/2	1/4	4/-	-/2	4/-
Arcyria incarnata	40/2		1/1		1/5	1/9	2/1	2/7	4/-	2/-		47/-
Licea minima	-/5	2/-	-/3	-/1	-/4	-/19		-/3	-/3			-/6
Mucilago crustacea	4/-		1/-			1/-	7/-	13/-	8/-	8/-	5/-	8/-
Perichaena chrysosperma	-/1		-/2		-/1	-/5		-/3	-/2	-/7	-/36	-/2
Trichia varia	1/-			-/1	1/-	3/1	2/-	3/-	13/-	6/-		16/-
Calomyxa metallica	1/1		-/3	-/1		-/1		-/3	-/2	-/9		-/1
Didymium dubium (*)		3/-		-/1	4/1	-/2			-/1	-/1	-/2	-/1
Enerthema papillatum	7/1		-/4		-/1	1/4	1/-	1/1	2/5			5/-
Physarum cinereum	1/-	16/-			1/-		2/-	2/1	1/-	1/-		-/4
Trichia decipiens	9/-	1/-				1/-	1/-	2/-	1/-	1/-		7/1
Trichia lutescens	4/2		-/2			-/2		-/1	-/1	-/1	-/1	15/3
Trichia munda	6/-		-/10	-/2	-/1	-/5		-/5		-/1		-/5
Arcyria pomiformis		1/-			-/1	-/2	2/1	1/1	1/-			2/-
Physarum bivalve		-/2			-/1	-/6	4/2	-/11	-/1	-/1		
Physarum oblatum			-/2			-/2	2/-	-/2	3/1	2/-	-/3	
Stemonitis axifera		-/1	3/-		2/-		1/-	2/1	5/-	8/-		
Stemonitis fusca	2/-		1/-					1/-	2/-	4/-	-/4	3/-
Craterium leucocephalum	5/-		2/-			-/1	2/-		1/-	5/-		
Didymium difforme		-/1		-/1		-/1		1/1			-/2	-/1
Didymium melanospermum			-/2			-/1	4/5	-/1	1/-	-/6		
Didymium squamulosum				-/1		-/2	2/-		-/3	1/-		-/6
Physarum leucophaeum		1/-	-/1				1/-		4/-	1/-		1/-
Physarum nutans			2/3		-/1	2/2	3/-	3/6				8/-
Comatricha laxa	8/2		-/1		-/1			1/1				6/3
Perichaena vermicularis					1/-	-/4				-/3	-/11	-/1
Trichia botrytis	6/-	6/-	-/2			-/2		1/1				
Trichia favoginea	2/-	1/-							2/-	1/-	-/2	
Badhamia utricularis	3/-						2/-		2/-			12/3
Comatricha typhoides							1/-	2/1	11/-	1/-		
Diderma radiatum						1/-		1/-	1/-	1/-		
Didymium clavus			3/1				2/-	1/-				1/-
Enteridium oliviaceum	7/-							1/-	-/1			5/-
Lamproderma arcyrioides (*)	4/-	5/-						2/-				1/-
Lamproderma sauteri (*)	2/-	12/-			3/-							4/-
Licea cf. *belmontiana*			-/3	-/2	-/4	-/6						
Licea parasitica	-/3		-/10					-/3				-/2
Paradiacheopsis fimbriata			-/6			-/20	-/4	-/3				
Physarum viride		2/-	1/-			-/1		2/-				
Prototrichia metallica (*)						-/4		1/-	1/-			8/-
Trichia contorta	1/4	2/-									-/15	11/3
Arcyodes incarnata		1/-				-/1		1/1				
Arcyria denudata					-/1	-/1				1/-		
Dictydium cancellatum		1/-							2/-	1/-		
Diderma niveum (*)	4/-	1/-						1/-				

Echinostelium brooksii [b]	-/26				-/1	-/7						
Enteridium splendens var. *juranum* [b]	2/-				3/-							8/-
Hemitrichia clavata		2/-							8/-	4/-		
Lamproderma scintillans							2/-		-/4	-/1		
Licea kleistobolus			-/1			-/6		-/1				
Licea operculata			-/9	-/1				-/1				
Licea variabilis	1/-		-/1									-/1
Macbrideola cornea			-/2			-/3						-/6
Perichaena depressa						-/2		1/3			-/1	
Trichia flavicoma [b]									-/3	-/10	-/1	
Tubifera ferruginosa		1/-					1/-				1/-	
Amaurochaeta atra	1/-								2/-			
Arcyria helvetica	1/-								1/-			
Arcyria obvelata		-/1			1/1							
Badhamia affinis									-/4			-/1
Cribraria violacea						-/4				-/5		
Dictydiaethalium plumbeum			1/-					2/-				
Diderma deplanatum		2/-									-/4	
Diderma effusum									1/-			1/-
Diderma trevelyani									6/-			1/-
Diderma umbilicatum										1/-		1/-
Fuligo intermedia											3/-	11/-
Fuligo septica									3/-		-/1	
Licea testudinacea					-/5	-/15						
Macbrideola macrospora [b]										-/2	-/2	
Paradiacheopsis cribrata [b]	-/1					-/2						
Perichaena pedata									-/1	-/2		
Physarum cf. *nudum*					-/1	-/4						
Physarum rubiginosum									1/-	1/-		
Physarum sp. A			-/2							-/1		
Stemonitis flavogenita	4/1											2/-
Stemonitis hyperopta		1/-								1/-		
Stemonitis smithii		1/-			1/-							
Trichia subfusca	1/-										1/-	

[a] The following 66 species were found only in one of the 12 study areas: *Badhamia* cf. *panicea*: SP 1/-; *B. foliicola*: GR 4/-; *B. macrocarpa*: IC 10/-; *Comatricha alta*: GR 1/-; C. *ellae* Härk. - Karstenia 18: 23. 1978: IC -/1; *C. longipila*: GR 1/-; *C. pulchella*: TP -/1; *C. rigidereta*: SP -/2; *Cribraria argillacea*: GR 1/-; *Cr. aurantiaca*: KM 1/-; *Cr.* cf. *atrofusca*: TP -/1; *Cr. microcarpa*: TP -/4; *Cr. vulgaris*: TP -/1; *Diacheopsis effusa* Kowalski - Mycologia 67: 623. 1975 (*): KM 1/-; *Dianema corticatum*: GR 2/-; *Diderma montanum*: GR 3/-; *Diderma* sp. A: MG 1/-; *D. spumaroides*: IC 1/-; *Didymium anellus*: GR 2/2; *D. bahiense*: GR -/1; *D. crustaceum*: CH -/1; *D. iridis*: SP -/1; *D. nigripes*: CH 2/-; *D. trachysporum*: GR -/1; *Echinostelium corynophorum* Whitney - Mycologia 72: 963. 1980: IC -/14; *Ech. fragile*: IC -/1; *Enteridium lycoperdon*: CH 1/-; *Hemitrichia abietina*: TP 1/1; *H. serpula*: NA -/1; *Lamproderma carestiae* (*): KM 1/-; *L. columbinum*: IC 1/-; *L. fuscatum* (*): KM 1/-; *Lamproderma* spec. (*): IC 1/-; *Lepidoderma aggregatum* Kowalski - Mycologia 63: 511. 1971 (*): KM 3/-; *Le. carestianum* (*): CH 3/-; *Le. granuliferum* (*): KM 4/-; *Lepidoderma* sp. A: SP -/2; *Leptoderma iridescens*: GR 2/-; *Licea biforis*: MG -/2; *L. castanea*: SP -/2; *L. marginata*: IC -/1; *Licea* sp. A: CH -/1; *Lindbladia tubulina*: MG 1/-; *Metatrichia vesparium*: NA -/3; *Oligonema fulvum*: GR -/1; *O. schweinitzii*: NA 1/-; *Perichaena corticalis*: SP 1/-; *P. liceoides*: CH -/2; *P. minor*: MG -/2; *Perichaena* sp. A: TP -/2; *Physarum carneum*: IC 1/-; *P.* cf. *leucopus*: CA 1/-; *P. contextum*: SP 2/-; *P. famintzinii*: IC 1/-; *P. luteolum*: SP 1/-; *P. mutabile*: IC 1/-; *P. notabile*: SP 1/-; *P. virescens*: KM 1/-; *Stemonitis* cf. *pallida*: CA 1/-; *St. virginiensis*: KM -/1; *Stemonitis* spec.: PU -/1; *Stemonitopsis subcaespitosa* (Peck) Nann.-Bremek.- Nederl. Myxomyc. 211. 1974: PP -/2; *Trichia alpina* (*): KM 18/1; *T. erecta*: KM 1/-; *T. scabra*: SP 1/-; *Willkommlangea reticulata*: CA 1/-. [b] For the following species names not cited in Martin & Alexopoulos (1969) references to the protolog are given: *Echinostelium brooksii* Whitney - Mycologia 72: 957. 1980; *Enteridium splendens* var. *juranum* (Meyl.) Härk. - Karstenia 19: 5. 1979; *Trichia flavicoma* (Lister) Ing - Trans. Brit. Mycol. Soc. 50: 558. 1967; *Macbrideola macrospora* (Nann.-Bremek.) Ing - Trans. Brit. Mycol. Soc. 78: 444. 1982; *Paradiacheopsis cribrata* Nann.-Bremek. - Proc. K. Ned. Akad. Wet. C 71 (1): 47. 1968

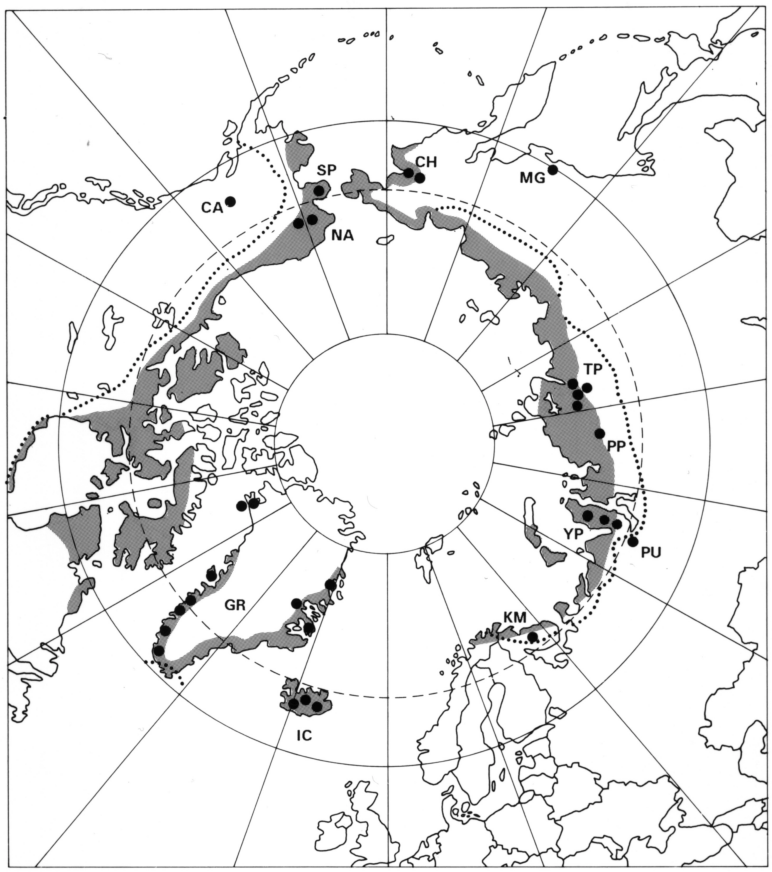

Figure 1 Locations of all collecting sites considered in the present paper (black dots). Study areas are identified by combinations of two letters (see Material and Methods for explanation). The shaded area indicates the extent of tundra regions, and a dotted line marks the approximate limit of the northern timberline.

(LE), the US National Fungus Collections (BPI), and the personal herbarium of M. Schnittler (stored at the Herbarium Haussknecht, Jena; JE). Nomenclature used for myxomycetes is essentially that of Martin & Alexopoulos (1969), except for a few species described recently, where a reference to the protolog is given in Table 1.
Names for vascular plants follow Czerepanov (1995) for Russia and Hultén (1968) for Iceland, Greenland and Alaska.

The assemblages of species associated with the different study areas were compared using a coefficient of community (CC) index (Mueller-Dombois & Ellenberg, 1974). The formula used to calculate this index is based solely upon the presence or absence of species: CC = 2c/(a + b). Here, *a* is the total number of species in the first data set being considered, *b* is the total number of species in the second data set, and *c* is the number of species common to both data sets. The value of CC ranges from 0 (when the data sets being compared share no species in common) to 1.0 (all species are present in both data sets). As an indicator for overall taxonomic diversity, we used the mean number of species per genus (S/G), as described by Stephenson et al. (1993).

Descriptions and locations of the 12 study areas are given below. Only those aspects of the environmental setting and vegetation that are important factors in determining the microhabitats potentially available for myxomycetes are mentioned. The range of latitudes represented by the various study areas extends from 59 ° to 77 ° N. Although some of the study areas are located south of the northern climatic limit of the boreal forest zone, the plant communities from which specimens were collected included only tundra, forest-tundra, and open (<60% canopy coverage) woodlands of the northern taiga that forms the transition zone to the tundra. Well-developed boreal forest communities with a closed canopy were excluded. As considered herein, tundra (*sensu* Bliss, 1988) includes vegetation types that range from tall shrub (generally 2-5 m high) to dwarf shrub heath (usually 5-20 cm high) to communities dominated by grasses, various herbaceous plants, lichens, or mosses. The three main vegetation types (tundra, forest-tundra, and woodland), as well as the tundra subtypes, often intergrade, frequently within relatively small distances. Therefore, an exact geographical delimitation is impossible. Locations of the all collecting sites assigned to the twelve study areas are shown in Fig. 1.

Iceland (IC): From the papers of Götzsche (1984, 1990), 332 specimens of myxomycetes from 17 collecting sites (64-66 °N, 14-21 °W) and numerous other localities represented by older herbarium collections were included in our database. The most productive sites were in areas near the coast, where *Betula pubescens* Ehrh. forms scattered forests. Other sites investigated for myxomycetes included tree

plantations of such species as *Larix sibirica* Ledeb. and *Picea glauca* (Moench) Voss as well as areas of dwarf shrub heath tundra.

Russia, Khibine Mountains (KM): This isolated mountain massif, approximately 50 km in diameter, forms an island in what is otherwise boreal forest. The southern part (67 ° 36 ’N, 33 ° 12 ’E), north of the city of Kirovsk, was the specific area investigated. The timberline in the Khibine Mountains occurs at an elevation of about 400 m, and the woodlands below, predominantly formed by *Picea abies* (L.) Karst. and *Betula pubescens*, are classified as light northern taiga. Avalanche gutters on south- to southwest-facing slopes are covered with dense herbfields of *Athyrium distentifolium* Tausch ex Opiz and the large composite *Cicerbita alpina* (L.) Wallr., which provide favourable substrata for nivicolous myxomycetes, an ecological group associated with decaying herbaceous plant debris wet by melting snowbanks and found predominantly in high mountains. At elevations above 650 m, a few areas support low thickets of *Betula nana* L., and these merge into mountain tundra. On north-facing slopes, various ericads form dense thickets, whereas south-facing slopes are characterised by herbfields dominated by numerous tall perennials. The very highest elevations support areas of lichen-rich tundra. During a fortnight stay, 119 specimens were recorded in 1994 (Novozhilov & Schnittler, 1997).

Russia, Polar Ural (PU): These mountains have a north-south orientation and reach elevations over 1850 m. Collecting sites were located in the vicinity of the city of Labytnangi (66 ° 58 'N, 66 ° 12 'E). This region falls within the transition zone that exists between forests dominated by *Picea obovata* Ledeb. and those in which *Larix sibirica* is dominant, and these two species form forest-tundra at elevations between 300 and 400 m. At higher elevations, areas of open tundra with patches of *Duschekia fruticosa* (Rupr.) Pouzar (to 3 m tall) occur. In stream valleys, shrubs (*Betula pubescens* and *Salix* spp.) to 5 m tall form azonal woodlands with a rich herbaceous biota in the understorey. From this study area, 123 specimens were recovered, mostly with the moist chamber technique.

Russia, Yamal Peninsula (YP): This study area is located in the lowlands of north-eastern Siberia. The specific site investigated was near the Ob' River (Siuniai-Sale, 66 ° 55 'N, 71 ° 20 'E). Although single, small trees of *Larix sibirica* sometimes occur, the region is within the tundra zone. Patches of "yernik" (thickets of *Betula glandulosa* Michx. and *B. nana*) and shrub tundra with stems of *Salix* spp. up to 1 m tall form a mosaic over the landscape. *Duschekia fruticosa* is present as a tall shrub. Only a few substratum collections, yielding 16 specimens in moist chambers, were available from this study area.

Russia, Putorana Plateau (PP): This study was visited in 1995. It consists of a series of hills (100 to 200 m elevation) called "Krasnyi Kamen" (69 ° 29 ‘N, 88 ° 32 ‘E) and is located approximately 80 km north of the city of Norilsk. Here, northern taiga is formed by *Picea obovata* and *Larix sibirica*, with rich herbfields of tall perennials such as *Cirsium helenioides* (L.) Hill and *Heracleum sibiricum* L. occurring in wet depressions. On hillsides, tall and large thickets of *Salix* spp., *Duschekia fruticosa*, and *Juniperus communis* form a forest-tundra. At elevations >200 m, dwarf heath tundra with *Betula nana* and various prostate ericaceous shrubs dominates. During one week, 103 specimens were collected.

Russia, Taimyr Peninsula (TP): A series of collecting sites, along a transect that extended from the northern taiga on the Kotui River (71 ° 30 ‘N, 103 ° 00 ‘E) to tundra (near Zhdanikha, at 72 ° 46 ‘N, 104 ° 50 ‘E) was investigated. At the first collecting site, *Larix sibirica* woodland with small, widely separated trees up to 10 m tall covers all except the stream valleys. More northward, but also in the natural meadows of the stream valleys, thickets of *Duschekia fruticosa* occur, intermixed with single, small *Larix* trees. In their shelter, *Juniperus communis* sometimes occurs. Although characterised by an extremely continental climate, this study area nevertheless produced 263 specimens, mostly from moist chambers (Novozhilov & Schnittler, 1996).

Russia, Magadan Region (MG): Collecting sites (59 ° 33 to 60 ° 30 ‘N, 150-155 ° E) were centred around the city of Magadan. This region is within the northern taiga, and plant communities investigated ranged from woodlands dominated by *Larix dahurica* Turcz. & Trautv., *Betula ermannii* Cham., and *Chosenia arbutifolia* (Pall.) A. Skvorts. to dwarf shrub tundra (with *Betula exilis* Sukatsch and dwarf species of *Salix*) and thickets of *Duschekia fruticosa*. This study area is represented by 91 specimens.

Russia, Chukchi Peninsula (CH): Several collecting sites, together yielding 179 specimens, were located near the mouth of the Anadyr River (64 ° 43 ‘N, 177 ° 29 ‘E). These ranged from lowlands to mountainous areas with elevations up to 500 m. The whole region belongs to the tundra zone, with *Betula nana* thickets up to 0.5 m tall dominating the lowlands. Mountainous areas are characterised by thickets of *Duschekia fruticosa* and *Pinus pumila* (Pall.) Regel, with the latter species forming very dense, low thickets, often with stems up to 10 cm in diameter. Extrazonal river floodplains are covered by open forests of *Chosenia arbutifolia* and *Populus suaveolens* Fisch., which contain trees up to 15 m tall.

USA, Seward Peninsula, Alaska (SP): This study area (65 ° 05-65 ° 50 ‘N, 163-164 ° E) falls entirely within tundra. Tall shrub communities dominated by *Salix alaxensis* (Anderss.) Cov. and *Alnus crispa* (Ait.) Pursh are present along stream drainages, but these give way to areas of dwarf heath tundra dominated by *Betula nana* and dwarf species of *Salix* on most slopes. Forests consisting of *Populus balsamifera* L. are present in a few widely scattered localities, and open woodlands of *Picea glauca* occur in the southwestern part of the general study area. This study area yielded 184 specimens.

USA, Central Alaska (AK): A total of 129 specimens came from various study sites located within the Alaska Range of Denali National Park and Preserve (63 ° 45 ‘N, 150 ° 00 ‘W). The vegetation of this study area is similar to that typically found throughout Interior Alaska (Viereck & Little, 1972). Subarctic alpine tundra occurs on the higher peaks and ridges, but this gives way to low shrub communities on most slopes and to tall shrub communities along stream drainages. *Picea glauca* woodlands occupy lower slopes and river terraces (Treu et al., 1996).

USA, Northern Alaska (NA): This study area (67 ° to 71 ° N, 149-161 ° W) consisted of a series of collecting sites in arctic tundra located on the north slope of Alaska and within the foothills of the east-west arching Brooks Range. Vegetation types investigated included open *Picea* woodlands, dry montane arctic tundra, moist arctic tundra, and wet lowland arctic tundra (Stephenson & Laursen, 1993). Field and moist chamber studies yielded 109 specimens from this study area.

Greenland (GR): The 328 specimens of myxomycetes reported from Greenland (60-77 ° N, 24-68 ° W) by Götzsche (1989) were recovered from a total of 35 collecting sites. The majority of these were along the southern part of the west coast, where small pockets of such trees as *Betula pubescens* and *Sorbus angustifolia* L. occur in sheltered localities. Collecting sites also included examples of tall shrub tundra and dwarf heath tundra. *Alnus crispa*, *Salix glauca* L., *Betula glandulosa*, and *B. nana* are among the more important species present in these communities. More than 95% of Greenland is covered with an ice cap, and a fairly complete cover of vegetation is restricted to areas near the coastline.

RESULTS AND DISCUSSION

Taxonomic composition

One hundred and fifty species representing forty genera were identified from the 1,976 specimens considered (Table 1). This total includes seven taxa for which identification to species was not possible. Three of these (designated as *Lepidoderma* sp. A, recorded from the Seward Peninsula, Alaska; *Licea* sp. A, found on the Chukchi Peninsula; and *Perichaena* sp. A, recorded from the Taimyr Peninsula) apparently represent undescribed species. Furthermore, members of the complex of small, corticolous species of *Comatricha* centred around *C. nigra* (Pers. ex J.F. Gmel.) Schroet. are notoriously difficult to identify. *Comatricha nigra* was one of the three most common myxomycetes in this study, occurring frequently but not exclusively on the bark of living trees and shrubs. Apparently, this taxon represents a species complex that includes two corticolous and rare extreme forms identified as *Comatricha rigidireta* Nann.-Bremek. (Seward Peninsula) and *Paradiacheopsis cribrata* Nann.-Bremek. (Iceland, Taimyr Peninsula). *Trichia flavicoma* (Lister) Ing and *T. munda* (Lister) Meyl., two other taxa that are closely related and difficult to separate, were found to be surprisingly common, occurring in 9 of the 12 study areas. Following the concept used by Götzsche (1990), we recognised as characteristic for *T. flavicoma* the clavate, comparatively large sporothecae not sharply separated from the short stalks, with an inconspicuously areolate peridium and a pale yellow spore mass. *Trichia munda*, as circumscribed herein, has much smaller sporocarps on longer stalks that reach 1-1.5 times the length of the almost spherical sporotheca. The latter is sharply differentiated from the stalk. The peridium in our specimens was clearly areolate, producing the appearance of a miniature *Trichia erecta* Rex but with a much duller, ochraceous spore mass.

Many species of myxomycetes, especially snowbank-associated and wood-inhabiting species, never or very rarely appear in moist chambers. On the other hand, many myxomycetes with tiny sporocarps are almost impossible to detect in the field. The most prominent example in this study is *Echinostelium minutum* de Bary, with tiny sporocarps that last in nature perhaps less than one day, or *Licea minima* Fr., with sessile fructifications possessing a long-lasting peridium, which enhances the chances of occasionally finding fructifications in the field (Table 1). As such, field collections and specimens obtained from moist chamber cultures supplement each other if one wants to survey the myxomycete biota of a region as completely as possible. Very probably, most species of myxomycetes cannot form fructifications from spores in moist chambers. Even the very rapidly developing members of the genus *Echinostelium* (often fruiting in moist chambers after just 2-6 days) never appeared again during the entire period of time (2-4 months) a moist chamber was maintained. If these species could complete their entire live cycle in a moist chamber, a second fructification peak should occur. If moist chambers simply reflect spore fallout, at least for a few of the more than 1,400 cultures considered for this study and maintained at room temperature, strictly tropical species of myxomycetes should have appeared, as a result of the occasional presence of spores brought in by long-distance dispersal. The absence of such forms is strong evidence that data obtained with moist chamber technique do reflect the real myxomycete assemblage of a region, thus supporting the hypothesis of Alexopoulos (1964) that for many species of myxomycetes microcysts or sclerotia may be much more important than spores as dormant stages.

In this study, the average number of species recorded for a given study area was 38.8, but if the one study area (the Yamal Peninsula) represented by only 16 specimens is excluded from consideration, the average number increases to 41.4. The northernmost location, the Taimyr Peninsula (71 ° 30 ‘N), produced one of the highest numbers of species (48). This study area, which has the northernmost woodlands on Earth, has a continental climate with relatively warm summers and also was surveyed rather intensively. The high number of species recorded is undoubtedly a result of these two factors.

Despite the high number of 150 species recorded, only 33 taxa were found to be widely distributed (present in 5 or more of the 12 study areas, Table 1). *Arcyria cinerea* (Bull.) Pers., *Comatricha nigra*, *Echinostelium minutum*, and *Lycogala epidendrum* (L.) Fr.) were recorded from at least 11 study areas. Only *E. minutum* occurred throughout all 12 study areas and was the most common species in moist chambers (recorded 178 times, occurring in 12 % of all 1453 cultures). It is also common in the temperate zone, as shown by a frequency of 49 % (312 of 632 moist chambers prepared with bark) in a study on temperate upland forests in southwestern Virginia (Stephenson 1989).

A very similar picture – a few common species among many rare ones – can be obtained from calculating the abundance of a particular species in the field or in moist chambers. Due to the different methodologies used in different components of this study, we calculated values for

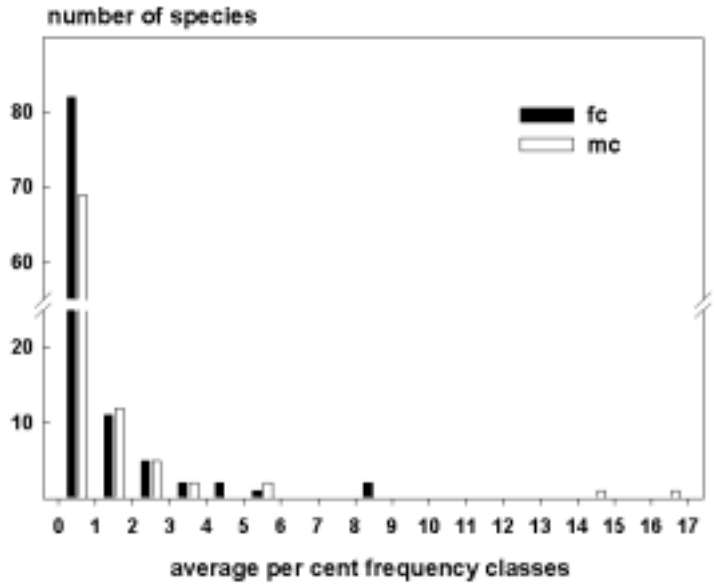

Figure 2 Average values of per cent frequencies for all species represented as field collections and/or moist chamber collections. The x-axis indicates average frequency classes from 0 - <1, 1 - < 2, ..., 16 - <17 per cent, whereas the y-axis indicates the number of species per frequency class for field collections (closed bars) as well as for collections from moist chambers (open bars).

average per cent frequency based on the proportion each species represented of the total of all field collections and/or all records originating from moist chambers for each study site. Fig. 2 shows the number of species for classes of per cent frequency (average value from all 12 study areas) for specimens from the field and from moist chambers. A similar pattern is evident, with 41 species occurring with a average frequency higher than 1 % in the field and/or in moist chambers (Table 1). Only seven species (*Arcyria cinerea*, *Comatricha nigra*, *Echinostelium minutum*, *Lycogala epidendrum*, *Mucilago crustacea* Wiggers, *Perichaena chrysosperma* (Curr.) Lister, and *Trichia varia* (Pers.) Pers.) had an average frequency higher than 5 % for either field or moist chamber collections. Both approaches, one looking at the general distribution and the other at the average abundance of a species, coincide in revealing only a limited number of myxomycetes (33 and 41 taxa) as the most consistently occurring and widely distributed species associated with plant communities in high-latitude regions of the Northern Hemisphere (Table 1). Twenty-seven taxa match both criteria.

In Fig. 3, the proportions of the orders of myxomycetes are shown in comparison to two temperate biotas - Germany (Schnittler et al., 1996), and the Netherlands (Nannenga-Bremekamp, 1991). When considering all species of myxomycetes ever recorded for a particular region, the proportions of the respective orders do not vary to any significant extent. However, when looking at the regularly occurring species only, members of the *Trichiales* clearly represent a higher proportion of the total number of species at high latitudes. On the other hand, the proportion of members of the *Liceales* decreases. In the latter order, the two largest genera by far are adapted to woody substrata; species of *Cribraria* prefer wood, especially thick conifer logs, whereas species of *Licea* are corticolous. At high latitudes, both types of substrata almost disappear beyond the northern timberline. In contrast, many members of the *Trichiales* manage to develop on small, decaying branches of shrubs with a diameter of less then 1 cm. For the twelve species of *Trichia* recorded in the present study, nine were found at least occasionally on litter, with two (*Trichia flavicoma* and *T. munda*) observed mostly on this substratum type.

Substratum - species relationships

From the 1,043 specimens obtained from moist chambers, 245 were from decaying wood, 403 from bark samples collected from living trees and shrubs, 352 from leafy litter or decaying herbaceous plant material, and 43 from the dung of herbivorous animals. Since the numbers of specimens for a particular species are affected by the amount and types of substrata collected, these figures do not necessarily reflect the naturally occurring proportions. Table 2 shows the summary data for the average yield of moist chambers from ten of the twelve study areas. Interestingly, litter had the highest percentage of moist chambers positive for myxomycetes; bark was less productive than usual for the temperate zone. However, 5-10 % of the plasmodia occurring in moist chambers prepared with litter could not be induced to fruit. For the 933 field collections, most of the specimens originated from wood (643) and litter (262), with only a few collections from bark (25) and dung (3). For a survey done predominantly in regions covered by tundra and forest-tundra, the high number of records from wood might be surprising. However, many species were found to occur on even tiny bits of wood, such as specimens of *Comatricha nigra* on small, decaying branches of *Betula nana* lying in the litter under shrubs.

Bryophytes and lichens are important components of many vegetation types found at high latitudes. In the present study, few specimens of myxomycetes were collected from lichens, but myxomycetes were observed to be fairly common on bryophyte-covered wood. Samples of litter used to prepare moist chamber cultures inevitably contained fragments of both lichens and bryophytes. No myxomycete species was recorded predominantly from either lichens or

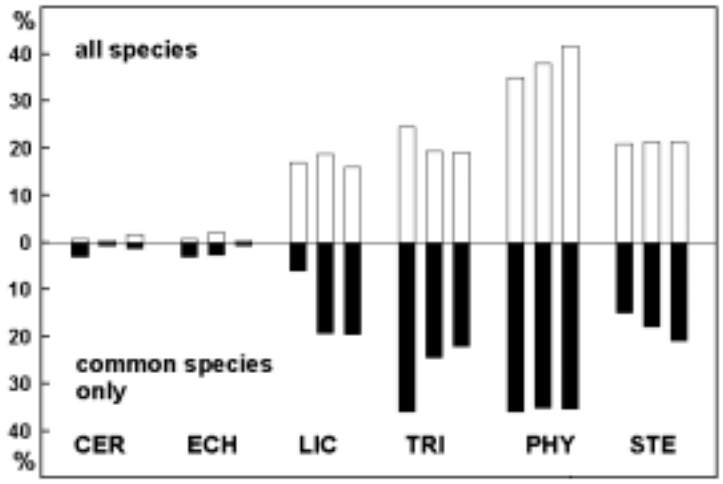

Figure 3 Proportional contribution of each order to the total myxomycete biota for high-latitude regions (first bar within each group of three), for Germany (second bar), and the Netherlands (third bar). For the upper half of the diagram (open bars) all species recorded for each region are considered (150 for high-latitude regions, 319 for Germany, and 245 for the Netherlands). In the lower half of the diagram (closed bars) proportions are given only for the regularly occurring species (34 for high-latitude regions, representing widely distributed species recorded from at least five study areas; 151 for Germany, categories G, *, and ** of the preliminary Red List (Schnittler et al., 1996); and 149 for the Netherlands, all species recorded more than three times (Nannenga-Bremekamp, 1991). Abbreviations used for the orders of Myxomycetes are CER = *Ceratiomyxales*, ECH = *Echinosteliales*, LIC = *Liceales*, TRI = *Trichiales*, PHY = *Physarales*, and STE = *Stemonitales*.

Table 2 Summary data for specimens of myxomycetes collected in the field and obtained from moist chambers (abbreviated as 'mc') for the twelve study areas. Since more than one myxomycete species may occur in a given moist chamber, the number of specimens obtained from a set of moist chambers for a single study area is usually higher than the total number of positive moist chambers. Exceptions may occur in study areas where many moist chambers were prepared with litter, because these moist chambers often have high proportions of plasmodia that cannot be induced to fruit. These non-fruiting plasmodia remain unindentified and are not considered in the numbers of specimens from moist chambers. Moist chamber data could not be reconstructed from the literature for Greenland and Iceland and are therefore not included in the totals given in the last column. ND - no data.

Study area	IC	KM	PU	YP	PP	TP	MG	CH	SP	CA	NA	GR	Total
wood: mc positive	ND	3	9	0	10	56	-	14	-	-	-	ND	92
mc prepared		7	11	1	14	83		22					138
% positive		*43*	*82*	*0*	*71*	*67*		*64*					*67*
bark: mc positive	ND	9	32	0	17	37	12	27	24	2	2	ND	162
mc prepared		71	37	7	19	61	15	32	27	5	9		283
% positive		*13*	*86*	*0*	*89*	*61*	*80*	*84*	*89*	*40*	*22*		*57*
litter: mc positive	ND	5	13	9	3	20	17	19	71	45	89	ND	291
mc prepared		32	19	25	14	49	33	31	139	61	142		373
% positive		*16*	*68*	*36*	*21*	*41*	*51*	*61*	*51*	*74*	*63*		*78*
dung: mc positive	ND	1	4	-	1	6	-	9	-	0	7	ND	28
mc prepared		13	6		5	25		12		3	14		78
% positive		*8*	*67*		*20*	*24*		*75*		*0*	*50*		*35*
total: mc positive	ND	18	58	9	31	119	29	69	95	47	98	ND	573
mc prepared	216	123	73	33	52	218	48	97	166	69	165	193	1,044
% positive	*ND*	*15*	*80*	*27*	*60*	*55*	*60*	*71*	*57*	*68*	*59*	*ND*	*55*
specimens from mc	125	18	101	16	76	249	29	111	84	56	95	83	1,043
field collections	207	101	22	0	27	14	62	68	100	73	14	245	933
number of species	48	40	35	11	29	48	31	48	54	43	25	54	150
number of genera	21	20	19	6	15	22	21	23	26	21	17	26	39
species / genus ratio	2.2	2.0	1.8	1.8	1.9	2.1	1.4	2.0	2.0	2.0	1.4	2.0	3.8

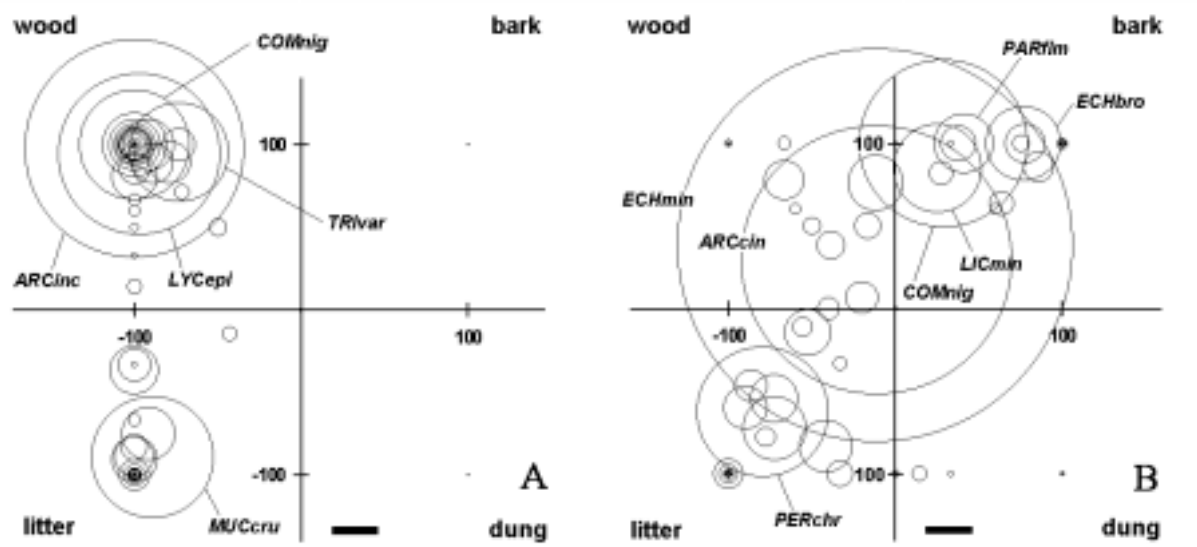

Figure 4 Ordination plot showing substratum preferences and total abundances for species represented by specimens obtained as field collections (A) and/or recorded from moist chambers (B). Each circle represents a particular species, with the diameter of the circle corresponding to the total number of specimens recorded for this species (bar = ten specimens). The position of the circle in the total space defined by a quadrate representing the four substratum types provides a measure of the degree of substratum specificity, e.g. a species occurring exclusively on bark would be found in the upper right (coordinates 100, 100), whereas one having half of the collections on bark and half on wood would be located in the upper middle (coordinates 0, 100). Abbreviations for species names are composed of the first three letters of the genus name (capitals) and epithet (small letters, compare Table 1).

bryophytes. In a few instances, a particular myxomycete seemed to display a preference for bryophytes. *Mucilago crustacea* occurred in association with low-growing vascular plants in open vegetation with bryophytes present and sometimes abundant, and the sporocarps of *Diderma deplanatum* Fr. often developed upon bryophytes in moist chambers prepared with samples from northern Alaska. However, this may reflect more of a coincidence (substratum moisture favours both groups of organisms) than a preference (Stephenson & Studlar, 1985). Since plasmodia usually choose elevated microsites in their habitats for forming fructifications, they might appear more often than expected by random upon bryophytes and lichens protruding the substratum surface.

Figs. 5A and B present absolute abundances (collection numbers) as well as substratum preferences for all species from field collections and from moist chambers, respectively. Species represented by field collections show a relatively high substratum specificity for either wood or for litter, with only a few species utilising both substrata to a similar extent (Fig. 4A). Common species confined almost exclusively to wood were *Arcyria incarnata* (Alb. & Schwein.) Cooke (wood 98 field collections/13 specimens obtained from moist chambers, bark -/9, litter 1/1, and dung -/2) and *Lycogala epidendrum* (wood 71/-, bark 1/-, litter 2/-). Interestingly, *Enteridium splendens* var. *juranum* (Meyl.) Härk. (wood 13/-), another species typically forming large fructifications on wood, was also fairly common. In contrast, species appearing in moist chambers usually show less substratum specificity (Fig. 4B). The two most common species (largest circles in Fig. 4B), *Echinostelium minutum* and *Arcyria cinerea*, are nearly ubiquists. As already noted, species typically occurring on wood do not well grow in moist chambers, and only a few of the more common species are specialists for either bark or litter. Examples are *Echinostelium brooksii* Whitney (wood -/4, bark -/30), and *Paradiacheopsis fimbriata* (G. Lister & Cran) Hertel (wood -/8, bark -/19). Litter was the predominant substratum utilised almost exclusively by only three of the more common species, and all other species recorded predominantly from litter are rare. Common litter species were *Physarum cinereum* (Batsch) Pers. (wood 2/-, bark 1/-, litter 21/3, dung -/2), *Physarum bivalve* Pers. (bark -/2, litter 4/15, dung -/7), and *Trichia munda* (wood 1/1, bark -/3, litter 5/24, dung -/1). Dung, as the substratum with the lowest species yield in this study, lacks any specialised species. The only species found most often on dung was *Didymium difforme* (Pers.) S.F. Gray (litter -/3, dung 1/4).

An interesting result of the present study is the occurrence of nivicolous (snowbank-associated) myxomycetes in the far north. In at least 3 of the 12 study areas, collections were made from obviously nivicolous situations (see Table 1), and 12 species were found predominantly in nivicolous situations. Most of these are rare, recorded only from 1 or 2 study areas, but a few species that are predominantly cryophilous were found to be fairly common. Prominent examples are *Didymium dubium* Rostaf. (recorded from 8 study areas), *Lamproderma sauteri* Rostaf. (4 areas), and *Prototrichia metallica* (Berk.) Massee (4 areas). The Khibine Mountains exhibited a whole biota of

nivicolous myxomycetes (Novozhilov & Schnittler, 1997), which suggests that these species also can be expected in other arctic regions.

How unique is the biota?

As to be expected for harsh environments, only about 20 % of the 150 species recorded in this study can be regarded as regularly occurring at high latitudes. Almost all of the 33 species widely distributed in high-latitude regions also are well-known also from boreal and temperate regions. Consequently, the arctic and subarctic myxomycete biota can be regarded as a depauperate version of that characteristic of the temperate zone. This conclusion is supported by consistently low species/genus (S/G) ratios for the 12 study areas investigated, where the calculated values varied from 1.4 to 2.2 (Table 2). Only the figure for the whole circumpolar region is considerably higher, reflecting mostly single reports of species typical for all of the temperate zone accumulated from all of the study areas (Table 1). These values are rather low when compared with those calculated for the myxomycete biotas of temperate and tropical areas, where S/G values usually range from 2.2 to 4.6 (Stephenson et al., 1993).

Compared to most other organisms, myxomycetes show very little evidence of endemism (Stephenson et al., 1993). Except for the seven taxa for which identification to species was not possible, all of the species listed in Table 1 also have been recorded from temperate regions of the world, and many of these also are known from tropical or subtropical regions (Martin & Alexopoulos, 1969). However, a few species appear to have distributions centred in high-latitude regions of the world. Possible examples include *Echinostelium brooksii*, rarely recorded elsewhere but found in 3 of the 12 study areas; *Trichia lutescens* (Lister) Lister (8 areas); and the closely related *Trichia flavicoma* and *T. munda*, together registered from 9 study areas. *Trichia flavicoma* was found to be fairly common in Alaska, whereas *T. munda* occurred throughout Eurasia from Greenland to the Chukchi Peninsula. Consequently, with further investigation, a certain degree of distinctiveness for the arctic and subarctic myxomycete biota may be recognised.

Possible distribution limits

If the hypothesis is accepted that species richness of myxomycetes decreases with increasing latitude, then the question of possible distribution limits for these organisms arises. Two main factors are conceivable as providing limits to the northernward distribution of myxomycetes – availability of suitable substrata and climate. Obviously, at a certain latitude the increasing severity of the climate leads to the disappearance of almost all plant species providing substrata for myxomycetes. Hence, the question becomes one of whether the myxomycetes or the plants providing their substrata and in turn the nutrients for the food organisms (mainly bacteria) utilised by myxomycetes drop out first.

Because of the inherent resistance of the various dormant stages (microcysts, sclerotia, and spores) in the life cycle of a myxomycete, low winter temperatures would seem to be a relatively unimportant factor. Indeed, the Taimyr Peninsula, with the most extreme winter temperatures of all the study areas, was not only rich in species but also harboured *Cribraria violacea* Rex, whose distribution is apparently centred in submeridional to tropical regions. A possible explanation may be the mean summer temperature, since for approximately one month temperatures are high enough to allow myxomycetes to complete their life cycle. Interestingly, even species developing large, compact fruiting bodies occur far to the north. Examples are *Lycogala epidendrum* (recorded from 11 study areas), *Mucilago crustacea* (9 areas), and *Enteridium splendens* var. *juranum* (3 areas). Two of these three species are wood inhabitants, whereas *Mucilago crustacea* was frequently observed in pure tundra regions, emerging from thin mats of raw humus and litter, sometimes covered with bryophytes and lichens (Stephenson & Laursen, 1993). Seemingly, this would be an example of a species with a distribution not limited by substratum availability and probably accepting a wide range of food organisms.

Substratum availability seems to affect first those species specialised for living on wood or the bark of living trees, since beyond the northern timberline larger logs disappear and only shrubs, the majority of which have relatively smooth bark, are present. Consequently, substratum availability might be the limiting factor for a wood-associated species like *Lycogala epidendrum*. A lone record from the island of Spitsbergen (ca. 78 ° N) seems to support this hypothesis. Here, *L. epidendrum* was found on the decaying remnants of a former log house, where the wood had been brought in by man (Elvebakk et al. 1996). Bark as a substratum seems to impose limits upon the number of species present by the high acidity of the bark of almost all trees and shrubs investigated. For the Taimyr Peninsula, pH ranges recorded for moist chamber samples collected from the most common trees and shrubs were 2.6 - 4.7 for *Larix gmelinii* (46 collections, mean 3.7 ± 0.1); 3.5 - 5.9 for *Salix* spp. (14 collections, mean 4.8 ± 0.2); and 4.7 - 6.4 for *Duschekia fruticosa* (9 collections, mean 5.6 ± 0.2). Probably, for many corticolous members of the *Physarales* and *Echinosteliales* that are adapted to higher pH values, this is a major limiting factor. In contrast, litter as a substratum is available as far north as shrubs (e.g. *Betula nana*) occur. Indeed, even in pure tundra regions, this substratum harbours myxomycetes. However, as already noted, very few species occurred regularly on litter. The most common examples were *Physarum bivalve*, *P. cinereum*, and *Trichia munda*. Compared with temperate regions, the arctic and subarctic biota is obviously depauperate for this ecological group. Evidence for a possible explanation is provided by the long development times recorded for litter-inhabiting species in moist chambers prepared with litter from the Taimyr Peninsula and the Putorana Plateau. *Physarum bivalve* had a development time ranging from 26-40 days (mean = 34 days, n = 7) and

Table 3 Pairwise comparisons of myxomycete biotas among the 12 study areas. Both coefficient of community indices (upper right) and numbers of species shared in common (lower left) are given. Abbreviations for study areas are the same as those used in Table 1.

	IC	KM	PU	YP	PP	TP	MG	CH	SP	CA	NA	GR
IC	***	0.34	0.48	0.20	0.42	0.42	0.35	0.50	0.45	0.40	0.30	0.55
KM	15	***	0.29	0.20	0.41	0.34	0.37	0.41	0.36	0.39	0.31	0.34
PU	20	11	***	0.30	0.44	0.58	0.52	0.67	0.43	0.49	0.30	0.49
YP	6	5	7	***	0.35	0.34	0.19	0.27	0.22	0.26	0.17	0.28
PP	16	14	15	7	***	0.55	0.43	0.44	0.36	0.42	0.22	0.46
TP	20	15	24	10	21	***	0.48	0.63	0.47	0.53	0.30	0.47
MG	14	13	17	4	13	19	***	0.53	0.54	0.55	0.25	0.42
CH	24	18	28	8	17	30	21	***	0.51	0.49	0.30	0.53
SP	23	17	19	7	15	24	23	26	***	0.67	0.33	0.50
CA	18	16	20	7	15	24	20	22	32	***	0.42	0.44
NA	11	10	9	3	6	12	7	11	13	14	***	0.33
GR	28	16	22	9	19	24	18	27	27	21	13	***

Trichia munda one ranging from 22-40 days (mean = 35 days, n = 6) (Novozhilov & Schnittler, unpubl. data). These development times are so long that a temperature limitation imposed by the short arctic summers cannot be ruled out. As such, the distribution of litter-inhabiting myxomycetes may be limited much more by climate than by substratum availability.

In general, myxomycetes are thought to have very large distributional ranges, and many species appear to be cosmopolitan or nearly so (Martin & Alexopoulos 1969). However, the data presented by Stephenson et al. (1993) as well as in this paper provide evidence that spatial distribution patterns of myxomycetes can be successfully related to differences in climate and/or vegetation. The overall high degree of similarity among the 12 study areas (expressed as coefficient of community indices in Table 3) certainly suggests that most species of myxomycetes have high dispersal capabilities. As pointed out by Eliasson (1991), species endemic to islands or other geographically isolated areas seemingly do not exist for the myxomycetes. With three exceptions, the average for the coefficient of community values that result from pairwise comparisons of one study areas with the eleven others ranges from 0.40 to 0.49. Exceptional in this regard were the Khibine Mountains (0.35), with a high proportion of nivicolous myxomycetes, the obviously underinvestigated Yamal Peninsula (0.26), and Northern Alaska (0.29), with extremely severe climatic conditions.

As additional data sets like the one presented herein or already generated for several other regions of the world (e.g., Stephenson et al., 1993, Lado, 1994) become available, it should be possible to assess biogeographical relationships and patterns of biodiversity for myxomycetes on a global basis as has been attempted for dictyostelid cellular slime moulds (Cavender, 1973, Swanson et al., 1999) and many other groups of organisms.

ACKNOWLEDGEMENTS

A major portion of this study was carried out while the second and third authors were visiting professors at Fairmont State College. The visit of the second author was made possible by a grant from the National Research Council. Field work in Alaska and Russia was supported by two grants (N 96-04-48209 and N 95-04-11790a) from the Russian Foundation for Basic Research (RFBR) and two grants (3974-88 and 5487-95) from the National Geographic Society. We are grateful to V. A. Mukhin for providing us with the opportunity to conduct field work in the Polar Ural Mountains and on the Yamal Peninsula. We acknowledge logistical support provided by the National Park Service in Alaska and by D. Bolsheianov of the Arctic and Antarctic Research Institute, St. Petersburg, Russia. Appreciation is extended to I. Yu. Kirtsideli, I. V. Cherniadieva, and E. Yu. Kuzmina (V.L. Komarov Botanical Institute, St. Petersburg) for collecting substratum samples for moist chambers in some areas of the Taimyr and Yamal Peninsulas.

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Karstenia 36: 19–40, 1996

The myxomycetes of boreal woodlands in Russian northern Karelia: a preliminary report

MARTIN SCHNITTLER AND YURI NOVOZHILOV

SCHNITTLER, M. & NOVOZHILOV, Y. 1995: The myxomycetes of boreal woodlands in Russian northern Karelia: a preliminary report. – Karstenia 36: 19–40. Helsinki. ISSN 0454-3402

Data on species composition and ecology of myxomycetes are presented for an island of the Keret Archipelago (66°16'N, 34°40'E) in the White Sea (Karelia, Russia). The area, which lies in the middle boreal zone, contains all major vegetation types of Northern Karelia and was used as a model system for studying the myxomycetes of boreal woodlands. Ninety-two species of myxomycetes of 32 genera were registered with certainty, 12 of these new for Russia. Four species (*Arcyria magna*, *Lamproderma gulielmae*, *Perichaena minor* and *Stemonitis nigrescens*) are recorded for the first time for Fennoscandia. Microhabitat preferences and abundance estimations are presented for all species. The influence of microhabitat availability and microclimatic conditions on distribution are discussed. This study reports comparable data for myxomycete diversity in the Russian part of Fennoscandia. The mean species per genus ratio of 2.88 indicates a high taxonomic diversity of myxomycetes on the island. Comparisons with other well-studied areas show highest coefficients of community with the boreal parts of Finland (0.62) and Sweden (0.55).

Key words: fungi, myxomycetes, North Karelia, species diversity

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Introduction

As shown by several studies in Alaska (Stephenson & Laursen 1993) and Scandinavia (Eliasson & Strid 1976, Härkönen 1979a, b, Schinner 1983, Johannesen 1984), the northern boreal zone seems to be one of the regions with the highest richness in myxomycetes. In contrast to the Scandinavian countries, which are relatively well studied, data about distribution and abundance of myxomycetes in northern Russia, the region occupying the greatest part of the boreal zone, are almost totally lacking. Some myxomycetes from the Russian part of Karelia were collected by Karsten (1866) and Hintikka (1919). The work reported here is the first part of a project studying myxomycetes in northern Russia. The data presented for the White Sea region will also help to elucidate the distribution patterns of myxomycetes world-wide.

Objectives and tasks of the survey

For the purposes of carrying out a quantitative biogeographical analysis of myxomycete biodiversity we adopted three principles.

1) Size and comparability: To provide comparable data, study areas should be of approximately equal and minimal size, while still including all vegetation types of the region.

2) Thoroughness of investigation: To provide the full species inventory, a systematic survey of all suitable microhabitats should be carried out together with moist chamber experiments.

3) Repeated survey: To ensure the recording of all phenological groups, at least two field surveys in a year are necessary.

On basis of these principles one of the small islands of the Keret Archipelago, Sredniy Island, was chosen for the study. Geology, soil and plant communities are representative for nearby Karelian areas and the adjacent islands. The main tasks of the work were:

1) to reveal the species diversity;

2) to compare it with that of neighbouring and remote territories;

3) to study the distribution of myxomycetes in the main plant communities of the island and the influence of some ecological factors on this distribution.

Materials and methods

The field work was carried out during three fortnightly periods in July / August 1993, the first half of September 1993 and in July / August 1994. Some data from adjacent islands were pooled with that from the main area of investigation, the Sredniy Island. All vegetation types were thoroughly examined. Common and easily recognized myxomycete species were only occasionally collected, but rare species and species not easy to recognize in the field were always collected. We defined all sporocarps that could arise from one plasmodium as one specimen. In practice, we assumed that sporocarps that share the same substrate and are separated by a distance that could be overcome by a migrating plasmodium belong to the same plasmodium. This reflects the biology of myxomycetes and is already accepted in some ecological and biogeographical works (Eliasson 1981, Stephenson 1988). From almost all collections, sporocarps were preserved as permanent slides in polyvinyl lactophenol and/or glycerol gelatin, to distinguish between limeless and lime-containing structures. In several cases, sporocarp structures were studied with a JEOL 35c scanning electron microscope at St. Petersburg. Samples for the moist chamber experiments were taken from the bark of each tree species on the island, especially from *Juniperus communis*, *Picea obovata* and *Populus tremula*, and also from litter of various herbaceous plants, mainly *Epilobium angustifolium*. Fifteen samples were taken from the frequently occurring faeces of willow grouse (*Lagopus* spec.) and capercaillie (*Tetrao urogallix*). A total of 125 moist chamber experiments were carried out. Moist chamber cultures were prepared as described by Härkönen (1977a, 1981a) and Stephenson (1985, 1989). To compare the species inventory of different territories or habitats, the Coefficient of Community (CC) was used as explained by Stephenson et al. (1993). The formula is based on the presence or absence of species; therefore the value of CC ranges from 0 (the data sets share no species) to 1.0 (all species are present in both data sets). As an indicator for species diversity we used the mean number of species per genus (S/G). A lower value for S/G implies a greater floral diversity than a high value, assuming an equivalent degree of investigation (Schmidt 1980, Stephenson et al. 1993).

Study area

The investigated area forms a part of the Keret Archipelago in the White Sea (66°12'-66°26' N, 34°30'-35°00' E), situated ca. 120 km south of the Polar Circle (see Fig. 1A). The most thoroughly investigated Sredniy Island (66°16' N, 34°40' E) covers about 30 square kilometres. The island is formed of archaic metamorphic rock, predominately granite and gneiss, often appearing as naked rocks and cliffs on the sea shore. The whole island is not more than 60 m above sea level. The climate is predominatly continental but with some oceanic influence. The mean annual rainfall is about 350 mm and the mean annual temperature is -0.2°C. The first snow falls in mid-September. A relatively stable frost period extends from the middle of November until April, but extended thaws may occur due to influence of warm air from the Atlantic Ocean. The snow cover in the forests may be up to 1.5 m. The period without frost is about 120 days, beginning in May and ending at the beginning of October. Because of the variable relief, producing rocky and dry woodland in elevated areas and damp woodland and mires in depressions, the diversity of vegetation is high (see schematic map in Fig. 1B). Except the extrazonal coastal tundra on very small islands of the archipelago (locally called "ludy"), all vegetation types also occur on Sredniy. Moreover, wood remnants from a timber factory form a special habitat attracting wood-inhabiting myxomycetes. Thus the island provides all potential myxomycete habitats of northern Karelia.

Vegetation and habitats. The following short description of the main vegetation types covers

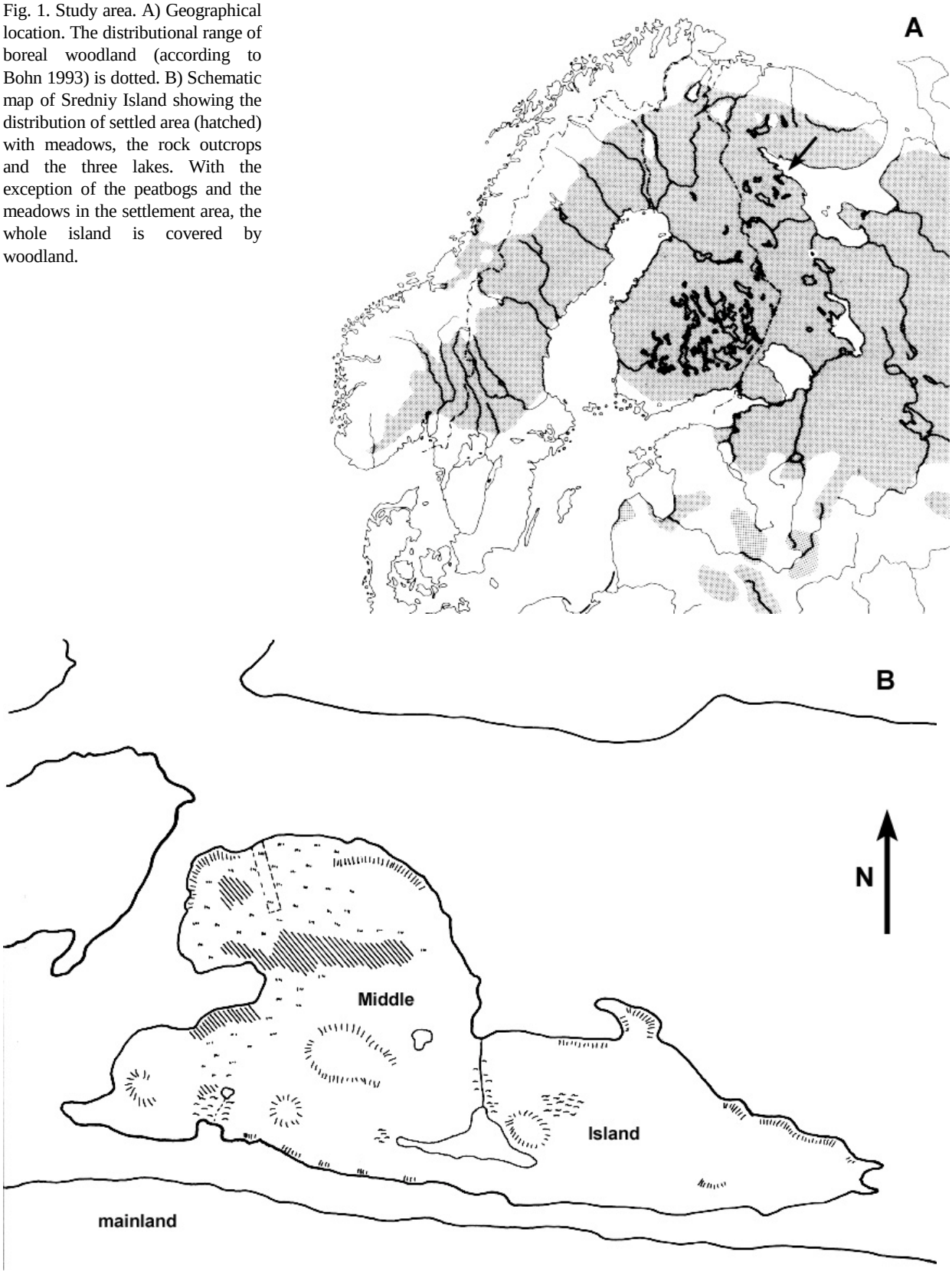


Fig. 1. Study area. A) Geographical location. The distributional range of boreal woodland (according to Bohn 1993) is dotted. B) Schematic map of Sredniy Island showing the distribution of settled area (hatched) with meadows, the rock outcrops and the three lakes. With the exception of the peatbogs and the meadows in the settlement area, the whole island is covered by woodland.

only those aspects that are of interest for the habitat description of myxomycetes. Nomenclature of the vascular species follows Flora Europaea (Tutin et al. 1964), the English names are used as in Stace (1991). For the few mosses and lichens mentioned the authors are given. The vegetation cover is characterized by spruce and spruce-pine woodland (30% of the area), dry pine-lichen woodland on rocky ground (ca. 15%) and damp spruce-birch-aspen woodland in the depressions (ca. 10%). Pure aspen stands are lacking. About 30% of the area are man-made meadows and a pioneer community of various willow (*Salix*) species, birch and willowherb (*Epilobium*). A further 10% are natural, damp meadows on coastal bays and blanket peat bogs in the inland depressions, seemingly bearing no myxomycetes. A brief description of the main habitat types follows.

Pine-lichen woodland. A very dry, open woodland with scattered, small pines (*Pinus sylvestris*) and a lot of lichens, eg. *Cladonia mitis* Sandst., *C. rangiferina* (L.) Weber ex Wigg., *C. stellaris* (Opiz) Pouzar & Vezda on the higher, rocky parts of the island. The water retention is low and it is moist only after rainfalls. Many of the pine trees have been blown down by wind, so numerous fallen trees and branches lie on the rocks.

Pine-spruce woodland rich in herbaceous plants. A medium-moist woodland, mainly with spruce (*Picea obovata*), also pine. The spruce trees are relatively thick, up to 80 cm stem diameter forming an almost closed canopy. Juniper (*Juniperus communis*) commonly occurs on more open places. The peeling bark of its stems up to 8 cm thick provides a very good substrate for corticolous myxomycetes. A rich vegetation of herbaceous plants, e.g. *Geranium sylvaticum, Vicia sylvatica*, and many *Pyrolaceae* forms a dense closed cover on the ground. This vegetation, up to 50 cm high, retains much dew in the autumn, producing the requisite moisture for myxomycetes. The fallen trees are mainly shaded, so decay proceeds faster than in the pine-lichen woodland.

D*amp, moss-rich spruce woodland.* A shady, very damp woodland type on turfy soils in depressions, often growing in close contact with the spruce-birch-aspen type (see below). The main tree is spruce and on the ground moss pillows predominate, typically with *Sphagnum girgensohnii* Russ. Scattered higher herbaceous plants occur, eg. *Carex loliacea* or *Viola epipsila*. Fallen trees often lie very wet on *Sphagnum* and decay quickly.

Spruce-birch-aspen woodland. The prevailing trees are spruce, aspen (*Populus tremula*), birch (*Betula pubescens*) and alder (*Alnus incana*). This woodland type usually occurs in depressions near lakes. In the lower storey a few bushes of rowan (*Sorbus aucuparia*), willows (eg. *Salix caprea*) and more rarely juniper are present. Aspen grows up to 30 m high, and its thick, scratched bark which is almost free of mosses and lichens, provides a microhabitat for corticolous myxomycetes such as *Perichaena* species. The large, often still erect trunks bear a persistent bark even while in progressive stages of decay. With the strongly decayed wood inside they offer a very suitable substrate for wood-inhabiting myxomycetes, eg. for *Diderma*. The forest canopy is almost closed, but more open than in the moss-rich spruce woodland. Three species of *Equisetum* are very frequent on the ground, but tall perennials are rare.

Pioneer community. This is a pre-woodland of willows (especially *Salix caprea* and *S. phylicifolia*), birch and willowherb (*Epilobium angustifolium*). This association is typical for disturbed places such as roadsides, devastated meadows and burned areas. Under dense stands of willowherb up to 2 m high, the previous years' stems lie deeply shaded, forming the main habitat for litter-inhabiting myxomycetes.

The old timber road. For several decades, up to the fifties, a timber factory was active on the island and a long plank road was built to the sea for transport and storage of the cut pine and spruce logs (see Fig. 1B). The thick, hollow layers of decaying timber are a unique attractor of wood-inhabiting slime moulds, acting as a 'natural moist chamber'. Recently, the pioneer community has begun to invade the timber road.

The species of myxomycetes

The following list includes all recorded species

in alphabetical order. The nomenclature follows Martin & Alexopoulos 1969, with a few exceptions for which references are given. In these cases the synonym according to this monograph is given. The abundance was estimated with a simple scale adapted from a percentage scale of Stephenson et al. (1993):

R - rare: recorded once or twice
O - occasional: recorded 3-5 times
C - common: 6-15 records
A - abundant: more than 15 records.

The species names are followed by the collection numbers of the first author (numbers of four digits, private collection) and/or the second author (numbers of five digits, herbarium St. Petersburg). The characters '...' at the end of the list stand for species that were so common that they were not always collected. Specimens whose determinations are considered by the authors as doubtful are given with the note 'cf.' (confirm). This often indicates scanty material or the remains of last-years fruitings. The abbreviation '(mc)' marks a specimen obtained from the moist chamber. For all species, short comments are given on ecology and microhabitat preference, and additionally for some rare and/or doubtful species, short taxonomic descriptions. Data for distribution within Russia will be presented in a furture paper (Novozhilov & Schnittler, in prep). Here species new to Fennoscandia are marked with two asterisks, those new to Russia with one.

A *Arcyria cinerea* (Bull.) Pers.: 5723(mc), 5730(mc), 5735(mc), 5740(mc), 5742(mc), 6759(mc), 47887(mc), 47890(mc), 47898(mc) ...

Regularly in moist chamber cultures with the bark of living trees, on almost all investigated tree species.

R *Arcyria denudata* (L.) Wettst.: 5755 = 47861

Only once collected from a decaying alder stem in damp spruce-birch-aspen woodland, unexpectedly rare.

R *Arcyria ferruginea* Sauter: 2719

Solely from one old log of pine or spruce; as in other regions not common on the island.

A *Arcyria incarnata* (Pers.) Pers.: 2706 = 47716, 2711 = 47690, 2715, 2729, 2791 = 47534, 2803, 5718(mc), 47382, 47543, 47363, 47712 ...

The most abundant species of the genus, preferring medium to strongly decayed wood of coniferous tree, only once on aspen or alder.

** * R *Arcyria magna* Rex: 2820 = 47400

A single, but large collection on a strongly decayed birch stem, in spruce-birch-aspen woodland.

Sporocarps densely crowded, but not gregarious, with up to 7 mm long expanding, red to pink plumes, short-stiped, the stipe filled with cysts 10-15 µm. Cup small, but deep; under the microscope evenly distributed, papillose warts up to 1.5 µm long appear inside. Plumes not firmly attached to the cup and easily blown away. Capillitium almost colourless under the microscope, ornamented with half-rings which are often spirally arranged. Spore mass red to pink, colourless in transmitted light, with irregularly distributed warts, 7.5-9.5 µm in diameter. The characters fit best *A. magna* var. *rosea* Rex.

C *Arcyria obvelata* (Oeder) Onsberg (1978), syn. *A. nutans* (Bull.) Grev.: 2720 = 47669, 2786, 2837, 5295 = 48396 ...

Seen only on coniferous wood, especially on the lower side of medium-decayed branches and stems.

C *Arcyria pomiformis* (Leers) Rost.: 2726, 2748 = 47533, 2756, 2843, 5296 = 48398 ...

As the previous species, but also capable of forming fruitings on small branches still with a solid and smooth surface.

R *Badhamia foliicola* Lister: 47563

Once on strongly decayed deciduous, moss-covered wood lying on the ground, in spruce-birch-aspen woodland.

R *Badhamia panicea* (Fr.) Rost.: 2815 = 47640

As the former species, on aspen.

* R *Badhamia populina* Lister & G.Lister: 5756 = 47346

On the bark of a thick, fallen spruce, moderately decayed. Sporocarps subglobose to ovoid, on short stipes or sessile, never plasmodiocarpous, 1-1.5 mm. Peridium white, rough and lime-incrusted; the brittle, eggshell-like lime layer

closely connected to the inner membranaceous layer. Dehiscence irregular. Capillitium coarse, typically 'badhamoid' as an isodiametric network of limy tubules. Spore mass deep dark brown, almost black, spores loosely clustered in groups of 15-20, clusters dissolving in the preparate, ovoid to globose-angular, coarsely warted and with a characteristic ridge around the spore, which is paler here than in other parts, diameter (9)-10-12-(16) µm.

R *Calomyxa metallica* (Berk.) Nieuwl.: 5757 = 47539

On strongly decayed wood of pine or spruce. Surprisingly, not yielded in moist chamber.

C *Ceratiomyxa fruticulosa* (Müll.) Macbr.: 2707, 2721 = 47635 ...

On strongly decayed wood, preferring the moist, lower side of old planks and stems.

R *Clastoderma debaryanum* A.Blytt: 47341, 47381 = 6768

In autumn after first frost, covering 2-3 square meters on the lower side of a moderately decayed but very moist plank, once together with *Licea minima*.

* A *Colloderma oculatum* (Lippert) G. Lister: 2766, 2774 = 47643, 2783 = 47622, 2810(cf.), 47591, 47359, 47474, 47422, 47473, 47476, 47477, 47480 ... (Figs. 2, 4)

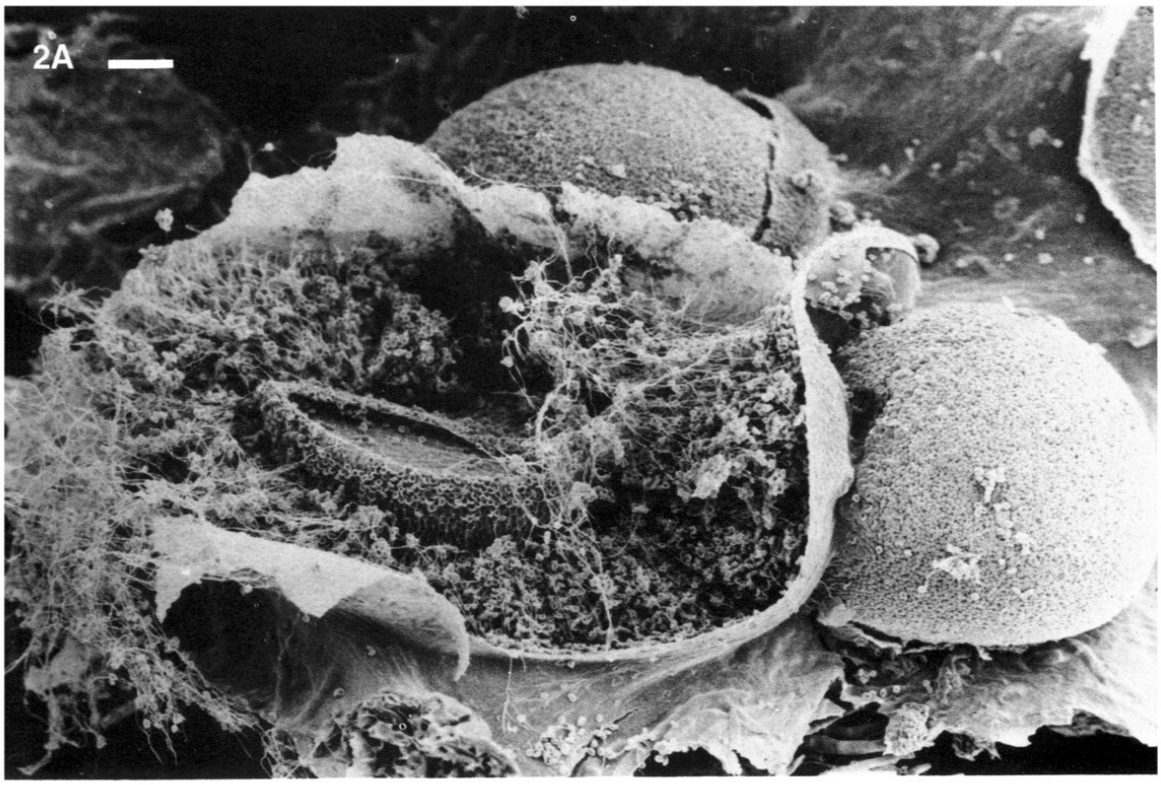
Locally very abundant with large, dense colonies of up to 150 sporocarps on 2-4 m high vertical rocks. Typically trickling water provides good conditions for a thin, slimy cover of liverworts and algae. Not occurring every year, absent in the dry summer of 1994. Development proceeds slowly; in 1993 marked plasmodia showed no visible change during two weeks. No records from wood or bark. Sporocarps form small up to very large, dense groups, globose to subglobose, sitting on a broad, gelatinous, stalk-like layer, 0.6-1.5 mm in diameter. At first white, they change to black with maturity; finally the gelatinous layer dehisces, showing the just iridescent peridium which is single, translucent, colourless in transmitted light, almost smooth. At the base is a flat but large and disc-like columella (see Fig. 2A). The capillitium rises from this columella and often is attached to the peridium. It consists of flexuous, thin threads, which are pale violet, often with darker, up to 1 µm thick granula, rather dichotomously branched, rarely anastomosing, without translucent sheet. The spore mass is almost black, violet brown under transmitted light, globose to slightly ovate, (11)-12-13-(16) µm, covered with not very regularly distributed, distant and up to 0.6 µm long spinulae (Fig. 2B, C). Some collections differ in a more cartilaginous and duller peridium and somewhat larger spores. These features are described for *C. robustum* Meylan, but considering the consistency of the sporocarps, we assume that they are not fully mature forms of *C. oculatum*. One scanty collection (2810, Fig. 4) of scattered sporocarps was found in a deep and fully shaded cavity under the timber road. The substrate was slimy wood without bark, covered with algae and liverworts. Water on the floor of the cavity, perhaps in connection with the sea, provides cool and damp conditions. This collection differs from the typical form in its smaller (0.3-0.5 mm) sporocarps, which are black with metallic reflections due to the very thin, translucent peridia (Fig. 4A, B). The sporocarps were fully mature and probably had already hatched off the gelatineous layer, exposing the very thin and iridescent true peridium. Here no columella was found. The capillitium is almost colourless, arising from the base, forming a large-meshed net, the tubulae hollow under SEM (Fig. 4D), up to 1.5 µm in diameter, smooth. The same minute, scattered fructifications, also on wood, were seen in the German Alps.

R *Comatricha dictyospora* Celak.: 2840

Once, on bark of a fallen spruce.

———

Fig. 2. SEM-photos of *Colloderma oculatum* (2783 = 47555). A) Three sporocarps, one open showing capillitium and columella. Bar = 100 µm. B) Detail of spore ornamentation. Bar = 1 µm. C) Spore. Bar = 1 µm. Photos Y. Novozhilov.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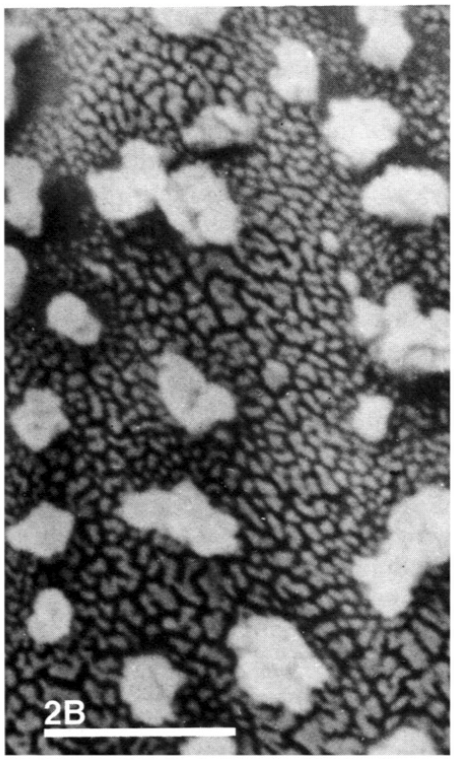

2B


2C

A *Comatricha elegans* (Racib.) G.Lister: 47573, 47575, 47605, 2738 = 47604, 2751 = 47841, 2795 = 47621, 2821, 5298 = 48403 ...

One of the most common species on the island. Often large fruitings on the lower side of big, fallen stems without bark, up to some thousands of sporocarps covering several square decimetres. Only seen on spruce and pine, often associated with *Arcyria pomiformis* and *Licea minima*.

Two varieties are present on the island: the long-stiped var. *elegans* (stipe up to 2 mm) and the shorter-stiped var. *pallens* (stipe 0.5-0.8 mm). The long-stiped variety seems to be the commoner.

A *Comatricha laxa* Rost.: 2725, 2746 = 47627, 2753 = 47851, 2772 = 47308, 2794, 2822 = 47410, 2834 = 47623, 47652, 47678 ...

Very frequent, also with strong preference for coniferous wood. Typically on small branches lying without bark on wet mosses, at Sredniy Island also on the timber road.

C *Comatricha nigra* (Pers.) Schroet.: 2708, 2709, 2720, 2737, 2741 = 47576, 2752, 2785, 5298 = 48403, 5728(mc), 5739(mc), 47339, 47458, 47569, 48391(cf.) ...

Shows the same preference as the two previous species but a wider microhabitat spectrum: also on bark of living pine, once collected on litter of willowherb.

One, small collection (2720) has sporocarps like *C. ellae* Härkönen (1977b, 1978), differing from *C. nigra* by smaller size (0.5-1 mm), shorter stalk and a well-developed surface net on the capillitium. The coppery colour typical of *C. ellae* is absent; our sporocarps are duller. The material is too scanty to be definitely identified as *C. ellae*.

O *Comatricha typhoides* (Bull.) Rost.: 2734, 2750, 2836, 48413

This species seems to be rarer on in Karelia than in the temperate zone. It prefers strongly decayed wood. Collected on alder, birch and on a horizontal plank, probably pine.

O *Craterium leucocephalum* (Pers.) Ditmar: 5758 = 47772, 47373, 47453, 47467, 47677, 47786

Occurring only in autumn on litter of *Epilobium* and on other herbaceous plants in the pioneer community.

C *Cribraria argillacea* (Pers.) Pers.: 2745 = 47380, 2777, 2797, 5285 = 48371, 5305 = 48419, 47492, 48401(cf.) ...

As typical for the genus, this species prefers strongly decayed wood of coniferous trees.

C *Cribraria aurantiaca* Schrad.: 2724 = 47350, 2733, 2792, 5290 = 48390, 5300 = 48408, 5304 = 48416, 47370 ...

The same microhabitat spectrum as the preceding species.

R *Cribraria cancellata* (Batsch) Nann.-Brem.: 2747 = 47371, 5289 = 48389

In spite of its strong preference for coniferous wood, surprisingly rare on the island.

C *Cribraria microcarpa* (Schrad.) Pers.: 2739, 2823, 5297 = 48402, 5297 = 48402, 5717(mc), 5744(mc), 6758(mc), 47351 ...

A probably abundant species on the island, since easily overlooked in the field. All records are from moderately decayed wood of coniferous trees, often from planks.

C *Cribraria minutissima* Schw.: 2790 = 47354, 5291 = 48392 ...

As for the previous species, but probably rarer.

O *Cribraria purpurea* Schrad.: 47781, 47785, 47790

All collections were found on the old timber road. It seems to be an autumn species requiring large, strongly decayed wood bodies, but then developing very extensive colonies, in one case covering about 20 square dezimeters.

R *Cribraria rufa* (Roth) Rost.: 5759 = 47343, 47702

Two collections in autumn, also on decayed coniferous wood. In contrast to the temperate zone rare on the island.

R *Cribraria splendens* (Schrad.) Pers.: 2804 = 47348

Once, on old coniferous planks in the pioneer

community on the margin of the timber road.

O *Cribraria vulgaris* Schrad.: 2735 = 47385, 2743, 2839 = 47390, 47352

Also one of the rarer species compared with the temperate zone; all collections on coniferous wood.

R *Diacheopsis* spec.: 2732 = 47686 (Fig. 3)

The collection was made on a stem of pine or spruce, lying on the grass of a small, natural meadow at the margin of a woodland near the seashore but not salt-influenced. We believe that the material belongs to an undescribed species, but our material (one colony of about 100 sporocarps) is not sufficient for a description. Sporocarps in a dense colony, but not gregarious; sessile, subglobose, oval, black without metallic reflections, up to 1.5 mm in diameter (Fig. 3A). Hypothallus thin, black to brown and separate for each sporocarp. Peridium membraneous, partly evanescent after dehiscence, remaining in the lower part of the sporocarp like a large collar. Columella absent. Capillitium radial arising from the base, branching and anastomosing with large meshes, forming a surface net with remaining free ends (Fig. 3C). Spores black in mass, black-brown by transmitted light, 11-12 µm in diameter, warted, the warts under SEM blunt to spinulose, partly coalescing (Fig. 3B, D). Plasmodium unknown. The form of the capillitium, failure of columella and structure of the capillitium clearly fit *Diacheopsis*, but the size of spores and the colour of the sporocarp differ from all described species (Kowalski 1975, Meyer & Poulain 1990).

* O *Dianema corticatum* Lister: 2796 = 47306, 5292 = 48395, 5777 = 47537, 5778 = 47538, 47307, 47500, 47547, 47590

Occurring in small colonies of depressed sporocarps on medium-decayed coniferous wood without bark. The yellowish, cartilagineous peridium is typical and allows previous-year's fructifications to be recognized.

* R *Diderma asteroides* (Lister & G.Lister) G.Lister: 2828 = 47559

Solely on a big trunk of aspen; the wood was strongly decayed and covered by very persistent bark.

C *Diderma globosum* Pers.: 5763 = 47443, 5764 = 47446, 5765 = 47502, 5766 = 47503, 5767 = 47550, 5768 = 47694, 5769 = 47775, 47445, 47487, 47460, 47546 ...

Common on the island, with a wide microhabitat spectrum from the decayed wood of several tree species to *Epilobium* litter in the pioneer community. Collected only in autumn.

O *Diderma radiatum* (L.) Morgan: 5770 = 47499, 5771 = 47509, 5772 = 47510, 5773 = 47398, 5774 = 47415, 47471

In contrast to the preceding species only collected on litter, also in autumn.

O *Diderma trevelyani* (Grev.) Fr.: 5303 = 48414, 5775 = 47448, 5776 = 47483, 47451, 47463, 47481

A further autumn species, seen only on willowherb litter in the pioneer community.

O *Didymium difforme* (Pers.) S.F.Gray: 5726(mc), 47454, 47455, 47501, 47688

Surprisingly rare on the island, only twice collected on litter in autumn, once appearing in the moist chamber on droppings of willow grouse (*Lagopus* spec.).

R *Didymium dubium* Rost.: 47894(mc), 47777

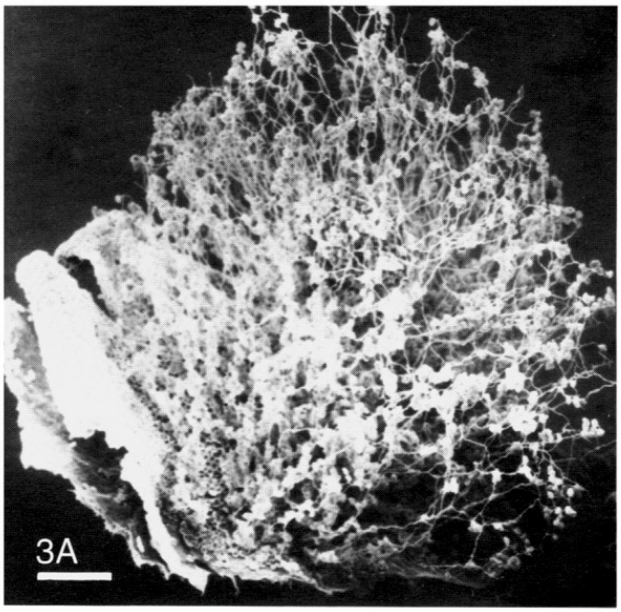
Occurring in autumn on litter of *Salix* and *Epilobium* in the pioneer community.

O *Didymium melanospermum* (Pers.) Macbr.: 2760 = 47299, 2768 = 47653, 2808 = 47655, 47345, 47773, 47365

In contrast to the other *Didymium* species with a weak preference for mosses, this species typically occurs on thick moss tussocks on soil or at the base of rocks, rarer on litter.

R *Didymium nigripes* (Link) Fr.: 2814, 5760 = 47494

Rare on the island, collected once in summer on bark of aspen and again on *Epilobium* litter in autumn.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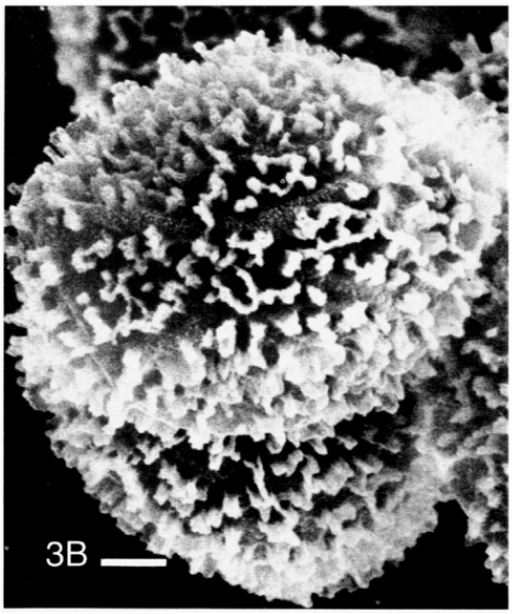
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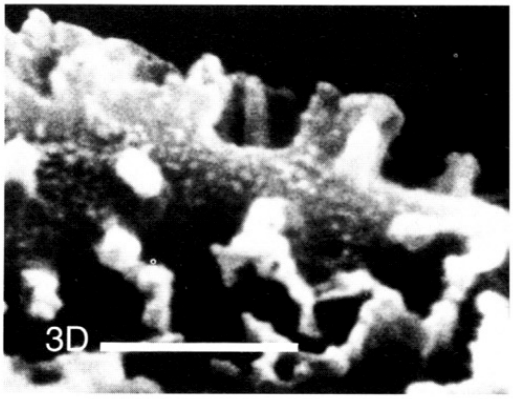
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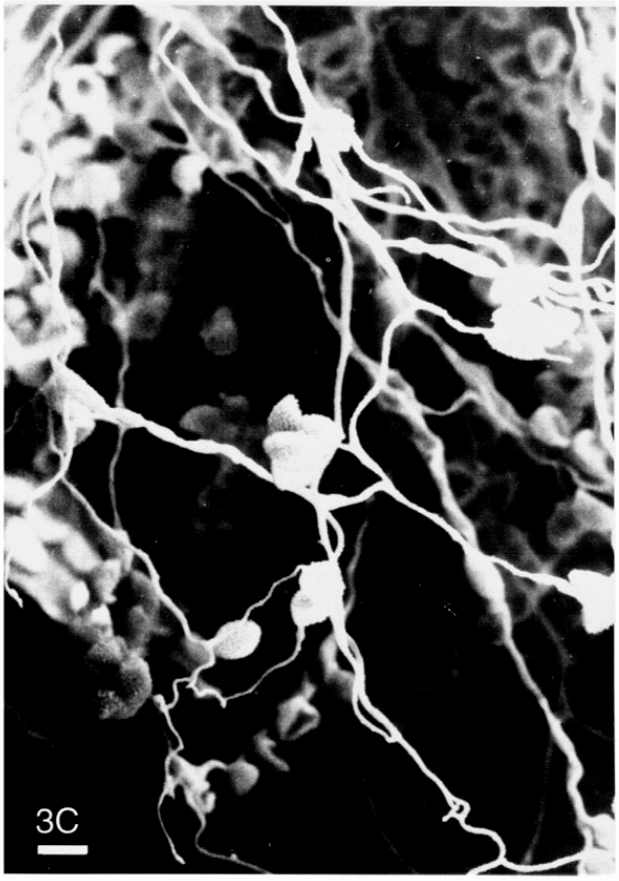
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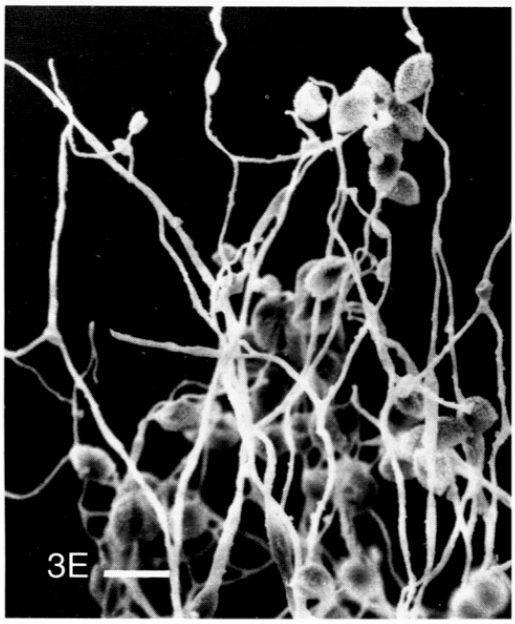
3E

C *Didymium squamulosum* (Alb. & Schw.) Fr.: 5761 = 47495, 5762 = 47511, 47464 ...

Occurring in autumn on litter, only seen in open places such as margins of the pioneer community or man-made meadows.

A *Echinostelium minutum* de Bary: 2831 = 47682(mc), 3222(mc), 5729(mc), 6761(mc), 47864(mc), 47906(mc) ...

Probably abundant on bark of living trees; regularly in the moist chambers, especially on juniper, also on aspen; not seen on the bark of coniferous trees.

A *Enerthenema papillatum* (Pers.) Rost.: 2713 = 47703, 2723, 2731, 2736, 5286 = 48373, 5733(mc), 6762(mc), 47536, 47714, 48410, 48417 ...

A very common species on moderately to strongly decayed coniferous wood, rather rare on bark of living pine.

R *Enteridium lycoperdon* (Bull.) Farr (1976), syn. *Reticularia lycoperdon* Bull.: 5797 = 47701

Surprisingly, only one small collection from litter in the pioneer community. According to Farr the generic name *Enteridium* should be used.

* R *Enteridium splendens* (Morgan) Macbr. var. *juranum* (Meylan) Härkönen (1979a), syn. *Reticularia jurana* Meylan: 48397

Found once in autumn, on strongly decayed wood and litter on the ground in the pioneer community.

C *Fuligo septica* (L.) Wiggers: 2712, 5299 = 48407, 48404 ...

Common, but not abundant on strongly decayed wood of the timber road, also on birch. All specimens belong to the nominate form or the var. *candida* (Pers.) R.E. Fries.

Fig. 3. SEM-photos of *Diacheopsis* spec. (2732 = 47686). A) Open sporocarp with capillitium, spores and remnants of the peridium. Bar = 100 µm. B) Spore. Bar = 1 µm. C) Detail of the wide-meshed capillitium. Bar = 10 µm. D) Spore ornamentation. Bar = 1 µm. E) Tips of capillitium. Bar = 10 µm. Photos Y. Novozhilov.

R *Fuligo leviderma* Neubert, Nowotny & Baumann (1995: 211): 2830

This recently described species was found once on the partially dead stem of a damaged birch at ca. 1 m height.

R *Hemitrichia clavata* (Pers.) Rost.: 47720

Only one collection on strongly decayed coniferous wood.

R *Lamproderma arcyrionema* Rost.: 5779 = 47526, 6766 = 47527, 47493

Only on litter in the pioneer community.

A *Lamproderma columbinum* (Pers.) Rost.: 2757 = 47574, 2758 = 47577, 2769 = 47571, 2775, 2798 = 47516, 47372, 47676 ...

All collections except one on moss-covered rocks. Often associated with *L. sauteri* and *Colloderma oculatum*, but preferring drier and thicker tussocks of mosses. One exceptional collection on slimy wood, in the same location as the scanty specimen of *Colloderma oculatum*.

** * R *Lamproderma gulielmae* Meylan: 5780 = 47615, 47717

In autumn, collected on litter of willowherb (*Epilobium*) and on leaves in the spruce-birch-aspen woodland.

* A *Lamproderma sauteri* Rost.: 2126 = 47581, 2759, 2769(cf.), 2781 = 47675, 2811(cf.), 2812 = 47613, 2826(cf.), 5781 = 47434, 5782 = 47779, 5783 = 47704 ...

The commonest *Lamproderma* on the island, like *L. columbinum* found on rocks and in the same association. As mentioned by Nowotny (1989), also our material is very variable. Stipes range from very short, almost sessile to half sporocarp diameter, spores 12-17 µm.

R *Leocarpus fragilis* Dicks.: 2780, 47680

On ground, mosses and litter, only seen in autumn.

O *Lepidoderma tigrinum* (Schrad.) Rost.: 5784 = 47383, 5785 = 47478 ...

An autumn species, also in the rock association and preferring the very wet, thin liverwort and algae cover. The typical, orange- to yolk-

coloured plasmodia are already seen in summer, but sporocarps occur only after the first autumn frosts and snowfalls, indicating a cryophilous species.

R *Licea castanea* G. Lister: 47668

One field collection on bark of dead pine.

O *Licea kleistobolus* Martin: 2832 = 47366(mc), 5724(mc), 6760(mc), 47888(mc) ...

More or less regularly in moist chamber cultures from bark of living *Juniperus*, more rarely of *Populus*.

A *Licea minima* Fr.: 2710, 2714 = 47310, 2718 = 47304, 2753, 2788 = 47406, 2799 = 47634, 5302 = 48411, 5307 = 48393, 5786 = 47695, 5737(mc), 47459, 47508, 47689, 48377 ...

An extraordinarily abundant species on wood, preferring the still solid surface of branches or planks without bark. Only on coniferous wood. The fructifications always have scattered sporocarps of variable size. Sometimes in association with the small *Cribraria* species.

R-O *Licea parasitica* (Zukal) Martin: 5750(mc) ...

Obtained once in moist chamber culture on dead bark of aspen. Some other, not fully mature records from other moist chamber cultures probably belong to this species.

C *Licea variabilis* Schrad.: 2716 = 47353, 2717, 2721, 5301 = 48409, 5787 = 47377, 47693 ...

All collections from more or less decayed coniferous wood.

O *Lindbladia tubulina* Fr.: 2833, 5308 = 48421...

Rare, but often with large fructifications, typical on litter of coniferous trees and on remnants on the roadways of the island. In 1994 on the latter substrate one aethalium has formed a patch of 30 square decimeters but dried out partly before maturation.

A *Lycogala epidendrum* (L.) Fr.: 2838, 47449, 47572, 48406 ...

Abundant on all strongly decayed wood rests on the island, no preference for coniferous or deciduous wood. One small specimen (47572) resembles strongly *L. exiguum*, but the SEM examination of the spore ornamentation showed smaller ridges (0.2-0.3 µm) and finer meshes (0.7-0.8 µm). Both characters are in the range of these for *L. epidendrum* (Eliasson & Sunhede 1980).

R *Macbrideola cornea* (G. Lister & Cran) Alexop.: 5752(mc), 6763(mc)

Two small, but typically developed groups of few sporocarps from the bark of living willow and aspen in the spruce-birch-aspen woodland, the second specimen together with *Perichaena minor*.

O *Paradiacheopsis fimbriata* (G. Lister & Cran) Hertel (1956), syn. *Comatricha fimbriata* G. Lister & Cran: 6764(mc), 47862(mc), 47911(mc)

The first specimen was obtained from bark of living willow in the spruce-birch-aspen woodland. The other two were from pine bark in the dry pine community on rocks, probably more common there than our results suggest.

R *Paradiacheopsis solitaria* (Nann.-Brem.) Nann.-Brem. (1967), syn. *Comatricha solitaria* Nann.-Brem.: 3139(mc)

Once, from living bark of juniper.

C *Perichaena chrysosperma* (Currey) A.List.: 3115(mc), 3132 = 47877(mc), 3146(mc), 47875(mc), 47881(mc) ...

Regularly found on living bark of aspen and juniper in moist chamber cultures, one of the most common corticolous species on the island. Surprisingly, the closely related *P. vermicularis* was not found.

O *Perichaena corticalis* (Batsch) Rost.: 2817 = 47758, 47342, 47868(mc)

Under loose bark of aspen, once from strongly decayed coniferous wood, once from bark of alder in moist chamber culture.

** * R *Perichaena minor* (G.Lister) Hagelst. var. *minor*: 3114(mc), 3119(mc)

Two specimens, both from bare bark of living aspen without any mosses or lichens.

* R *Physarum auriscalpium* Cooke: 47614

Once, from the already decayed bark of a fallen trunk of aspen in an old spruce-alder woodland.

R *Physarum bitectum* G.Lister: 5788 = 47709, 5794 = 47469, 47389

Collected in autumn, on litter of willowherb in the pioneer community.

R *Physarum bivalve* Pers.: 5789 = 47362, 47489

In the same locality and at the same time as the preceding species.

** * R *Physarum* cf. *carneum* G.Lister & Sturgis: 47551

One, very scanty collection on mosses.
Only six, scattered sporocarps, stalked and globose, total height 0.6-0.8 mm, diameter 0.5-0.6 mm. Hypothallus discoid, separate for each sporocarp. Peridium membraneous, slightly impregnated with yellow lime granules. Stalk cylindrical, stout, reddish-yellow, translucent in transmitted light, limeless. Capillitium consisting of short hyaline tubules, with angular nodes 40-45 µm in size, white. Columella absent. Spores dark brown in mass, brown by transmitted light, with blunt spinulae up to 1 µm, which are verrucose on top (SEM).

R *Physarum cinereum* (Batsch) Pers.: 5790 = 47450, 47444

On willowherb litter in the pioneer community.

C *Physarum contextum* (Pers.) Pers.: 5793 = 47468, 5794 = 47469, 5795 = 47498, 5796 = 47517, 6765 = 47673, 47360, 47521, 47705, 47441 ...

All collections except one on litter in the pioneer community; once collected on strongly decayed coniferous wood.

O *Physarum decipiens* Curt.: 5716(mc), 5721(mc), 5745(mc), 47880(mc) ...

Sometimes recorded from moist chamber cultures, strongly preferring bark of living aspen, once from juniper. These preference was long ago mentioned by Fries (1912).

R *Physarum globuliferum* (Bull.) Pers.: 2800 = 47356, 5791 = 47295

Two records from moderately decayed coniferous wood partially moss-covered.

O *Physarum leucophaeum* Fr.: 2727 = 47298, 2827, 2842, 5720(mc), 5725(mc), 5749(mc), 47562

Surprisingly not very common on the island, on dead wood, mostly of aspen, more rarely on spruce, often associated with mosses. The records from moist chamber cultures result from mossy, living or dead bark of aspen.

R *Physarum leucopus* Link: 47765

One record from strongly decayed wood of *Populus tremula*.

A *Physarum nutans* Pers.: 2778, 2792 = 47642, 2805 = 47296, 2825, 2841, 5792 = 47364, 48380(cf.) ...

One of the commonest species on the island, on all kinds of well-decayed wood. Two records are from moss tussocks on rocks (see notes under *P. viride*).

O *Physarum oblatum* Macbr.: 2816 = 47561, 3116(mc, cf.), 3117(mc, cf.), 5722(mc), 5732(mc), 47303 ...

This species seems to be specialized on living bark. Recorded from aspen, but more often from juniper, not from pine nor spruce. It appears after only two to four days incubation in moist chamber cultures, but not all specimens were obtained fully mature.

O *Physarum virescens* Ditmar: 2813 = 47347 ...

While the bright yellow plasmodia of this species are very conspicuous, the brown-greenish fruitings may easily be overlooked. It prefers big moss tussocks on the ground, especially *Dicranum*; once recorded from a *Sphagnum* bog.

A *Physarum viride* (Bull.) Pers.: 2722 = 47636, 2761 = 47658, 2762 = 47321, 2763, 2764, 2767 = 47522, 2770 = 47631, 2776 = 47335, 2782(cf.), 2789, 2805, 2806, 2819 = 47421, 5754(mc), 47606 ...

Occurring on two substrate types: often on decayed wood of conifers, more rarely on deciduous trees, and on the moss and liverwort layers of rocks. Here it prefers medium-wet

places between the pure slimy algae layers and the big moss tussocks. In particular, the colour of the lime (ranging from orange to faded greyish yellow) and the spore diameter (ranging from 9.5 up to 14 µm) vary widely without relation to the microhabitat. Specimen 2805 fits well the description for *Physarum bethelii* (Hagelstein) Bilgram but due to the difficulty of separating *P. bethelii* from *P. viride* (see Marx & Schubert 1992), we hesitate to name this as a separate species. The colour of the lime (the most distinctive feature of *P. viride* var. *aurantiacum*, also recorded) probably has no taxonomic value and depends mainly on the availability of inorganic ions, as suggested by Aldrich (1982). The species concept of *P. viride* and *P. nutans* likewise should be scrutinized in this light.

O *Stemonitis axifera* (Bull.) Macbr.: 2730 = 47358, 2744, 5736(mc), 47399, 47793, 48405 (cf.)

This species is not very common but shows a broad spectrum of habitats, extending from living bark (juniper) to strongly decayed wood. One record from litter.

O *Stemonitis fusca* Roth: 2728, 2779 = 47336, 2818, 2829, 5727(mc), 5734(mc)

Another species inhabiting wood in all stages of decay. In moist chamber cultures forms resembling to *S. nigrescens* occurred. Specimen 2779, growing on moss tussocks in a spruce-birch-aspen woodland, can be assigned to var. *rufescens* Lister.

O *Stemonitis hyperopta* Meylan: 2749, 2753, 47588

All records from decayed wood. Two specimens have very small spores of 5-5.5 µm diameter, ornamentated with warts forming an incomplete net. These characters are close to *S. microsperma* B.Ing.

** R *Stemonitis nigrescens* Rex: 5798 = 47728

One record from dead aspen.

* R *Stemonitis virginiensis* Rex: 3140(mc)

One record from a moist chamber culture with bark of living juniper, after drying and rewetting of the culture.

R *Symphytocarpus confluens* (Cooke & Ellis) B.Ing & Nann.-Brem. (1967), syn. *Stemonitis confluens* Cooke & Ellis: 2742 = 47620, 5799 = 47679

Two records on very solid, cut wood of spruce without bark. The 30 cm thick stem pieces had lain relatively dry for one year. After a few nights outside the store, exposed to the night dew, coralloid, white plasmodia appeared on two pieces. After 10-24 hours aethalia were formed. In one case, a 2 cm thick piece of wood was sawn off to collect the specimen, and after three hours a new plasmodium occurred on the sawn surface. This strongly indicates that the solid inner wood is the microhabitat of the plasmodia.

O *Symphytocarpus flaccidus* (A.List.) B.Ing & Nann.-Brem. (1967), syn. *Stemonitis splendens* Rost. var. *flaccida* A. Lister: 2835 = 47610, 5310, 5731(mc, cf.)

A species with a broad microhabitat spectrum, recorded from litter as well as living bark and decayed wood of coniferous trees.

O *Trichia botrytis* (J.F.Gmel.) Pers.: 5800 = 47674, 47515, 47528, 48376(cf.)

Compared with the temperate zone rare on the island; all records from coniferous, strongly decayed wood of the old timber road.

O *Trichia contorta* (Ditmar) Rost.: 2754 = 47379, 2824, 5801 = 47486, 6769 = 47349

Three records from each of spruce, alder and birch, one from litter with small remnants of wood. Specimen 6769 with its long tapered capillitium tips (20-45 µm) falls under var. *attenuata* Meylan.

A *Trichia decipiens* (Pers.) Macbr.: 2740, 2771, 2773, 2793, 2802, 5284 = 48370, 5287 = 48374, 5288 = 48378, 47437, 47540, 47542, 47544, 47545, 47711, 47759, 47645 ...

The commonest *Trichia* on the island, on all kinds of moderately to strongly decayed wood and with a slight preference for conifers.

C *Trichia favoginea* (Batsch) Pers.: 2807 = 47651, 5802 = 47496, 47601, 47462 ...

Only the form with spores bearing a complete net of prominent ridges and prolonged

sporocarps was found (= *T. favoginea* s.str.). On strongly decayed wood, mostly from conifers, once from aspen.

* R *Trichia lutescens* (Lister) Lister: 2755 = 47679

One record under bark of a dead and moderately decayed, but still erect small birch in a spruce woodland.

R *Trichia cf. subfusca* Rex.: 5306 = 48420(cf.)

The single, scanty record is from previous-year remnants of sedges in a dense stand near a lake.

C *Trichia varia* (Pers.) Pers.: 5293, 47386, 47514, 47602, 47794 ...

Common, but more rare than *T. decipiens*; on all kinds of strongly decayed wood.

R *Tubifera ferruginosa* (Batsch) J.F.Gmel.: 2801 = 47684

Surprisingly rare, only one collection on the upper side of a strongly decayed spruce trunk of already spongy consistency.

Results and discussion

Besides the numerous myxomycete fructifications which were merely observed in the field, 348 collections were made in the investigation area. Sixty-one of these were made from moist chambers.

Ninety-three species of 32 genera were recorded with certainty. Two species represented by very scanty collections are regarded as doubtful. These, the newly described *Fuligo leviderma* and the undescribed *Diacheopsis* species are excluded from further analyses. If an adequate intensity of investigation can be assumed, the species/genera ratio of 2.88 indicates, first, a high taxonomic diversity of myxomycetes and, second, a high diversity of suitable microhabitats. The high degree (44%) of species classified as rare shows the difficulty of investigating the group in sufficient degree.

Comparison with other surveys

To estimate the representativeness of this survey for the myxomycete flora of the northern boreal zone, a comparison can be made with Finland (Härkönen 1979a, b, 1981b, 1989) and Sweden (Eliasson 1975, 1977, Eliasson & Lundqvist 1979, Eliasson & Strid 1976, Eliasson & Sunhede 1972, Fries 1899, 1906, 1910, 1912, Harling 1952, Santesson 1948, 1964). From the whole of Finland, 154 myxomycete species are known, and a further 14 are probable. If species recorded only in the southern biological provinces of Varsinais-Suomi and Uusimaa (belonging to the northern temperate zone) are excluded, 126 species remain. A compiling of the published Swedish records yields 171 species and a further 11 which are probable. If here also the part of the country belonging to the temperate zone is excluded (all biological provinces south of the line Värmland, Västmanland, Uppland), 102 species are recorded. Tab. 1 shows species richness and the degree of similarity with the myxomycete flora of northern Finland and Sweden. Some other well-studied areas are included for comparison: northeastern United States, northwestern and southern India (data recalculated from Stephenson et al. 1993), and Hawaii (Eliasson 1991). The community coefficient of 0.62 with northern Finland indicates the expected close relationship with this area. For northern Sweden the value is lower (0.55), perhaps because of the nivale species of the Swedish mountains (see Fries 1906, 1910). This ecological group is completely absent from Sredniy island; within Karelia nivale myxomycetes are recorded only from the Khibine Mountains 200 km northward (Novozhilov & Schnittler, in press).

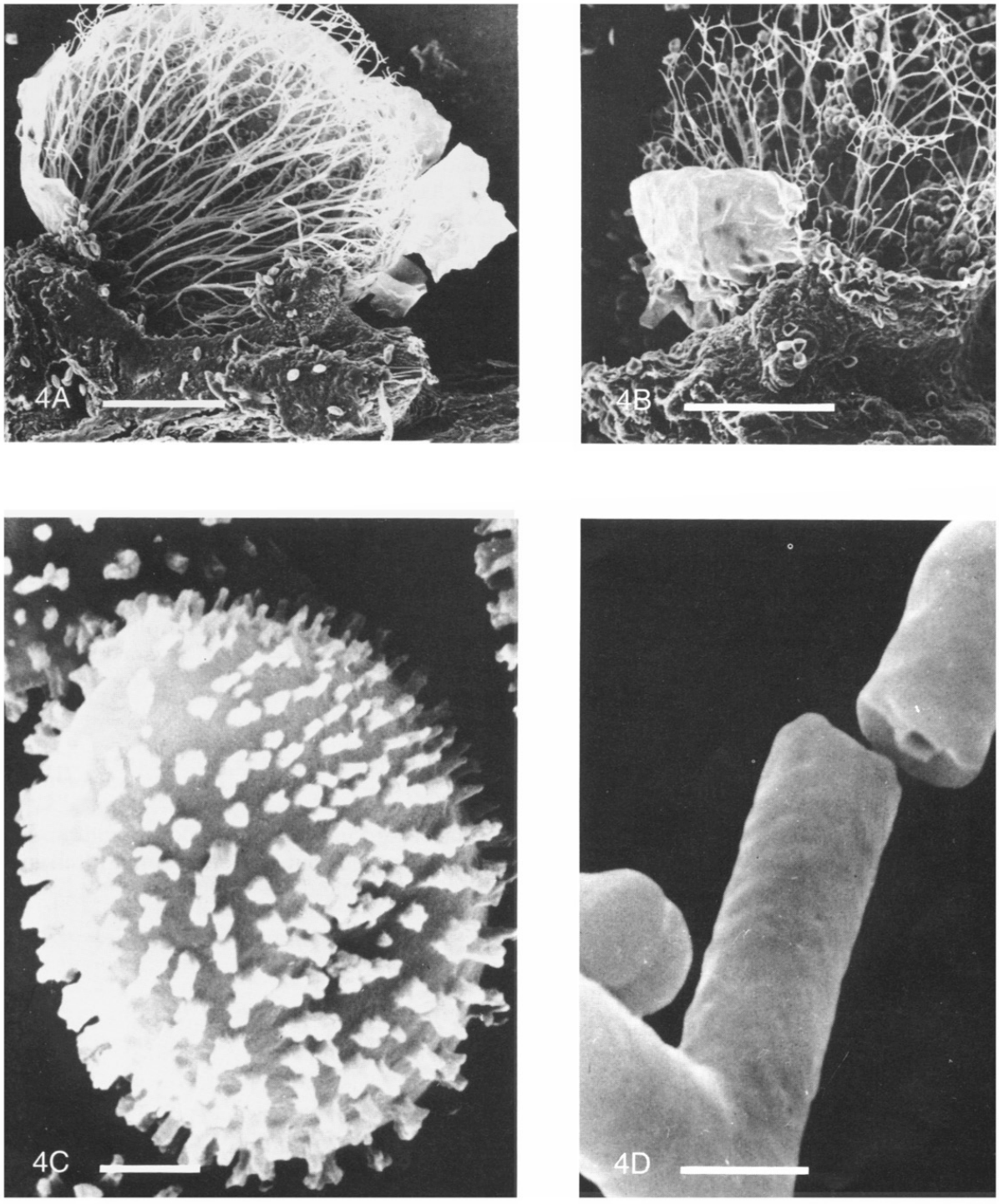

Fig. 4. SEM-photos of *Colloderma cf. oculatum* (2810). A, B) Two opened sporocarps with capillitium and remains of the peridium. Bar = 100 µm. C) Spore. Bar = 1 µm. D) A broken thread of the capillitium showing the tubular structure. Bar = 1 µm. Photos Y. Novozhilov.

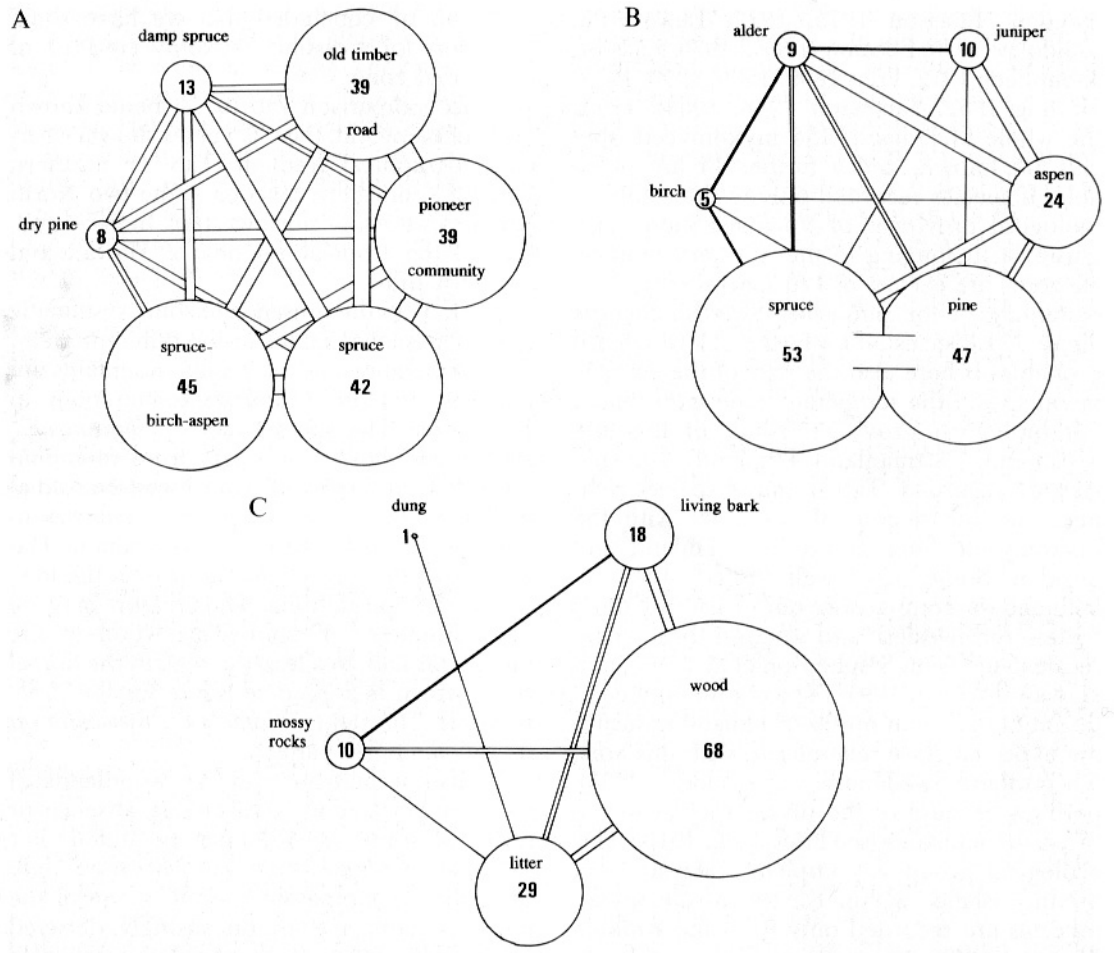

Fig. 5. Relationships of myxomycete occurrences within communities (A), on tree species (B, only for the inhabitants of bark and wood and in the various microhabitats (C). The size of the circles represents the number of species collected in the respective structure (numbers inside), the thickness of the connecting lines the degree of similarity (calculated as CC).

It can be concluded that we have some indicators for a distinct myxomycete flora of the boreal zone:

1. In comparison with other better-known areas of the world, the CC values show a clear-cut geographical gradient (Tab. 1): northern Finland - northern Sweden - the two North American areas - northwestern India - and, finally, the tropical regions of Hawaii and southern India.

2. Shifts in the presence of some systematic groups are conspicuous in the different areas. The boreal zone and especially mountains are relatively rich in *Cribrariaceae*, but poor in *Physaraceae*. The species ratio *Cribrariaceae* / *Physaraceae* shows a gradient from mountain areas (Cheat Mountain, northwestern India) over the boreal and temperate territories to the tropical areas (Tab. 2). Mountainous Hawaii also has more *Cribrariaceae* than the lowlands of tropical India. One reason may be the dominance of coniferous wood in the mountains and, to a lesser extent, in the boreal zone, which is a good substrate for the *Cribrariaceae*. The ratio *Trichiaceae* / *Stemonitaceae* reveals a similar pattern.

3. In comparison with the woodlands of the temperate zone, a surprising absence or rarity of some species must be noted. For example, *Cribraria rufa* was recorded only once. In the temperate zone it is one of the most frequent species on strongly decayed coniferous wood. Not recorded were also *Metatrichia vesparium* and *Trichia scabra*, while *Arcyria denudata*,

Cribraria cancellata, *Hemitrichia clavata*, *Cribraria rufa* and *Didymium difforme* were rarely seen; all species known as common from the temperate zone. On the other hand, species such as *Comatricha elegans* and *C. laxa*, which are regarded as rare in Central Europe, are very common on the island. The comments in the Finnish checklist (Härkönen 1979) confirm this. For the species mentioned above, in the investigation area as well as in Central Europe suitable microhabitats are available, since a climatic limitation must be assumed.

Distribution in the various plant communities, microhabitat and substrate preferences

The myxomycete richness of the different plant communites does not correspond to their relative extensions. The dry pine-lichen-woodland is like a desert. Only a few species survive on the surface of the mostly barkless, small pine stems and trees lying on the lichen tussocks. The occurrence of *Paradiacheopsis fimbriata*, which was found on *Pinus* bark in this community, is worth noting. The richest community in terms of myxomycete abundance, not species number, is the pine-spruce woodland. Although covering only a small area compared with the pine-spruce woodland, the spruce-birch-aspen woodland includes the highest number of species of all communities. The main reason is the occurrence of deciduous trees, with myxomycetes that do not appear on coniferous wood. The damp, *Sphagnum*-rich spruce woodland is poor in myxomycetes, only *Physarum virescens* seems to be adapted to live in big moss tussocks. The old timber road, as an artificial community, is closely connected with the pioneer community, and often a specimen could not be assigned to one of these with certainty. Fig. 5A presents a schematic diagram of the species recorded in the communities and their degree of similarity.

The distribution of the wood-inhabiting species on the main tree species is interesting (Fig. 5B): As expected, the two conifers are closely similar. Providing about 80% of all wood biomass in the region, they harbour the highest number of species (56). The rather rare deciduous trees aspen, alder and birch together bear only 30 species. Juniper provides practically no wood biomass, but has a unique flora of corticolous species. Only the cracked bark of aspen shares some of these species. This results in a relatively isolated position in the similarity diagram.

Five groups can be distinguished among the microhabitats (see Fig 5C). Here a lower average degree of similarity is shown compared with the similarities between communities and between tree species. The bark of living trees has few, but relatively specialized species. *Licea kleistobolus* regularly occurs on the bark of juniper and *Physarum decipiens* has a strong preference for the thick, scratched bark of aspen. More or less strongly decayed wood is the most important substrate for ca. 70% of all species recorded. Strong species preferences are often obvious. *Comatricha elegans* represents a species group restricted to coniferous wood. Other species, such as *Diderma asteroides*, are on deciduous trees. Large trunks of aspen are a rare microhabitat in the investigation area, perhaps insufficiently investigated. The most suitable litter substrate in the study area were the of previous years' stems of willowherb (*Epilobium*). Leafy and needle litter yielded only occasional myxomycetes. In contrast, a whole association was found on willowherb, with all species collected in autumn. The most common species were *Craterium leucocephalum*, *Diderma globosum*, *trevelyani* and *radiatum*, as well as *Didymium squamulosum*. The occurrence of *Lamproderma arcyrionema* on litter was unexpected. In contrast to reports from desert areas (Blackwell & Gilbertson 1984, Stephenson 1989), dung of birds and animals was less important as a microhabitat. In 15 samples used in moist chamber experiments only *Didymium difforme* was found as one large colony in the droppings of willow grouse (*Lagopus* spec.).

Moss-inhabiting Myxomycetes

A fascinating discovery was the occurrence of myxomycetes at moss communities on rocks. There are frequent vertical steps in the granite rocks on the island, which separate the damp woodlands from the dry pine-lichen community. If water trickles over for a long period of time, a thin cover of liverworts and blue-green algae is

Tab. 1. Comparison of the recorded species inventories of the study area (Rs), northern Finland (Fe), northern Sweden (Su), two areas of northeastern United States - Mountain Lake (Am1) and Cheat Mountain (Am2), and areas in northwestern (In1) and southern (In2) India and Hawaii (Ha). The number of species shared by the territories (upper right) and the community coefficient (lower left) are given. The last column shows the number of species recorded with certainty for each territory.

	Rs	Fe	Su	Am1	Am2	In1	In2	Ha	species
Rs	*	68	58	52	37	39	31	36	92
Fe	0.62	*	68	59	40	45	44	39	126
Su	0.55	0.56	*	48	34	40	31	29	102
Am1	0.51	0.50	0.46	*	43	51	44	47	106
Am2	0.49	0.43	0.43	0.53	*	38	16	23	56
In1	0.46	0.44	0.45	0.56	0.57	*	35	34	77
In2	0.33	0.39	0.31	0.43	0.20	0.39	*	50	77
Ha	0.38	0.35	0.29	0.47	0.30	0.40	0.51	*	94

formed, especially under big cushions of musci. During the summer 1993, these moss layers provided a very good microhabitat, especially in eastern exposure. The communities are nevertheless unstable, and in the exceptionally warm summer of 1994, when there was no trickling water, only dry scraps of dead liverworts were found on these rocks. Two sub-associations of myxomycetes can be distinguished. One prefers thicker tussocks of musci (more than 0.5 cm), in particular *Drepanocladus uncinatus* (Hedw.) Warnst., *Dicranum fuscescens* Turn. and *Cynodontium strumiferum* (Hedw.) De Not. These tussocks, wet inside but with dry leaf tips, are enriched with small detritus particles. *Lamproderma columbinum*, *L. sauteri* and *Didymium melanospermum* (the latter often at the base of the rocks) fruit here. The second sub-association contains *Colloderma oculatum* and *Lepidoderma tigrinum*, two species that are able to fruit on very thin (less than 0.5 cm), slimy layers of liverworts, covered with a water film. These microhabitats are found at 1-3 m height on rocks, that are provided with trickling water. Often large moss tussocks on the upper margin of the rock function as a water reservoir. Both species form sporocarps directly on the water film of the liverworts, which corresponds to the well-developed slime-sheet of their plasmodia. Artificial destruction of this sheet quickly leads to infection with fungi. *Physarum viride* and *P. nutans* were surprisingly also found on the rocks, very often at the transition between the sub-associations. But sporocarps were only seen when at least some leaf tips of the mosses protruded the water film.

These findings add a new perspective to the discussion of bryophilous myxomycetes (Stephenson & Studlar 1985). The moss layers were situated on rocks, the plasmodia had therefore to live within the moss layers. There was no wood available as an alternative substrate and the only conclusion is that some myxomycete species are well-adapted to living together with mosses and within moss layers. The huge colonies, especially of *Colloderma oculatum*, suggest that moss layers are a normal microhabitat. A possible food source for the plasmodia may be blue-green algae. Ing (1983) has described a myxomycete association in similar microhabitats in England, but with an almost completely different set of species.

Conclusions

We draw three conclusions from our findings:

1. Many species show a distinct phenology. For instance, all the litter species were only found in the autumn survey. *Clastoderma debaryanum* occurs only after the first frosts, as also confirmed by repeated records from the German Alps (unpublished).

2. Some species show surprisingly strong microhabitat preferences. A more precise description of the microhabitats should clarify this in the future.

3. Some species prefer different microhabitats in the boreal zone than they do in other regions. One example is *Arcyria cinerea*,

Tab. 2. Species numbers of *Cribrariaceae* (C) and *Physaraceae* (P) and the ratio *Cribrariaceae* / *Physaraceae* (C/P) in the compared territories. The last three rows give the analogous values for *Trichiaceae* (T, excluding *Arcyriaceae*) and *Stemonitaceae* (S). Abbreviations for territories as in Tab. 1.

	Rs	Fe	Su	Am1	Am2	In1	In2	Ha
C	10	8	11	14	9	9	1	6
P	19	31	21	21	6	15	35	28
C/P	0.53	0.26	0.52	0.67	1.50	0.60	0.03	0.21
T	7	14	11	15	11	10	4	5
S	22	25	23	23	14	20	20	19
T/S	0.32	0.56	0.48	0.65	0.79	0.50	0.20	0.26

which was not found on decaying wood, but was abundant on the bark of living trees, very similar to the situation in Finland (Härkönen 1977a). Another case is *Colloderma oculatum*, which in atlantic regions prefers the moss-covered bark of living trees (B. Ing, personal communication) but in Central Europe the species can be found on moss-covered wood slimy from algae. In the more continental region investigated here (the distribution boundary for the species?) it seems to prefer mossy rocks provided with trickling water. Possibly, myxomycetes accept other microhabitats on the margin of their range while they are more stenoecious.

In the attempt to clarify the world-wide distribution pattern of myxomycete species, we suggest that the following should be taken under consideration:

- The relatively strong microhabitat preferences of some species may vary within their distribution range: To verify this demands intensive surveys within representative but limited areas containing all suitable microhabitats, obligatorily with moist chamber experiments.

- Because the microhabitat seems to be the primary factor limiting the distribution and considering the dispersal through spores, areal boundaries in myxomycetes are not as clear-cut as in higher plants. This means that an extraordinarily suitable microhabitat may produce a record in a region where the species does not occur regularly. Clear distribution patterns can be obtained therefore only if microhabitat and local abundance are recorded simultaneously.

- The distribution of myxomycetes seems to be limited by climate, not only between the tropics and temperate regions but also within the Holarctic. Extreme conditions (eg. a very warm and dry summer) can also lead to exceptional records or failure of species (eg. *Colloderma oculatum* in the summer of 1994). To obviate this requires repeated surveys in a selected investigation area.

Acknowledgements. We are grateful to the organization 'Biopractica' (Dr. A. Balachonov, Dr. A. Markov, Dr. M. Molitvin) for providing us the opportunity to do field work at the biostation of St. Petersburg University. The survey was carried out within the project "Russian Arctic Mycoflora", supported by the International Science Foundation. The laboratory work was supported by a stipendium for the second author from the German Academic Exchange Service (DAAD). We wish to express our thanks to Mrs. Barbara Piechotka for technical assistance in the moist chamber experiments; and finally to J. Reynolds (Dublin), who did not hesitate to correct our English.

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Received on 4 May 1995

Nordic Journal of Botany

Nivicole Myxomycetes of the Khibine Mountains (Kola peninsula)

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Novozhilov, Y. & Schnittler, M. 1997. Nivicole Myxomycetes of the Khibine Mountains (Kola peninsula). – Nord. J. Bot. 16: 549-561, Copenhagen. ISSN 0107-055X.

Data on species inventory and ecology of myxomycetes, especially snow-line species, are presented from the Khibine, a small mountain area situated in the central Kola peninsula (Russia, 67°38'N, 33°37'E). Fourty species of myxomycetes belonging to 18 genera are recorded. Among them 12 species can be regarded as nivicole. For these taxonomic descriptions are given, their abundance is estimated, microhabitat preferences are described and commented on. *Diacheopsis effusa*, *Lamproderma cf. fuscatum* and *Lepidoderma aggregatum* are new for Fennoscandia.

Due to their geographical position, the Khibine mountains are more comparable with the Scandinavian mountains than with the mountain areas in the Russian Arctic which are influenced by a more continental climate. Therefore, the present paper leads together with previous reports of other authors to the conclusion, that nivicole myxomycetes can be expected in all suitable places throughout the Scandinavian mountains.

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Introduction

Reports of snow-line myxomycetes have been presented only from a few regions of the world. These nivicole slime moulds are an ecologically defined group, limited to higher mountains, where on open places near the melting snow a cover of herbaceous plant refuse forms suitable microhabitats. Well investigated are the western and central Alps (Meyer et al. 1992, Schinner 1981, Gottsberger 1966) and the mountains of California (numerous works by Kowalski). In contrast to other ecological groups of myxomycetes only poor information is available about Fennoscandia (Norway: Karsen 1943, northern Sweden: Schinner 1983, Fries 1906, 1910). Many species of this fascinating group are only known from a few localities.

This paper presents a first survey of the myxomycete flora of the Khibine mountains. Regarding the snow-line species, the results are discussed in comparison with the present knowledge about their distribution in Scandinavia.

Materials and Methods

The field work was carried out during two weeks (15-30 July 1994). All vegetation types were thoroughly examined. Common and easily recognizable myxomycete species were only occasionally collected, but rare species and those not easily recognized in the field were always collected. We defined all sporocarps that could arise from one plasmodium as one specimen. In practice, we assumed that sporocarps that share the same substrate and are separated by a distance that could be overcome by a migrating plasmodium belong to the same plasmodium.

Accepted 6-1-1996

From almost all collections sporocarps were preserved as permanent slides in polyvinyl lactophenol and/or glycerol gelatin, to distinguish between limeless and lime-containing structures. In several cases sporocarp structures were studied with a JEOL 35c scanning electron microscope at St. Petersburg.

Samples for moist chambers were chosen from bark of *Picea*, *Juniperus* and from the litter of various herbaceous plants, especially from *Cicerbita alpina* and *Epilobium angustifolium*. The moist chamber experiments were carried out as described by Härkönen (1977).

Study area

The Khibine mountains, situated in the central part of the Kola peninsula (67°36'-67°55'N, 33°23'-34°12'E) are the remainders of a strongly eroded plateau with a diameter of approximately 50 km and an elevation of about 1000 m, furrowed by deep valleys down to 300-400 m (Fig 1A). The region is characterized by a subarctic, but oceanic climate. The average monthly temperatures range from about –15°C in January to approximately +15°C in July, but with greater fluctuations than in surrounding lowlands with a more continental climate. In the deep-cut valleys the winter temperature can reach exceptionally up to +9°C. In June inversions lead to the contrasting effect, and the temperature can drop to –5°C. Usually, at the first half of June, the snow melts in the valleys, but may remain on the slopes somewhat longer, with some snow fields up to August. Therefore, the climate of these mountains is extraordinary for the taiga zone of Karelia and is more comparable with the oceanic part of Norway (see also Walter & Breckle 1986). A detailed overview about the climatic conditions is given by Seschko (1972).

This study was mainly carried out in the valley of the Wudjawrjokk River near the Polar-Alpine Botanical Garden of Kirovsk (67°38'N, 33°37'E). It is one of the big valley systems of the Khibine mountains, situated ca. 15 km northeast of Apatity in the southern part of the mountains. The investigated part of the valley lies in south-eastern direction, the ground plain is ca. 320 m above sea level. Fig. 1B gives a scheme of the collection localities.

Vegetation and collection localities

The region exhibits different vegetation types, ranging from taiga on the lower slopes to arctic mountain tundra on the plateau. A detailed analysis was made by Mischkin (1953). The following short descriptions include only aspects interesting for the habitat description of myxomycetes. The locality numbers are shown in Fig. 1B. Nomenclature of the mentioned plant species follows Flora Europaea (Tutin et al. 1964), the English names are used as in Stace (1991).

Damp spruce woodland (localities 7a-7c, 10, 15)

A relatively rare association of the valleys, mostly near the rivers and on the lower slopes. Spruce (*Picea abies* ssp. *obovata*) has the best growing conditions here, forming stems up to 25 m height and 70 cm diameter. Due to the long distances between the trees (5-20 m) and their narrow, pyramid-shaped form the canopy is not closed. This provides enough light for a close cover of tall herbaceous plants. Rotten spruce stems lie on their branches and therefore the stems do not touch the ground directly. As a consequence, the decay of the stemwood is delayed, and the bark is much longer attached to the wood.

Birch (*Betula tortuosa*) and rowan (*Sorbus aucuparia* ssp. *glabrata*) are regulary in-between these communities. Very rare are grey alder (*Alnus incana* ssp. *kolaensis*) and willows (*Salix caprea*, *S. phylicifolia*). The two mentioned willows are usually tree-forming, but tall trees are an exception in the investigation area.

Dry spruce-birch woodland (localities 4, 5, 8, 14)

This is a very open type of woodland occurring especially on the south-exposed slopes of the valleys. The main trees are predominantly birch, scattered spruce, sometimes mixed with rowan and juniper (*Juniperus communis*). The latter grow as small shrubs with stems mostly 1-2 cm in diameter. The ground flora is poor in species and harbours only small herbaceous plants. During a period of warm and dry weather in summer this woodland type dries out quickly.

Birch-rowan woodland (localities 2, 3a, 3b, 11a, b, 12a-c, 13)

Due to the heavy snow pack in winter, spruce does not extend higher than 350 m. Therefore the middle range of the mountain slopes up to 500 m are covered only with rowan and birch, sometimes grey alder, often forming a lot of small, procumbent stems. In spring the slopes warm up quickly and provide good conditions for a lot of tall herbaceous plants. Under moist conditions (locality 2) the large perennial *Cicerbita alpina* grows in large stands. In places with high snow movement the fern *Athyrium distentifolium* becomes dominant, and climbs higher than the boundary of the woodland. In light and drier places (locality 11b) junipers form bigger shrubs up to 8 cm in stem diameter.

The most interesting locality (12) was an avalanche gutter within dense woodland on the south to southwest-exposed, steep slope of the

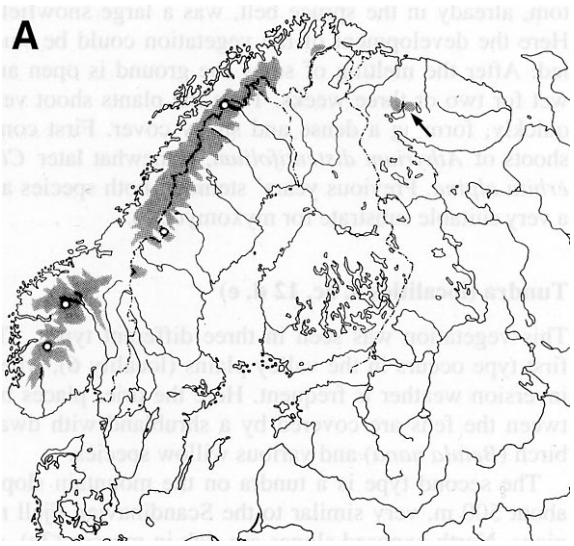
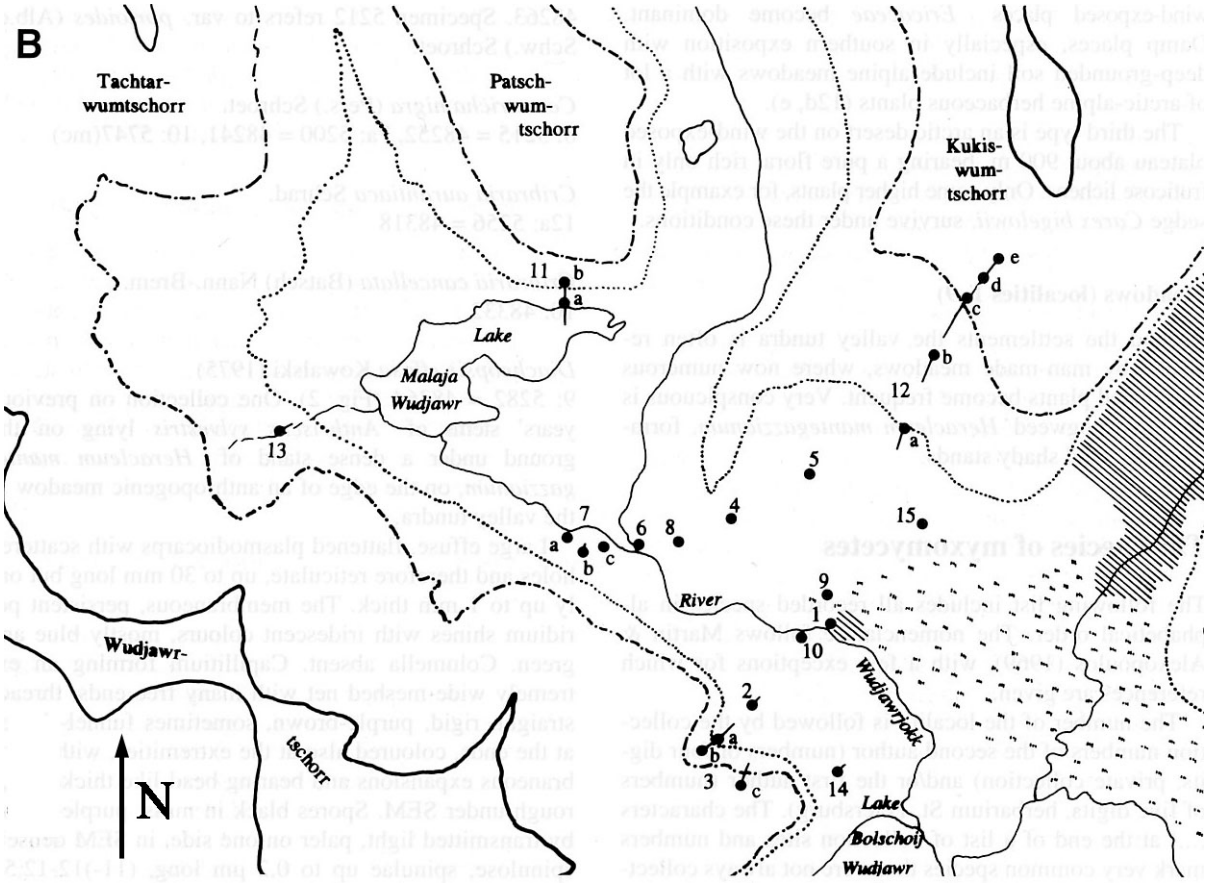


Fig. 1 A Geographical position of the Khibine mountains within Fennoscandia. Mountaineous areas higher than 1000 m, well corresponding with the distribution of alpine tundra (Walter & Breckle 1986), are dotted. The arrow marks the investigation site; points indicate localities from which nivicole myxomycetes in Scandinavia are known. From north to south these reports are: Fries (1910) and nearby Schinner (1983), Fries (1906), Schnittler (1991, unpublished) and Karsen (1943). – Fig. 1 B Schematic map of the Wudjawrjokk valley representing the localities, 1:25000. Only those which yielded myxomycetes are shown, not all investigated sites. A line extending from a point roughly symbolizes exposition (direction) and steepness of the slope (length). Dotted line: 400 m level (corresponding with boundary of spruce), dotted and full line: 500 m level (corresponding with woodland boundary), full line: 900 m level (the high plateau). Shaded areas: settlements on the margin of Kirovsk (large patch), the Botanical Garden (small patch), inbetween meadows.



Kukiswumtschorr mountain. The gutter reaches from almost 600 m to about 375 m and was open over a width of 10-25 m. Up to 500 m it was framed on both sides with dense birch-rowan woodland. On the open ground the fern *Athyrium distentifolium* formed very dense mats of old leaves on black, humid soil about granite rocks, shaded by the living leaves up to one meter long. With higher altitudes the big composite

Cicerbita alpina became dominant, growing more scattered in small clusters. On the bottom, already in the spruce belt, was a large snowfield. Here the development of the vegetation could be studied: After the melting of snow the ground is open and wet for two or three weeks. Then the plants shoot very quickly, forming a dense and shady cover. First come shoots of *Athyrium distentifolium*, somewhat later *Cicerbita alpina*. Previous years' stems of both species are a very suitable substrate for myxomycetes.

Tundra (localities 6, 3c, 12 d, e)

This vegetation was seen in three different types. The first type occurs in the valley plains (locality 6), where inversion weather is frequent. Here the drier places between the fens are covered by a shrubland with dwarf birch (*Betula nana*) and various willow species.

The second type is a tundra on the mountain slopes about 500 m, very similar to the Scandinavian Fjell regions. North-exposed slopes are rich in mosses (3c), on wind-exposed places *Ericaceae* become dominant. Damp places, especially in southern exposition with deep-grounded soil include alpine meadows with a lot of arctic-alpine herbaceous plants (12d, e).

The third type is an arctic desert on the wind-exposed plateau about 900 m, bearing a pure flora, rich only in fruticose lichens. Only some higher plants, for example the sedge *Carex bigelowii*, survive under these conditions.

Meadows (localities 1, 9)

Around the settlements the valley tundra is often replaced by man-made meadows, where now numerous introduced plants become frequent. Very conspicuous is the giant hogweed *Heracleum mantegazzianum*, forming dense and shady stands.

The species of myxomycetes

The following list includes all recorded species in alphabetical order. The nomenclature follows Martin & Alexopoulos (1969), with a few exceptions for which references are given.

The number of the locality is followed by the collection numbers of the second author (numbers of four digits, private collection) and/or the first author (numbers of five digits, herbarium St. Petersburg). The characters '...' at the end of a list of collection sites and numbers mark very common species that were not always collected. Specimens whose determinations are considered by the authors as doubtful are given with the note 'cf.' (confirm), often indicating scanty material. The abbreviation '(mc)' marks a specimen obtained from a moist chamber.

For the species collected in nivicole situations brief descriptions with comments on ecology and distribution are given.

Arcyodes incarnata (Alb. & Sch.) Cooke
3b: 5195 = 48221

Arcyria cinerea (Bull.) Pers.
3c: (mc), 5: (mc), 10: 5748(mc), 12a: 5260, 6754(mc), 13: 6756(mc) ...

Arcyria obvelata (Oeder) Onsberg (1978, syn. *A. nutans* (Bull.) Grev.)
5: 5738(mc)

Arcyria pomiformis (Leers) Rost.
7a: 5197 = 48237

Ceratiomyxa fruticulosa (Muell.) Macbr.
7a: 5203 = 48249, 11a: 5254 = 48315, 12b: 5212 = 48263. Specimen 5212 refers to var. *porioides* (Alb.et Schw.) Schroet.

Comatricha nigra (Pers.) Schroet.
6: 5215 = 48252, 7a: 5200 = 48241, 10: 5747(mc)

Cribraria aurantiaca Schrad.
12a: 5256 = 48318

Cribraria cancellata (Batsch) Nann.-Brem.
10: 48332

Diacheopsis effusa Kowalski (1975)
9: 5282 = 48364 (Fig. 2). One collection on previous years' stems of *Anthriscus sylvestris* lying on the ground under a dense stand of *Heracleum mantegazzianum*, on the edge of an anthropogenic meadow in the valley tundra.

Large effuse, flattened plasmodiocarps with scattered holes and therefore reticulate, up to 30 mm long but only up to 1 mm thick. The membraneous, persistent peridium shines with iridescent colours, mostly blue and green. Columella absent. Capillitium forming an extremely wide-meshed net with many free ends, threads straight, rigid, purple-brown, sometimes funnel-shaped at the ends, coloured also at the extremities, with membraneous expansions and bearing bead-like thickenings, rough under SEM. Spores black in mass, purple-brown by transmitted light, paler on one side, in SEM densely spinulose, spinulae up to 0.2 µm long, (11-)12-12,5(-13) µm in diameter.

Our collection agrees well with the original description and seems to be the first record outside the type locality, the Californian Sierra Nevada (Kowalski 1975). *Diacheopsis effusa* is distinguished from other species of the genus by the plasmodiocarpous habit, the spore ornamentation and the persistent peridium. Similar by habit are *D. serpula* (Kowalski 1975, with fugacious peridium and lirate spore ornamentation), *D*

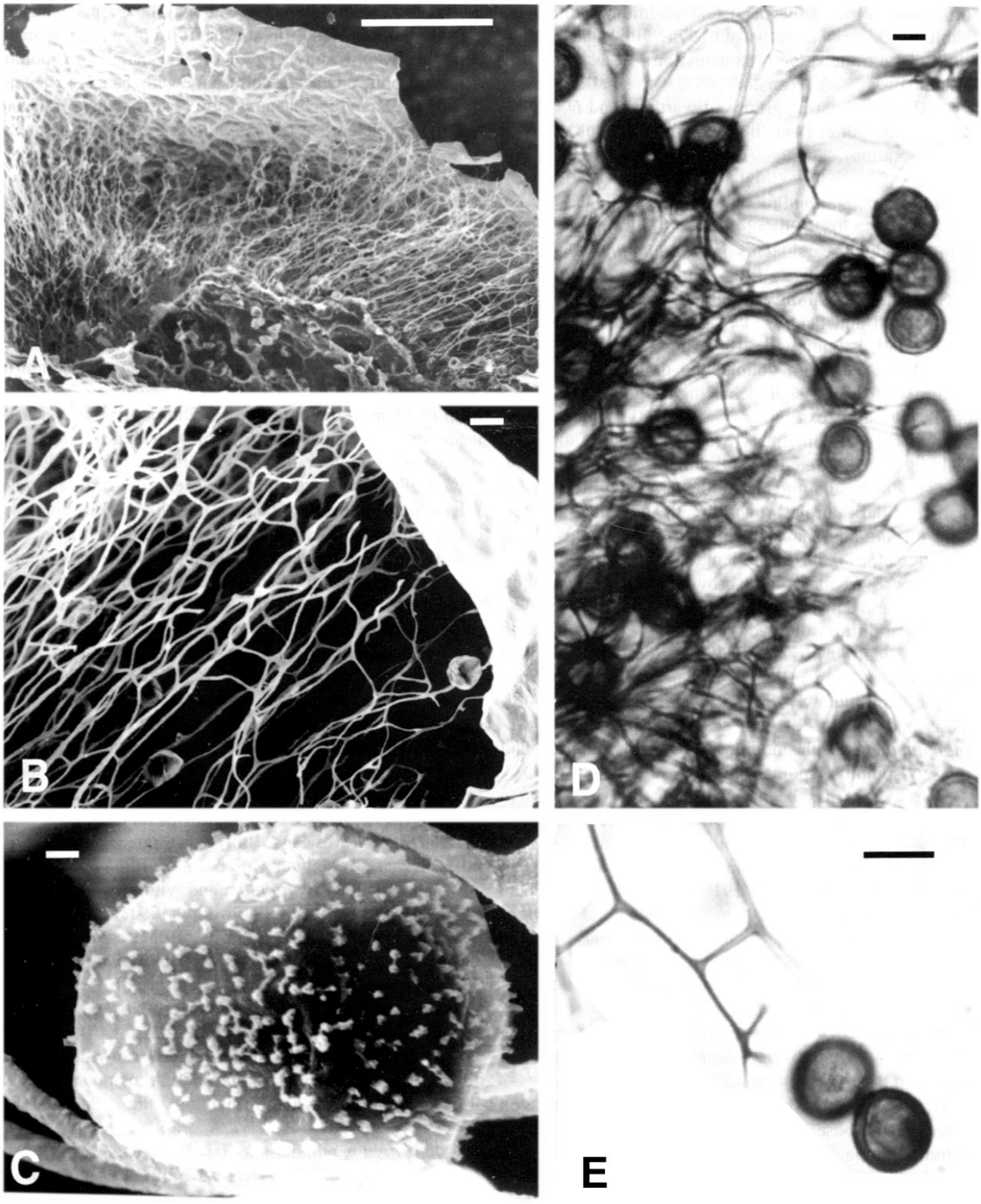


Fig. 2 SEM- (A-C) and LM-photos (D-E) of *Diacheopsis effusa* (5282). A Open plasmodiocarp showing the capillitium and the hypothallus on the bottom. Bar = 100 µm. B Capillitium and peridium. Bar = 10 µm. C Spore. Bar = 1 µm. D Capillitium and spores, embedded in polyvinyl lactophenol. Bar = 10 µm. E Spores in optical section. Bar = 10 µm. Photos Y. Novozhilov.

vermicularis (Nann.-Brem. & Y. Yamam. 1987, with smaller densely warted spores bearing groups of wartlets) and *D. reticulospora* (Meyer et Poulain 1990, with a reticulose spore ornamentation).

Diderma deplanatum Fr.
3a: 5249 = 48308, 12d: 5240 = 42292. Both records on lying, previous years' stems of *Cicerbita alpina* in shaded woodland.

Sporocarps forming curved, sometimes branched, ring-shaped and depressed plasmodiocarps, about 0.1-0.2 mm tall, 1-2 mm wide, 10-20 mm in length, white or ochraceous. Peridium double, the outer layer a thick, brittle, whitish lime shell dehiscing irregulary, often disappearing and exhibiting the inner membraneous, slightly rugose, sometimes iridescent layer. Columella lacking or represented by an elongate, usually narrow ridge on the base of the plasmodiocarp. Capillitium consisting of dark purple-brown threads, branched and seldom forking and anastomosing with hyaline tips, often bearing spines 0.5-1 µm in length or bead-like thickenings. Spores in mass dark, brown by transmitted light, minutely and densely spinulose, diameter 10-12 µm.

The capillitium of specimen 5240 is very similar to that of *Diderma niveum* (5219). Both specimens have spinulae 0.5-1 µm in length and bead-like thickenings on the capillitium. But *D. niveum* forms sporocarps and has spores with scattered spinulae, *D. deplanatum* grows plasmodiocarpous with minutely and densely spinulose spores.

The species has been found in a few localities in Scandinavia and is not known as obligately nivicole. The very similar *D. niveum* occurs usually near the snowline and has been found in similar situations in Scandinavia (Fries 1906, 1910). Our records indicate that these species are very closely related and may represent two forms of one species (with *D. niveum* as the snowline form).

Diderma niveum (Rost.) Macbr.
12b: 5219 = 48274. One small collection on litter of a dense *Athyrium distentifolium* tussock in an open avalanche gutter.

Only eight, clustered, spherical sporocarps, sitting on a constricted base, 0.7-1.5 mm in diameter, white. Peridium double, the outer layer crustaceous, smooth, fragile, the inner layer membraneous and thin. Columella large, about half of the sporocarp diameter, ochraceous or yellow-orange. Capillitium very abundant, elastic, the threads brown-violet, thickened, often with nodules and spinulae, colourless at the ends. Spores black in mass, violet-brown by transmitted light, spinulose, 9-11 µm in diameter. The well developed spinulae (1-2 µm in length) on the capillitium were not mentioned by Nowotny (1990) or Martin & Alexopoulos (1969), other characters correspond with their descriptions.

From Scandinavia known by Fries (1906, 1910) and Karsen (1943), see *D. deplanatum* for discussion.

Didymium difforme (Pers.) S.F. Gray
7c: 5743 (mc)

Didymium dubium Rost.
1: 5266 (with *Trichia alpina* 5281), 12d: 5231 = 48285, 5233= 48287. On litter of *Epilobium* and *Athyrium*, in shady situations in woodland, also along the margin of an avalanche gutter.

Plasmodiocarps scattered, pulvinate, up to 1 mm in diameter, branched, flattened and sometimes reticulate up to 15 mm long and up to 0.5 mm tall, grey, or dark brown due to the absence of lime. Peridium a single layer, shining, membraneous, covered more or less densely with lime crystals. Columella absent, but some fruitings have a thick lime layer on the base like a flat columella. Capillitium thin, wavy, quite elastic, dark-brown with little swellings, furcated and hyaline at the ends. Spores black in mass, violet-brown in transmitted light, 9.5-12.5 µm in diameter, minutely and densely verrucose, warts up to 0.5 µm long (SEM), sometimes forming a broken reticulum.

Our collections include two forms. No. 5266 has a sparsely branched, dark purple brown capillitium with rather thick swellings. The spores are black in mass, brown in transmitted light, 11-12.5 µm in diameter and rather densely verrucose without a broken reticulum. This fits the description given by Nannenga-Bremekamp (1990) for *D. leptotrichum* (Racib.) Massee (syn. *D. nivicolum* Meylan). But it also agrees well with an exsciccate of Meylan (01.05.1915, Jura, Switzerland) which he named *D. dubium*, and with nivicole forms of *D. dubium* described by Nowotny (1991, specimen 1304 of his collection). No. 5233 has a pale capillitium with many branches and spores 9.5-11 µm in diameter, which are verrucose with a broken reticulum (SEM and oil immersion) and the specimen corresponds with the description of *D. dubium* s.str. of Nannenga-Bremekamp (1990). Thus, our specimens suggest a broader concept of the species as used by Martin & Alexopoulos (1969), including the snowline forms.

Echinostelium minutum de Bary
3c: 5746(mc), 6752(mc), 6753(mc), 4: (mc), 5: 5753(mc)

Hemitrichia clavata (Pers.) Rost. 7b: 48357, 13: 48352

Lamproderma arcyrioides (Sommerf.) Rost.
1: 5268= 48338, 12d: 5237 = 42289, 5218 = 48278, 5234 = 48129, 5241 = 42293 ... On litter of various plants, in particular *Epilobium* and *Athyrium*.

Sporocarps crowded to clustered, stalked, globose or ovoid, 0.8-1.5 mm in diameter, 1-2.5 mm in total

hight, iridescent blue, green and purple. Hypothallus separate on each sporocarp, discoid, reddish brown. Stipe thick, stout, rigid, not tapering towards the apex, up to 1 mm in length, prolonged to a columella up to the centre of the sporocarp, sometimes shorter, quite massive. Peridium membraneous, thin, dehiscing irregularly in large, shining fragments. Capillitium with few free ends, reddish brown except at the hyaline extremities, sometimes colourless in the middle part also, expansions common on the primary branches. Spores dull brown or black in mass, pale violet-brown by transmitted light, minutely warted, 8-11 µm in diameter.

The features of the capillitium are different in our collections. The capillitium of specimen 5237 is colourless not only at the tips, but also in the middle part of the net. This and No. 5234 may be assigned to var. *leucotrichum* (M. Meyer, pers. comm.) The other characters agree with the description by Kowalski (1970). No. 5268 has a very short stipe and a dark brown capillitium which is colourless only at the extreme tips, probably representing an intermediate form between *L. carestiae* and *L. arcyrioides.* According to spore features (10-11 µm and minutely warted) it can be closer related to *L. arcyrioides.* One of the most common snowline species (Kowalski 1970), within Fennoscandia known from Torne Lappmark (Fries 1910) in similar habitats, from different parts of Finland (Härkönen 1979) and also from north-west Russia (Novozhilov 1986).

Lamproderma carestiae (Ces. & de Not.) Meylan
1: 5186 = 48350. Eight aggregated sporocarps on litter of *Epilobium angustifolium.*

Scattered sporocarps on short stipes, ovoid, 0.8-1.5 mm in diameter. Stipe not more than 0.5 mm in length, sometimes absent. Peridium membraneous, thin, splitting in large pieces, iridescent blue and green. Columella tapering slightly towards the apex, reaching more than one half of the sporocarp. Capillitium a dense network with many free ends, black, hyaline only at the tips. Spores purple-brown in mass, dark violet-brown in transmitted light, minutely and densely spinulose, 11-12.5 µm in diameter.

According to Kowalski (1970) the main distinctive characteristics of this taxon are the short stipe, the dark brown capillitium and the densely spinulose and uniformly coloured spores 10-12 µm in diameter. It is known as nivicole and may be connected with *L. arcyrioides* by intermediate forms (Kowalski 1970, our observations). Cited by Fries (1912) as *L. violaceum* Fr.

Lamproderma fuscatum Meylan (in Martin & Alexoupolos 1969 included in *L. carestiae*).
12a: 5269 = 48321. Four sporocarps under bark of a lying stem of *Betula* at the margin of the avalanche gutter.

Sporocarps stalked, globose-ovoid, ferrugineous, 1-1.2 mm in diameter. Peridium membraneous, appearing thick, long persistent after dehiscence especially at the base of the sporocarp, slightly brown-iridescent, pale ferrugineous in transmitted light. Hypothallus discoid, red-brown and separate for each sporocarp. Stipe black, up to 0.8 mm long, prolonged into a columella reaching the centre of the sporocarp. Capillitium thick and stout, straight threads, furcated with a narrow angle, main branches opaque, black, thinner threats in the periphery ferrugineous under a microscope, only the most outerward tips pale ferrugineous-hyaline. Spores ferrugineous in mass, light violet-brown by transmitted light, regularily covered with fine, spinulose warts, 8-10 µm in diameter.

According to several authors (Meylan 1932, Kowalski 1970, Nowotny 1989) the species is well distinguished from *L. carestiae* by smaller spores and the conspicuous ferrugineous colour of all parts. Our collection agrees with these descriptions. But, compared with a specimen from the French Alps (Meyer 12726) it differs by the rigid, easily breaking capillitium threads furcated in a narrow angle. Beside slightly smaller spores the French sporocarps have a slender, flexuous capillitium with curved threads, which are thinner and translucent ferrugineous in transmitted light. Here the branches have a widther angle and are often dilated. Therefore, we hesitate in assigning our collection surely to *L. fuscatum*.

Lamproderma sauteri Rost.
3c: 5189 = 48231, 5190 = 48232, 5191 = 48229, 5192 = 48228, 5193 = 48230(cf.), 12b: 5214 = 48267, 12c: 5204 = 48256, 5205 = 48257 ,5206 = 48266, 12e: 5227 = 48281, 12d: 5235 = 48288, 3b: 5252 = 48311 ... Records were mainly on mosses covering small, shady and hidden rocks and boulders provided with trickling water, more rarely on fern litter.

Sporocarps clustered, stalked, globose to ovoid, 0.8-2 mm in diameter. Peridium membraneous, rather persistent, slightly iridescent, usually dull blue or green. Hypothallus well-developed, discoid and separate for each sporocarp, or common to a group of sporocarps, reddish brown. Stipe length highly variable, up to 2 mm. Columella tapering slightly towards the apex or truncate, reaching to the centre of the sporocarp, often rather massive. Capillitium dense, forming an intricate, flexuose net, the branches sometimes with nodular enlargements, ends more or less elongated, free, colourless at the extremities. Spores black in mass, purple-brown in transmitted light, with dense spinulose ornamentation, often paler on one side, 12-17 µm in diameter.
Our specimens can be separated into two groups. One has a capillitium with elongate, straight and often furcate tips, the other shows more intricate and curved capillitium tips. Some specimens (eg. 5193) have the

proportions and habit of *L. columbinum* but the peridium is only slightly iridescent, rather thick and persistent for a long time. Others, as 5190, 5204 probably represent the type variety (var. *sauteri*, M. Meyer, pers. comm.). A common and variable cryophilous species, but still with only a few reports from Scandinavia (Fries 1912, Karsen 1943) and southern and central Finland (Härkönen 1979).

Leocarpus fragilis Dicks.
11a: 48314

Lepidoderma aggregatum Kowalski (1971)
12b: 5207 = 48265, 12e: 5229 = 48283, 5228 = 48282 (Fig. 3 A-C). Found on the avalanche gutter, substrates are *Cicerbita* in one case, other records were from *Vaccinium* stems in the upper part of the gutter where tall herbaceous plants are already rare.

Sporocarps hemispheric, pulvinate on broad base, white or pinkish-cream, 1.5-2.0 mm in diameter and densely clustered, in habit very similar to *Diderma alpinum*. Hypothallus hidden by the broad base of sporocarp. Peridium single (membraneous layer firmly attached to the crustaceous layer), opaque, not iridescent, covered with lime scales, these 30-50 µm in diameter and conglomerated forming a dense crust. Columella pulvinate, large, filled with lime scales, creme to pinkish. Capillitium abundant, firmly attached to columella and peridium, composed of long, straight, rarely branched and smooth threads, rough under SEM. Threads 0.5-1 µm in diameter, rarely bearing enlarged nodules, with hyaline blunt ends. Spores in mass purple-brown, violet-brown in transmitted light, spinulose, 11-15 µm in diameter. The up to 1 µm long spinulae are widely scattered and branched at the ends (SEM). The specimen fits exactly the original description (Kowalski 1970), but differs from a collection made in the French Alps (Nowotny 1990) by the abundant, long, straight and very narrow violet-brown threads of the capillitium. Our collections have a thin and straight capillitium, the French specimen has a thicker and darker capillitium. Described from Washington, Cascade mountains. The first record for Fennoscandia.

Lepidoderma granuliferum (Phill.) R.E.Fries
12b: 5208 = 48268, 5224 = 48279, 5226, 5263 (Fig. 3 D-F). Collected from mats of previous years' *Athyrium* leaves in the avalanche gutter.

Effused plasmodiocarps, scattered or clustered, flattened, up to 5 cm long, rarely in combination with small sessile, hemispherical sporocarps. Peridium double but layers hardly separated, opaque and dull brown, more or less covered with a thick layer of densely packed lime scales, these rather large, 40-60 µm in diameter, yellowish to pinkish. Columella mostly absent, sometimes present as a small ridge. Capillitium yellowish-brown, consisting of a dense and regular network of branched, rather thick tubes with expansions and vesicles up to 30 µm in diameter, which are round or elongate and filled with large lime nodules. This is a unique character within the genus. Spores purple-brown in mass, violet-brown by transmitted light, densely spinulose, (13-)15-18(-20) µm in diameter, spinulae up to 0.8 µm long, sometimes furcate at the ends (SEM).

Another nivicole *Lepidoderma*, according to present knowledge more widely distributed than the former species, collected twice in Scandinavia (Fries 1910, Karsen 1943).

Licea minima Fr.
2: 5248 = 48307, 23: 5278 = 48353

Lycogala epidendrum (L.) Fr.
6: 48251

Physarum cinereum (Batsch) Pers.
1: 5187 = 48349, 3a: 5251, 5272 = 48345, 5273 = 48346, 5274 = 48347, 5275 = 48348, 10: 5283 = 48365, 12a: 5271 = 48343, 12b: 5217 = 48277, 12d: 5230 = 48284, 14: 5242= 42294, 5244 = 48302, 5245 = 48303, 5246 = 48304, 5247 = 48305, 15: 5280 = 48354 ... The most common myxomycete in the region, particularly abundant on the collapsed, previous year's stems of *Cicerbita alpina* lying on wet ground.

Sporocarps scattered, often gregarious, subglobose, always sessile, 0.3-0.8 mm wide, sometimes forming small plasmodiocarps up to 2 mm long, grey to dark with silvery and iridescent colours. Peridium membraneous, single, with very different quantity of lime. Columella absent. Capillitium with small, rounded lime nodes, these sometimes branched and confluent resulting in a badhamioid habit. Spores in mass brown, pale brown in transmitted light, 8-11 µm in diameter, densely and minutely warted, the warts irregularly distributed.
Also in this case a pair of taxa with *P. vernum* as the nivicole form seems to exist. According to the spore features our collections clearly fall under *P. cinereum*.

Physarum bivalve Pers.
3c: 5746(mc), 11a: 5719(mc)

Physarum leucophaeum Fr.
7a: 5199 = 48239

Physarum virescens Ditmar
1: 48331

Physarum viride (Bull.) Pers.
12a: 5258 = 48320, 12b: 5213 = 48264

Stemonitis axifera (Bull.) Macbr.
11b: 5741(mc)

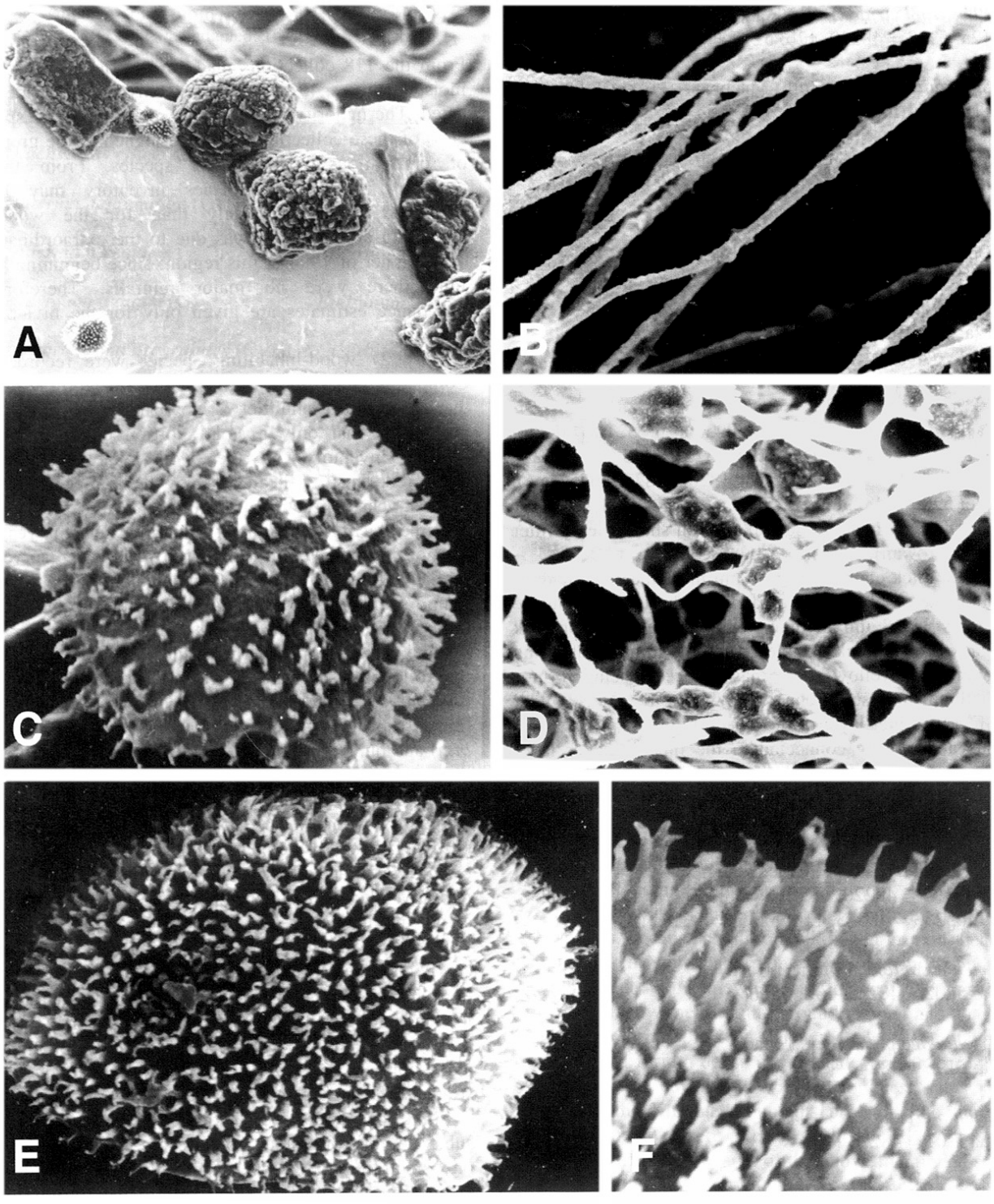


Fig. 3 SEM-photos of *Lepidoderma aggregatum* (5229). A Lime scales on the peridium. Bar = 10 µm. B Capillitium threads. Bar = 10 µm. C Spore. Bar = 1 µm. SEM-photos of *Lepidoderma granuliferum* (5224). D Capillitial threads bearing lime nodes. Bar = 10 µm. E Spore. Bar = 1 µm. F Detail of spore ornamentation showing the sometimes branched spinulae. Bar = 1 µm. Photos Y. Novozhilov.

Stemonitis hyperopta Meylan
12a: 5270 = 48341

Stemonitis smithii Macbr.
12a: 5257

Stemonitis virginiensis Rex
12a: 6755(mc)

Trichia alpina (Fr.) Meylan 1: 5188 = 48348, 5264 = 48324, 5265 = 48326, 5267 = 48330, 5281 (with *Didymium dubium*), 48323, 48325, 12b: 5210= 48260, 5211 = 48262, 5220 = 48269, 5221 = 48270, 5222 = 48271, 5223 = 48272, 5225 = 48280, 48273, 6757(mc), 12c: 5209 = 48258, 19d: 5232, 5239 = 42291 ... Rarely on *Athyrium* mats but abundantly on shaded leafy litter (birch, rowan).

The thick elaters up to 10 µm in diameter with short attenuate or blunt and furcate tips, the large, spinulose spores 13-18 µm in diameter, and the black or dark black-brown, thick, double-layered peridium contrasting against the yellow spore mass after dehiscing form a distinguishing set of characters within the genus. Under SEM the outer layer of the peridium is thin, membraneous and closely connected to the inner, thicker layer showing a spongy structure.

A common nivicole and mountain species. In the Khibine mountains it was one of the abundant litter species.

Trichia botrytis (J.F.Gmel.) Pers.
3b: 5194 = 48220, 6: 5216 = 48253, 7a: 5198 = 48233, 11a: 5253 = 48313, 11b: 5255 = 48317, 13: 5277

Trichia contorta (Ditmar) Rost.
7a: 5202 = 48235, 19d: 5236

Trichia decipiens (Pers.) Macbr.
7a: 5196 = 48240

Trichia erecta Rex
7a: 5201 = 48238

Trichia favoginea (Batsch) Pers.
12a: 5259 = 48336

Tubifera ferruginosa (Batsch) J.F.Gmel.
12a: 5261 = 48322

Results and Discussion

From the 118 collections made in the field and from moist chambers, 40 species of myxomycetes were identified. The majority (about 60 %, representing 12 species) of these collections can be assigned to the group of cryophilous-nivicole litter species. From this ecological group the species inventory may be registered more completely than for the wood-inhabiting species. This was due to the extraordinary dry summer of 1994 in this region: since beginning of June there were no major rainfalls. Therefore, abundance estimates are given only for the nivicole species.

Only 27 wood-inhabiting species were recorded. Compared with a survey at the White Sea, 200 km farther southward (Schnittler & Novozhilov, in press), it is obvious that only a small portion of the whole species inventory of the wood-inhabitants was registered. This is indicated also by the high percentage of last-year's fructifications among the collected specimens. High abundance fluctuations between years are not unusual. This was shown by a repeated survey in the White Sea region: compared with the more humid summer 1993, in 1994 at almost the same time only one fifth of the species was recorded.

For the moist chamber experiments 123 samples from the following substrates were collected: living bark (*Juniperus*, *Picea*, *Alnus*, *Salix* and *Sorbus*), plant refuse (especially from *Athyrium*, *Epilobium* and *Cicerbita*) and dung (lemming, *Lemmus lemmus* and willow grouse, *Lagopus* spec.). Only 20 samples (15 %) yielded myxomycetes, a small number compared with other studies (Nowotny 1986, Härkönen 1977, own experiences). The records belong to nine species, whereof *Arcyria cinerea* and *Echinostelium minutum* were found regulary. The optimal substrates were bark samples of spruce and juniper.

Beside the extraordinary weather situation in 1993, it can be assumed that wood-inhabiting myxomycetes in the Khibine mountains are less abundant than in the lowlands of the central boreal zone. Reasons may be:

- The woodlands of the Khibine mountains, belonging to the northern boreal zone, are very light. A lot of substrates suffer from direct sunshine and dry out quickly.
- Some deciduous trees, known as a very good substrate for corticolous species, are absent or form only small trees or shrubs: aspen, alder and willow.
- Juniper grows only as small shrubs, mostly missing the peeling bark of old individuals, known as a very suitable microhabitat for corticolous myxomycetes.
- The short vegetation period and the heavy snowpack in winter may hinder the development of species known as bryophilous, which often need a long time for sporocarp formation. In spite of the relative abundance of such microhabitats, only *Lamproderma*

Tab. 1 Microhabitat preferences of the cryophilous-nivicole group of litter myxomycetes. The first listed substrate was preferred. The symbol '-' refers to occurrings on the valley plain. For estimation of abundance, a simple estimation scale according to Stephenson (1993) was adapted: R - rare: recorded once, O - occasional: 1 -3 records, C - common: 3 - 5 records, A - abundant: more than 5 records.

species	substrate	light	exposition
Diacheopsis effusa (R)	*Anthriscus*	open	-
Diderma deplanatum (O)	*Cicerbita*	shadow	NO, SSW
Diderma niveum (R)	*Athyrium*	open	SSW
Didymium dubium (O)	*Epilobium*, *Athyrium*	shadow	-, SSW
Lamproderma arcyrioides (C)	*Cicerbita*, *Heracleum*, *Athyrium*	open shadow	-, SSW
Lamproderma carestiae (R)	*Epilobium*	open	-
Lamproderma fuscatum (R)	wood, under bark	shadow	SSW
Lamproderma sauteri (A)	mostly moss covers on rocks, *Cicerbita*	mostly shadow, once open (600 m)	NO, OSO, SSW
Lepidoderma aggregatum (O)	*Athyrium*, *Cicerbita*	open	SSW
Lepidoderma granuliferum (C)	*Athyrium*	open	SSW
Physarum cinereum (A)	*Cicerbita*, rarely on *Delphinium* (intro-duced), *Epilobium*	shadow	-, NO, SSW
Trichia alpina (A)	leafy litter, *Epilobi um*, rarely *Cicerbita*	shadow, rarely open	-, NO, SSW

sauteri has been found here.

On the other hand, the Khibine mountains provide good conditions for cryophilous-nivicole litter myxomycetes. This ecological group can be separated into two subgroups, based on phenology and habitat requirements (Tab. 1). The first subgroup contains the 'true' nivicole species, *Diacheopsis effusa*, *Diderma niveum* and the *Lepidoderma* and *Lamproderma* species (with the exception of *Lamproderma sauteri*). According to Schinner (1981), their habitat requirements can be characterized as follows:

- open ground,
- a more or less thick layer of herbaceous plant refuse,
- high snow cover in winter (may be for providing a dormant period, or simply for protection from hard frosts)

and an exposition, providing

- enough water from the melting snow to keep the substrate wet over 2-3 weeks,
- relatively high daily temperatures (for plasmodium growth), alterating with lower night temperatures (possibly for inducing fructification).

These habitats occur only very locally in the Khibine mountains, because conditions like open ground, heavy snow pack in winter and plants providing much herbaceous biomass are somewhat contradictory. Only a short time after snow melting, the ground is open and able to warm up during the day. Then the plants shoot very quickly and form a dense cover shadowing the ground. Therefore, the developing window for these species is small, in the Khibine mountains probably the second half of June. We were already slightly too late and did not found fresh sporocarps of the above-mentioned species. From the slopes around the Kirovsk Botanical Garden obviously the best place was the avalanche gutter described above, wet enough for tall perennials and with high snow cover hindering tree growth.

Surprisingly, also in the plains of the valley grounds species of these group were found, especially on places with high umbellifers. The reason may by the frequent inversion weather in the area. Probably the man-made meadows can serve as a secondary facultative habitat.

The second group of species is more cryophilous, growing predominantly in summer under cool and wet conditions on litter, especially in shady woodland. *Physarum cinereum*, *Didymium deplanatum* and *D. dubium*, perhaps *Trichia alpina* and *Lamproderma sauteri*, can be placed here. Their ecological requirements may be summarized as:

- shady ground,
- high moisture over a longer period (about two months)
- a more or less thick layer of herbaceous plant refuse.

Such habitats are common in the valleys of the Khibine mountains, also indicated by the abundance of *Physarum cinereum*. The most important substrate is formed by hollow, collapsed previous year's stems of *Cicerbita alpina* or *Cirsium heterophyllum*. The microclimate is moist and cold; here we found fresh sporocarps during the investigation time (July), especially of *Physarum cinereum* and *Lamproderma sauteri*.

Somewhat different are the microhabitats of two species. *Trichia alpina* was found predominantly on shaded leafy litter (especially rowan) between small boulders. Another exception was *Lamproderma sauteri*, preferring moss layers on rocks and boulders with running water. An extreme example was a place in the alpine tundra (565 m, locality 3c), a stony depression on a NO-exposed slope. On the ground floor was a two meter pack of big granite stones; their sides were covered with mosses, mainly the arctic-alpine liverwort *Gymnomitrium concinnatum* (Lightf.) Corda. Under the stones runs water from a nearby snowfield. *Lamproderma sauteri* seems to be the most cryophilous species, which does not need higher temperature in any phase of its development. Also the other growth places were very shady, often almost hidden, e.g. moss-covered rocks under tree roots.

Due to their geographical position and climate, the Khibine mountains have some features in common with the Scandinavian mountains. In comparison to the Ural and Siberian mountains, the following features are remarkable, indicating good conditions for snowline myxomycetes:

- the climatic conditions allow a relatively high snow cover also on slopes,
- the woodland boundary is formed by light birch woodlands, not by coniferous trees,
- high perennials grow also on the slopes, in a drier, more continental climate they are limited to damp valleys (eg. Putorany mountains in Siberia),
- some plants forming suitable substrates, such as *Athyrium distentifolium*, *Cicerbita alpina* or *Cirsium heterophyllum*, are common in the Khibine as well as in the Scandinavian mountains, but absent farther east,
- *Epilobium angustifolium*, an important substrate for litter myxomycetes, is replaced quantitatively by a smaller, closely related species in the Siberian mountains (*E. latifolium*). In contrast to the dense stands of *E. angustifolium* the latter species grows only scattered and does not provide a suitable substrate.

Our results together with the previous cited studies indicate, that nivicole myxomycetes can be expected throughout the Scandinavian mountains. R.E. Fries found nivicole species in habitats very similar to the Khibine mountains, also on *Cicerbita alpina*. A collection (Schnittler, not published) from the Jotunheimen Mountains in Norway yielded some nivicole species, with previous year's stems of the tall perennial *Aconitum septentrionale* as the main substrate. The nivicole species seem to be widely distributed in Scandinavia but occur only very locally. Because of the poor degree of investigation compared with the wood-inhabiting species (see for example Härkönen 1979) species new for Fennoscandia might be expected.

Acknowledgments – We are grateful to the staff of the Polar-Alpine Botanical Garden for offering us the possibility for field work around Kirovsk. The survey was carried out within the project "Russian Arctic Mycoflora", supported by the International Science Foundation. The laboratory work was supported by a stipendium from the German Academic Exchange Service (DAAD) for the first author. For sending us comparison material and confirmation of the determinations for the *Lamproderma* and *Lepidoderma* species we wish to thank Mrs. M. Meyer, St.-Paul, France. For linguistic revision we are indebted to Mr. H. Fox, Athy, Ireland.

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Nova Hedwigia 66 1—2 205—222 Stuttgart, Februar 1998

Late-autumn Myxomycetes of the Northern Ammergauer Alps

by

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With 2 figures and 1 table

Schnittler, M. & Y.K. Novohilov (1998): Late-autumn Myxomycetes of the Northern Ammergauer Alps. – Nova Hedwigia 66: 205-222.

Abstract: An inventory including data on abundance and microhabitats of myxomycetes is presented from a valley system of the Northern Ammergauer Alps with montane mixed fir forests. The area belongs to the northern Limestone Alps and is situated near Garmisch-Partenkirchen, Bavaria (47°31'N, 10°24'E).
During a two-week period in late October more than 6 km of narrow creek valleys were surveyed exhaustively. Sixty-five species of myxomycetes belonging to 27 genera were recorded and their microhabitats classified. For 40 species, found with fresh sporocarps, abundance estimations are added. A group of 11 species, found exclusively with fresh sporocarps and mostly in humid and cool environments, can be regarded as a late-autumn aspect. Previously considered as rare, some of them were found to be surprisingly common, providing evidence for a distinct late-autumn flora of montane but non-nivicolous myxomycetes.
Some species (*Barbeyella minutissima*, *Colloderma oculatum*) have a remarkable preference for decorticated logs coated with unicellular algae which form gelatinous layers. Evidence for a stable association of these slime moulds with algae is presented.

Keywords: northern European Alps, myxomycetes, species inventory, ecology.

Introduction

The true slime moulds (Myxomycetes) are a small group of organisms, including ca. 1000 described taxa. Besides Spain (Lado 1991, Lado & Pando 1994) and the Netherlands (Nannenga-Bremekamp 1974-1983), Germany can be regarded as one of the best investigated countries in continental Europe. The newest checklist (Schnittler et al. 1996) comprises 319 recorded species. But about 50% of these are represented by only one or a few collections; often exact microhabitat requirements are unknown. Due to the difficulties of recording (mostly small, fugacious fructifications commonly occurring only a few days in the year, often in hidden habitats) systematic surveys of myxomycetes including ecological data, as presented by Krieglsteiner (1993) for the Bavarian Forest, are rare.

For alpine myxomycetes, the papers by Meylan (see Kowalski 1975) from the Swiss Jura provide most of our taxonomic knowledge. The Alps have been investigated more recently by Meyer et al. (1992, French Savoie), Gottsberger (1966, Steiermark) and partially Nowotny (Upper Austria, since 1983). While these studies focus on nivicolous myxomycetes, this paper deals with non-nivicolous alpine species.

Materials and methods

The study area is a steep and narrow, often canyon-like valley system in the Northern Ammergauer Alps, situated 4-5 km northwest of Garmisch-Partenkirchen (Bavaria). The chosen sectors are located in a radius of less than 3 km (10° 24' 20" E, 47° 31' 55" N) at elevations between 850 and 1300 m. The main valley 'Lahnenwiesgraben' lies in the shadow of a mountain massive ('Kramerspitz', 1982 m). At 1140 m it is divided by a steep and high ridge into a northern part called 'Sulz-' or 'Wiesgraben', and a southern part named 'Stepberggraben' which was not investigated. All examined sectors lack roads or footpaths, having steep slopes, sometimes including limestone cliffs, with inclinations between 25 and 50°. Small creeks provide a continuously humid microclimate.

In terms of potentially natural vegetation, the whole area is fir-beech woodland (*Aposerido-Fagetum* Oberdorfer), the most frequent vegetation type in the northern limestone Alps between 700 and 1500 m (see Seibert 1968). The main tree species are fir (*Abies alba*), beech (*Fagus sylvatica*), mixed on the valley bottom with deciduous trees like sycamore (*Acer pseudoplatanus*), ash (*Fraxinus excelsior*) and elm (*Ulmus montana*). In spite of no visible influence of forestry on the valley bottom and the presence of all tree species typical of the natural vegetation, their relative abundances may be influenced by human impact. Fir grows probably less abundantly, often replaced by spruce (*Picea abies*), elm may be rarer than in former times because of Dutch elm disease. Nevertheless, large elm trees still exist. All sectors contained decayed wood of various size, with logs and trunks of old, fallen trees up to 1 m in diameter. Therefore, the area can be regarded as an example of an almost undisturbed myxomycete habitat.

For relief and vegetation, five sectors were differentiated in the part of the valley system studied. Their location is indicated in Gauss-Krüger coordinates (± 100 m); all are situated within the grid map quadrant 8432/3. The following brief descriptions cover only aspects of interest for myxomycete habitats. Nomenclature of the vascular plants follows Flora Europaea (Tutin et al. 1964-1993), the vernacular English names are used as in Stace (1991).

1: R 442898-442990 H 526555-75, 875-950 m
The lower part of the 'Lahnenwiesgraben'; width on the bottom 20-40 m. Montane woodland with tall firs and many deciduous trees; a rich flora of understorey shrubs like hazel (*Corylus avellana*) and species of honeysuckle (*Lonicera*), but also herbaceous plants as *Streptopus amplexifolius* indicate rich and moist, but well-drained soils. This sector is E-orientated and situated in the shade of the Kramer massive, having moderately cool and humid microclimate. The S-exposed lower slope is significantly warmer.

2: R 442865-98 H 526550-60, 950-970 m
A canyon-like, deep and rocky part, with the upper end formed by a small waterfall. The orientation is ENE, excluding direct sunlight, leading to a very damp and cool microclimate. Trees are mostly spruce, more rarely fir; fallen logs lie often directly over the creek.

3: R 442860-75 H 526560-70, 970-1030 m
A short adjacent side valley, SE-orientated, relatively steep and with significantly warmer microclimate, obtaining sunshine especially in the morning. Mainly beech forest, mixed with old fir trees and occasionally spruce.

4: R 442750-442810 H 526512-50, 1100-1240 m
A further canyon-like, rocky part with dolomite cliffs; very cool and damp due to the NE-orientation, sheltered by the 'Stepbergeck' ridge and therefore lacking direct sunshine. The dominating tree is spruce.

5: R 442700-50 H 526510-12, 1240-1260 m

The open, W-orientated upper part of the 'Sulzgraben'. The spruce woodlands of the N-exposed slope are often interrupted by avalanche gutters with almost pure stands of *Pinus mugo*. Due to the more open forest canopy, the microclimate is much dryer, the valley bottom is scattered with boulders.

The time of this investigation (October 14-23, 1994) was preceded by a week of initial snowfall (10-15 cm); night frosts with temperatures dropping to minus 5-10°C announced the winter. From October 10th onward, two weeks of clear, sunny days like an Indian summer brought warm air. At night it was still cold but not freezing, during the day the air warmed up to 25°C in sunny places. The valley system served as a trap for the cold air, leading to extended dewfalls. Day-time temperatures on the valley bottom ranged between 5 and 15°C. Dew evaporation needed almost the whole day, and often the understorey vegetation remained continuously wet.

The valley bottom and the first 20-40 m of the slopes on both sides with no visible impact of forestry were investigated. In this strip not broader than 100 m all larger logs and most of the smaller, decaying tree trunks, moss-covered boulders, larger moss tussocks and, at regular distances, litter on the ground were checked. This resulted in often less than 500 m per day being investigated. Interesting microhabitats were inspected with magnifying spectacles (3x), sometimes wood pieces were collected to be checked later with a dissecting microscope. Occasionally pH values of substrates were measured with a solid-state pHuture probe and a pHmeter Orion 610. For all collected specimens, valley sector, tree species and microhabitat features were noted in the field.

The microhabitat was classified according to the following list of abbreviations:

cor - bark of living trees (all corticolous species obtained in moist chambers).
wood1 - dead, but undecayed wood, often from still erect or freshly wind-blown trees, with bark firmly attached.
wood2 - slightly decayed wood, bark still attached but cambium already rotten, wood ± solid.
wood3 - moderately decayed wood, bark already loose or falling off, wood still in good shape, but appearing softer and often with abundant fungal colonization.
wood4 - strongly decayed, partly destroyed and brittle wood, mostly (except *Betula*-logs) without bark, wood soft and of spongy consistency, mostly from thicker logs.
woodA - decorticated, slightly to moderately decayed wood of logs thicker than 15 cm, from very moist (water-saturated air) and shady places, covered by a thin slimy layer of algae and liverworts.
woodM - mostly decorticated wood, moderately to strongly decayed and covered with thicker (> 1 cm) tussocks of mosses (often *Paraleucobryum* sp.), sometimes liverworts (*Mylia* spp.), enriched with detritus.

Although checked in the field and with moist chamber technique, litter and animal dung revealed no myxomycetes and they were therefore omitted from the list above.

Scattered throughout all valley sections, samples were obtained for moist chamber cultures. Forty-six moist chamber experiments were carried out, running 2.5 months. Cultures were prepared as described by Härkönen (1977, 1981).

Common and easily recognized myxomycete species were usually registered directly in the field, but rare species and those difficult to recognize in the field were always collected. As in other ecological and biogeographical works (Eliasson 1981, Stephenson 1988) we defined all fructifications that could have arisen from one plasmodium as one specimen. In practice, we assumed that sporocarps that shared the same substratum and were separated by a distance that could be overcome by a migrating plasmodium belonged to the same plasmodium. For estimation of abundance, the percentage scale of Stephenson et al. (1993) was adapted, based on the proportion of a species in the total number of records (about 500 over the survey):

R - rare (<0.5%): recorded once or twice, O - occasional (0.5-1.5%): 3-6 records, C - common (1.5-3%): 7-15 records, A - abundant (>3%): more than 15 records.

These abundance estimations were applied only to specimens found with fresh sporocarps. Therefore, they characterize only the late-autumn aspect, and not the occurrence over the whole year. For determination, sporocarps were often preserved as permanent slides in polyvinyl lactophenol and/or glycerol gelatin, to distinguish between limeless and lime-containing structures. In several cases specimens were examined with a JEOL 35c scanning electron microscope.

Observations

The following annotated list includes all recorded species in alphabetical order. The nomenclature follows Martin & Alexopoulos (1969), with a few exceptions. The estimation of abundance is followed by the scientific name and the collection numbers of the first author, combined with the number of the respective valley sector after a slash. The string '...' at the end of the list indicates common species of which not all records were preserved. Determinations considered as doubtful are given with the note 'cf.' (confer). The symbol '(-)' indicates specimens with withered sporocarps, '(mc)' those obtained from moist chamber experiments. In these cases no estimations of abundance are given. Otherwise, all collections were found in fresh condition in the field. After a semicolon, the microhabitats are listed in the order of their frequency. For rare and/or doubtful species taxonomic descriptions were added.

R *Arcyria cinerea* (Bull.) Pers.: 5324/1; wood3.

O *Arcyria denudata* (L.) Wettst.: 5351/1, 5424/1, 5458/3(cf.); wood3-4.

C *Arcyria helvetica* (Meylan) Neubert, Nowotny & Baumann (Carolinea 47: 43. 1989), syn. *A. incarnata* var. *helvetica* Meylan (Bull. Soc. Vaud. Sci. Nat. 46: 55. 1910): 5317/1, 5338/1, 5341/1, 5373/2, 5415/3, 5427/2, 5448/4; wood(1-)3-4. - Sporocarps scattered or in small colonies, stalked, up to 2 mm high, before capillitium is expanded. Stalk 0.4-0.9 mm in length, solid, with only a few spore-like cells, dull red to almost black at base, under transmitted light translucent red, with fibrous structure. Hypothallus translucent, membranous, separate for each sporocarp or common to the whole group. Capitulum pear-shaped to globose, 0.4-0.8 mm in diameter, 0.7-1.2 mm in length, when fresh dark to bright vinaceous, but fading to greyish, brown-red or pinkish with age. Peridium persistent, sometimes enveloping the whole capitulum, but more often separated into thinner, partly fugacious upper flakes and a persistent calyculus. The latter often occupying the whole lower half of the capitulum, with a somewhat irregular plicate, slightly shining peridium in fresh sporocarps, appearing pale reddish under the microscope, ornamented with warts tending to be connected by inconspicuous ridges to a network. The upper parts of the peridium are colourless and almost smooth. Capillitium a dense network forming a plume of 1.5-2 fold the capitulum size, only loosely attached to the calyculus centre, with almost colourless to pale reddish threads 5.5-6.5 µm wide, ornamented with conspicuous, short and broad cogs, often fimbriate at the ends and 1-1.2 µm high. Fresh spore mass vinaceous; spores under the microscope very pale pinkish, globose, almost smooth, 6.8-7.2-(7.5) m.

This form could be recognized in the field by the conspicuous carmine-red colour and the often persistent upper peridium. In valley sector 1 it occurred only in the upper part (above 900 m), preferring a colder microclimate, on spruce/fir and beech logs.

O *Arcyria incarnata* (Pers.) Pers.: 5337/1 ...; wood4. - More frequent in the lower parts of the valley system, often but not always with already weathered fructifications. Forms merging into *A. helvetica* were not observed.

R *Arcyria oerstedtii* Rostaf.: 5342/1; wood3. - These and the following species were found only once on beech logs from the S-exposed slope.

R *Badhamia panicea* (Fr.) Rostaf.: 5314/1; wood2.

A *Barbeyella minutissima* Meylan: 5359/1, 5367/1, 5388/1, 5404/2, 5435/2, 5442/4, 5447/4 ...; woodA, wood4. - The species occurred almost entirely on decorticated spruce and fir logs covered with algae having a slimy, gelatinous matrix embedding their cells (subsequently called slimy-algae). This was also observed in other valleys at this time (eg. 'Partnachklamm').

R *Calomyxa metallica* (Berk.) Nieuwl.: 5413/2, 5445/4; wood4. - Recorded only from the coldest and most humid valley sectors, this species was seen in clusters of 10-50 densely crowded, rarely single sporocarps forming up to 1 cm long colonies. Sporocarps were sessile on a broad base, 0.6-1.2 mm in diameter, angular due to mutual pressure with a tendency to reduce the peridium on the contact surfaces. Hypothallus common for one colony, with the same features as the peridium; the latter persistent but easily separated from the spore mass due to shrinkage in mature dry sporocarps, conspicuously shiny but not iridescent, resembling a pale brown cellophane layer; under the microscope translucent, pale brown with some violet tints, smooth. Capillitium formed by inconspicuous, free and very elastic threads, rarely branched, under transmitted light almost colourless, with a halo due to densely arranged spines (SEM), without ornamentation 1-1.5 µm wide.

Spores in mass pale grey-brown with coppery tint, under the microscope globose, almost colourless, with regularly distributed, fine spines up to 1 µm in length, (9.5)-10.0-10.7(-11) µm in diameter.

In moist chamber culture this species forms solitary, bright-yellow to greyish-violaceous, very small sporocarps. As noted in Martin & Alexopoulos (1969) sporocarps developed in the field can coalesce into pseudoaethalia, described as var. *intermedia* by Meylan (1910).

C *Clastoderma debaryanum* A. Blytt: 5330/1, 5344/1, 5345/1, 5390/1, ...; wood4. - Four of the seven records of this species, all fresh, were from the lower side of well-decayed fruitbodies of Poriales, still attached to their host logs, the other collections are from well-decayed beech and alder twigs. Besides one doubtful mention by Killermann (1946), these seem to be the first German records. All specimens were found in dense, but not crowded and often large colonies. The sporocarps up to 1.5 mm high fit well the description for the type variety.

- *Collaria* cf. *rubens* (Lister) Nann.-Bremek. (Proc. K. Ned. Akad. Wet. C 70: 209. 1967), syn. *Comatricha rubens* Lister: 5888/1(mc); wood3. - Sporocarps forming a small group sharing either a common hypothallus or scattered and separate, 1.5-2.3 mm in height, long-stalked. Hypothallus a small disk with irregular margins, black to brownish. Stalk 1.5-2 mm in length, continuously tapering upwards (diameter decreasing from 15 µm at the base to 3 µm at the apex), black, under the microscope fibrous, opaque, dark red-brown to black in the upper part, dividing into 2-4 main capillitial branches. Capitulum globose, erect, bright copper-brown, 0.1-0.3 µm in diameter. Peridium fugacious, except for a small collar at the base of the capitulum, smooth and very pale brown under transmitted light. Capillitium arising from a few main branches, with relatively sparse, curved and slender threads, ending free at the periphery without a surface net, pale brown under the microscope, about 1 µm wide. Spores in mass copper-brown, globose to ovoid, very pale brown under transmitted light, ornamented with distant and irregularly distributed spines less than 0.5 m, (7)-7.5-7.8-(8) µm in diameter.

The specimen fits the description given by Nannenga-Bremekamp (1991) except for the collar which should be more prominent and the very long stalk (described as only 2-3 times longer than the capitulum). Due to the scanty material (only a few sporocarps, *Pinus* bark of a dry, S-exposed slope), we cannot clearly assign it to this species.

A *Colloderma oculatum* (Lippert) G. Lister: 5388/1, 5405/2, 5444/4 ...; woodA, wood4. - Sporocarps widely scattered, 0.2-0.4 µm in diameter, when fresh sessile on and within a thick gelatinous layer, which often elevates the sporocarp up to 3 times above the surface; later, after drying, iridescent with brilliant blue colours and sessile on a broad base directly on the substratum. Peridium very thin (when drying, the sporocarp usually breaks off from the gelatinous layer), under the microscope colourless and smooth. Columella absent. Capillitium a branched network arising from the base of the sporocarp, with colourless to pale violet-brown, mostly free-ending threads which are very lax, 0.5 to 1.5 µm wide, surrounded by a fine, inconspicuous and colourless sheath, at the ends branched, the finest tips almost colourless, sometimes with darker thickenings up to 3 µm thick. Spores in mass dull brown to black, under the microscope dusty violet-brown, globose, ornamented with regularly distributed, small darker warts, (10.5)-11 µm in diameter.

The very small, always single sporocarps were remarkable. This feature contrasts with the dense colonies of significantly larger sporocarps found on rocks in Karelia (Schnittler & Novozhilov 1996). Also the capillitial threads surrounded by a translucent sheath and the absence of a small columella differ from the Karelian collections. The species was often found associated with *Barbeyella minutissima*, and like this species, it shows a preference for slimy-algae-covered wood. Mostly the sporocarps were still immature, as indicated by the white to greyish colour and shrinkage when drying.

O *Comatricha nigra* (Pers. ex J.F. Gmel.) Schroet.: 5322/1, 5391/1, 5406/2 ...; wood4, wood3. - Found mostly weathered, but two fresh colonies were associated with *Barbeyella minutissima* and *Colloderma oculatum*; here with scattered, small sporocarps showing very long, slender stalks.

- *Comatricha tenerrima* (M.A. Curtis) G. Lister: 5318/1(-); wood3. - One scanty record from a thin, fallen *Fagus* twig.

R *Cribraria argillacea* (Pers.) Pers.: 5343/1; wood4.

R *Cribraria atrofusca* G.W. Martin & Lovejoy: 5389/1; wood4. - Sporocarps scattered, long-stalked, 0.6-1.4 mm high, capitulum globose to urniform, ± erect, 0.3-0.45 mm in diameter. Hypothallus an inconspicuous extension of the stalk, dark purple-brown. Stalk 0.7-1.2 mm in height, 4-5 times longer than the capitulum, shiny purple-brown, under transmitted light translucent-opaque red-brown, fibrous. Peridium a bright silvery-shining, purple-brown, deep cup-shaped to urniform calyculus, occupying half of the diameter of the capitulum, under the microscope hazel-brown, with wavy transverse shrinkage lines and slightly darker, clustered granula (2)-2.5-3 µm in size. Upper part an irregular network of barely free-ending threads, with small, slightly thickened nodes, which show dense granulation contrasting with the threads. Peridium often persistent between the net meshes, shining silvery under the dissecting microscope, under transmitted light appearing as a pale, almost colourless aura around threads and nodes. Spores as a mass purple-brown, with transmitted light very

pale brown, globose to slightly ovoid, with fine, more or less regularly distributed warts underlaid by a coarse network of inconspicuous, pale ridges, giving the spores a somewhat angular shape in optical section; spores 8.2-8.6 µm in diameter.

This is seemingly the first German record, the specimen was associated with *Echinostelium minutum* and small colonies of *Colloderma oculatum* and *Barbeyella minutissima* on a single, brown-rotted *Alnus* log lying in a dense *Molinia* stand in a small alder swamp.

- *Cribraria cancellata* (Batsch) Nann.-Bremek.: 5356/1(-), 5394/1(-); wood4, woodM.

- *Cribraria microcarpa* (Schrad.) Pers.: 5885/1(mc), 5886/1(mc); wood3-4. - Two records each of a few sporocarps, both from decorticated, moderately decayed wood of alder and pine (*Pinus sylvestris*).

- *Cribraria* cf. *montana* Nann.-Bremek. (Proc. K. Ned. Akad. Wet. C 76: 476. 1973): 5407/2(-); woodA. - The single record, associated with *Barbeyella minutissima*, consists of a few mouldy sporocarps thus preventing a reliable determination.

- *Cribraria purpurea* Schrad.: 5371/1(-); wood4. - One very large colony spread over an area of 3-4 m^2 on a much-decayed spruce log of already spongy consistency.

O *Cribraria rufa* (Roth) Rostaf.: 5393/1, 5401/3 ...; wood4. - Only two small fresh colonies found on S-exposed slopes of the warmer valley sections.

- *Cribraria violacea* Rex: 5887/3(mc); cor. - One record from *Tilia* bark.

R *Dianema depressum* (Lister) Lister: 5323/1; wood3. - The single collection consists of some plasmodiocarps from the lower side of a dead *Sorbus* branch buried in leaf litter. The grey brown fructifications are easily overlooked, therefore this species might be commoner.

O *Diderma asteroides* (Lister & G. Lister) G. Lister: 5396/3, 5416/3, 5456/3 ...; wood4. - Recorded only from the warmest section of the valley system in five colonies on thick (> 50 cm diameter) *Abies*, *Pinus* and *Fagus* logs, once associated with the *D. floriforme*. All fructification phases beginning from the milky-white plasmodium were observed; remnants from the previous year were found twice on the same logs indicating a relative constancy of occurrence.

R *Diderma floriforme* (Bull.) Pers.: 5395/3; wood3.

A *Diderma montanum* (Meylan) Meylan: 5375/2, 5397/3, 5446/4, 5459/3, 5460/3 ...; wood2-4, woodM. - Fresh, often still developing fructifications in all cooler valley bottoms, mostly on moderately decayed wood of spruce and beech, often on mossy, loose bark.

R *Diderma umbilicatum* Pers. (Syn. meth. Fung. 165. 1801), syn. *D. radiatum* var. *umbilicatum* (Pers.) Lister: 5449/4; wood4. - Only one collection, macroscopically similar to *D. montanum* and associated with this species, differing in slightly larger spores: 10-11 (vs. 8.5-9.5 µm diameter in *D. montanum*) and larger columellae: 0.8-0.9 (vs. 0.2-0.4) mm. In contrast to the view expressed by Martin & Alexopoulos (1969), this taxon is clearly separated from *D. radiatum* (L.) Morgan (Nannenga-Bremekamp 1991), but the occurrence with *D. montanum* in the same microhabitat suggests that intermediate forms may exist.

R *Echinostelium minutum* de Bary: 5417/1, 5884/1(mc); wood4, cor. - One field record from a brown-rotted alder log, the other from bark of living pine on a S-exposed valley slope.

- *Enerthenema papillatum* (Pers.) Rostaf.: 5889/3(mc); cor.

R *Enteridium lycoperdon* (Bull.) Farr (Taxon 25: 514. 1976), syn. *Reticularia lycoperdon* Bull.: 5399/3, 5411/3; wood2-3.

R *Enteridium splendens* var. *juranum* (Meylan) Härkönen (Karstenia 19: 5. 1979), syn. *Reticularia jurana* Meylan: 5385/1; wood2. - Observed once on a slightly decayed, still solid beech log, in a bright, open part of a valley.

- *Fuligo septica* (L.) Wiggers var. *septica*: 5392/1(-).

- *Fuligo leviderma* Neubert, Nowotny & Baumann (Myxomyc. II: 211. 1995): 5325/1(-), wood3. - One aethalium on a partly dead, still erect *Ulmus*; probably developed before the frost period.

A *Hemitrichia clavata* (Pers.) Rostaf.: 5355/1, 5366/1, 5379/1, 5380/1 ...; wood3-4, woodM. - Only seen in the lower valley regions, mostly on *Fagus*.

A *Hemitrichia serpula* (Scop.) Rostaf.: 5328/1, 5332/1, 5364/1, 5368/1, 5374/2, 5381/1, 5384/1 ...; wood3-4, woodM. - Abundant especially in the lower valley regions; on fallen twigs and thinner logs between litter, always on the lower side.

O *Lamproderma arcyrionema* Rostaf.: 5333/1, 5349/1 ...; wood3, woodM.

A *Lamproderma columbinum* (Pers.) Rostaf.: 5312/1, 5348/1, 5357/1, 5365/1, 5367/1, 5400/3, 5403/2, 5409/2, 5430/2, 5447/4 ...; woodM, wood4. - One of the commonest species throughout all valley sectors, found as fresh, large and conspicuous colonies on thick moss beds covering rocks or fallen logs.

R *Lamproderma* cf. *sauteri* Rostaf.: 5370/1, 5376/2; woodM. - Sporocarps in large colonies, gregarious, up to 3 mm high. Stalk 1-2 mm long, dull black and opaque under the microscope. Hypothallus prominent, a black disk of irregular shape, at least the size of the capitulum, sometimes merging with those of the neighbouring sporocarps, under transmitted light violet-brown. Capitulum globose, erect, 0.8-1 mm in diameter. Peridium persistent, iridescent with metallic blue and violet colours, flaking away only in overmature sporocarps as large, irregular pieces, under transmitted light pale violet-brown, smooth, sometimes with remnants of capillitium tips. Stalk tapering into a blunt-ending columella attaining about one half the diameter of the capitulum. Capillitial threads arising from the apex of the columella, sometimes becoming flattened and then up to 6 µm wide, under the microscope pale violet-brown, the outer, branching and anastomosing tips almost colourless, free or attached to the peridium with fine but not funnel-shaped ends. Spores in mass dull brown to almost black, under the microscope uniformely violet-brown, globose, ornamented with regularly distributed, dark warts not exceeding 0.5 µm in length, (14)-15-18-(20) µm in diameter.

Features such as larger spores, shorter stipe and the capillitium arising only from the apex of the columella exclude *C. columbinum*. But not all characters agree with those for *L. sauteri* (eg. spores without a paler side as mentioned in Nowotny 1989 without exception, in Kowalski 1970 as often occurring). For the moment we place these specimens under *L. sauteri*, which is not strictly a snowline species, as seen in the arctic Khibine mountains (Novozhilov & Schnittler 1996) and highly variable.

A *Lepidoderma tigrinum* (Schrad.) Rostaf.: 5354/1, 5358/1, 5359/1, 5383/1, 5408/2, 5425/2, 5434/4, 5443/5, 5453/3, 5457/3 ...; woodM, woodA. - Frequently still developing, the orange-yellow plasmodia were extraordinarily conspicuous and abundant. Seen on all localities with *Barbeyella minutissima* and *Colloderma oculatum* (woodA), but more frequently on loose, mossy and algae-covered bark of *Picea* and *Abies* logs and trunks. As indicated by observations from Karelia (Schnittler & Novozhilov 1996), this species forms an association with *Colloderma* but has a wider ecological spectrum.

- *Licea kleistobolus* G.W. Martin: 5883/5(mc); cor. - Obtained only once from pine bark of a dry, S-exposed valley slope.

- *Licea operculata* (Wingate) G.W. Martin: 5317/1(-); wood3. - Two sporocarps were found in the field, within a colony of *Arcyria helvetica*.

R *Licea pygmaea* (Meylan) B. Ing (Trans. Brit. Mycol. Soc. 78: 443. 1982), syn. *L. pusilla* var. *pygmaea* Meylan: 5412/2; woodA. - Always scattered, small sporocarps of various size ranging from (0.05)-0.1 to 0.4 mm, half-ovoid in shape if still closed but of asterisk-like appearence when open, height $^1/_2$-$^2/_3$ of the diameter, without a dirty margin or any visible hypothallus, showing a system of prominent ridges when dry; colour dark brown when filled with spores. Peridium under the dissecting microscope brown, inside conspicuously shining, but outside granulose and mat, breaking along dehiscence lines, under transmitted light bright yellow-brown, smooth, but with prominent warts of 0.8-1.0 µm diameter on the dehiscence lines. Spore mass black, under the microscope greyish brown, globose to ovoid, ornamented with very fine, regularly distributed warts and a thin-walled germination pore occupying less then $^1/_{10}$ of the optical section, (11)-11.5-12.5-(13) µm in diameter.

Considering only the small differences from *L. minima* (duller in all parts) and *L. pusilla* (smaller sporocarps and spores), the distinction of this taxon requires confirmation by further collections.

- *Lycogala epidendrum* (L.) Fr.: 5311/1, ...; wood3-4. - Mostly found with older and partly decayed aethalia suggesting a fructification peak before the initial frosts.

- *Macbrideola cornea* (G. Lister & Cran) Alexop.: 5890/1(mc); cor. - Obtained once from bark of living *Acer pseudoplatanus*, together with *Perichaena chrysosperma*.

- *Metatrichia vesparium* (Batsch) Nann.-Bremek.: 5331/1(-), 5352/1(-), 5418/1(-), ...; wood3-4. - Found with mouldy sporocarps and more commonly in the lower valley sectors.

- *Perichaena chrysosperma* (Currey) Lister: 5881/1(mc); cor.

R *Perichaena corticalis* (Batsch) Rostaf.: 5420/1; wood3.

- *Perichaena vermicularis* (Schw.) Rostaf.: 5882/3(mc), cor. - Bark of living *Ulmus* yielded a small group of sporocarps. The thick, dark brown peridium together with a scanty capillitium is typical for the corticolous form of this species.

- *Physarum* cf. *leucophaeum* Fr.: 5353/1(-); wood3. - One, strongly withered collection.

R *Physarum nutans* Pers.: 5316/1; wood3. - Only one fresh colony was recorded from a *Picea* log.

R *Physarum viride* (Bull.) Pers.: 5319/1, 5321/1; wood3. - This species, usually common in montane spruce forests earlier in the year (observations from Thuringia), was found only twice on *Sorbus*.

- *Symphytocarpus* cf. *confluens* (Cooke & Ellis) B. Ing & Nann.-Bremek. (Proc. K. Ned. Akad. Wet. C 70: 219. 1967), syn. *Stemonitis splendens* var. *confluens* (Cooke & Ellis) Lister pro parte: 5433/2; wood1. - One older aethalium on bark fissures on the trunk of a thick, recently wind-broken spruce, in 2.5 m height.

A *Trichia botrytis* (J.F. Gmel.) Pers.: 5346/1, 5372/2, 5387/1, 5454/5 ...; wood4-3. - Specimen 5454 approaches in habit *Metatrichia floriformis* (Batsch.) Nann.-Bremek., but showing the typical opaque stalk and ochraceous colour of capillitium and spores.

R *Trichia* cf. *contorta* (Ditmar) Rostaf.: 5423/1; wood3. - One scanty specimen, found under the bark of a decayed *Sorbus* log. A form with aberrant capillitium; simple, rarely branched threads lying free

in the spore mass, ornamented with three spiral bands, 2-3(-4.5) µm wide, tips blunt or elongated, 4-8 µm long.

A *Trichia decipiens* (Pers.) Macbr.: 5329/1, 5334/1, 5336/1, 5347/1, 5414/2, ...; wood4-3.

A *Trichia favoginea* (Batsch) Pers.: 5320/1, 5335/1, 5362/1, 5398/3, 5452/5, 5461/3(cf.) ...; wood4. - As already pointed out by Neubert et al. (1993: 264), intermediate forms between *T. favoginea* and *T. persimilis* seem to be absent in Europe. Therefore, in contrast to Farr (1958), each species is here treated separately.

A *Trichia floriformis* (Schw.) G. Lister: 5326/1, 5361/1, 5402/1, ...; wood4.

A *Trichia persimilis* P. Karst.: 5327/1(cf.), 5339/1, 5360/1, 5363/1, 5369/1, 5382/1, 5386/1, 5429/2, 5450/4(cf.), 5451/5 ...; wood4. - Though sharing the same microhabitat, all specimens assigned to this species could be separated even macroscopically from *T. favoginea* by the globose shape of the sporocarps. Microscopically they differed clearly by the fragmentary spore net consisting of small ridges, except 5451 which had an almost closed net.

C *Trichia scabra* Rostaf.: 5419/1, 5422/1, 5426/1, 5431/1; wood4-3. - All records were from the lower part of valley section 1, below 900 m.

A *Trichia varia* (Pers. ex J.F. Gmel.) Pers.: 5313/1, 5340/1, 5350/1, 5378/1, 5421/1, 5428/2, 5432/2 ...; wood4-3, woodM. - Observed frequently in all parts of the valley except the very shady and moist sections 2 and 4. One large colony was observed on frozen, decayed *Petasites* leaves, with developing sporocarps changing from white to yellow in colour, as usual during sporocarp formation.

The following species were all found together on heaps of cut hay in a 5 x 10 m large piece of open grassland in front of a shelter for controlling water levels in the rivulet. It lies on the lowermost southern slope of section 1, therefore receiving some hours of sunshine per day. *Perichaena vermicularis* was seen in the lignicolous form with a fragile, translucent yellow peridium like an *Arcyria*, and a well-developed capillitium. *Physarum vernum* is known as being preferentially nivicolous.

Diderma hemisphaericum (Bull.) Hornem.: 5437
Didymium bahiense Gottsb. (Nova Hedwigia 15: 365. 1968): 5438(-)
Didymium difforme (Pers.) S.F. Gray: 5441 ...
Didymium squamulosum (Alb. & Schw.) Fr.: 5891(mc), 5315 ...
Perichaena vermicularis (Schw.) Rostaf.: 5439/1
Physarum cinereum (Batsch) Pers.: 5436
Physarum vernum Somm.: 5455.

Discussion

Sixty-five species of myxomycetes were identified from 156 collections and numerous fructifications seen only in the field. Nine species were obtained only from moist chamber experiments. These and the seven records from litter are excluded from all further analyses. Compared with the number of species that can be expected in alpine regions (Gottsberger 1966), only a small proportion was recorded. The main reason is the almost complete absence of nivicolous and summer myxomycetes in late autumn. With a fructification period starting earlier, as suggested by regular observations of mouldy colonies along with numerous fresh fructifications, the *Trichia* species were the commonest myxomycetes found in the survey (>26 % of all observations). This corresponds with findings from the climatically similar Upper Austria (Nowotny 1993).

Additionally, a number of species considered to be rare was found, often with high abundances (estimations in brackets). In this group we include *Arcyria helvetica* (C), *Barbeyella minutissima* (A), *Calomyxa metallica* (R), *Clastoderma debaryanum* (C), *Colloderma oculatum* (A), *Diderma montanum* (A), *D. umbilicatum* (R), *Lamproderma columbinum* (A), *L.* cf. *sauteri* (R), *Lepidoderma tigrinum* (A) and *Licea pygmaea* (R). From these species, all recorded colonies were observed in fresh condition. Except for some remnant stalks of *Lamproderma*, very probably from the previous year, no weathered specimens were seen. Therefore, it is likely that they are absent in summer and early autumn. The common feature of these late-autumn species is their obvious ability to develop under cold conditions, as indicated by their occurrence in the moist and cool parts of the valley system. 66% of all observations in the valley sectors 2 and 4 belong to this group, compared with 28% in the warmer sectors. The preferred substrata of this group are strongly decayed (37% of the records), moss-overgrown (31%) or algae-covered wood (22%).

For the latter microhabitat, a typical example was seen in valley sector 4. Shaded by large spruce and beech trees, a *Picea* log of 70 cm diameter lay between rocks, 1.5-2 m above the creek. During the whole day the wind-preserved log was wet from dew, but even during the early morning the rivulet prevented it from freezing and developing hoarfrost, as seen in the more open valley regions. Only the outer layer, about 0.5 cm, of the decorticated log was smooth and covered by a thin, greenish and slimy sheet of algae, overgrown with scattered, small threads of liverworts (see Tab. 1). The myxomycete association, here formed by huge colonies of *Barbeyella minutissima* and *Licea pygmaea* with scattered sporocarps of *Colloderma* and *Lepidoderma*, extended for 2 m primarily on the lower side of the log directed towards the rivulet and preserved from rainfall. A similar association was observed in other valley sections too, but lacking *Licea pygmaea*. As suggested by the still solid and undecayed wood within this log and by similar observations on Karelian rocks (Schnittler & Novozhilov 1996), the algal layer seems to form the microenvironment of the plasmodia.

For three larger collections of *Barbeyella minutissima* and *Colloderma oculatum* (all woodA) the algae were determinated (Tab. 1); mostly species with a thick, translucent gelatinous slimy layer embedding the cells. Such algae are typical of wood and rocks staying continuously moist over a longer period. As observed in fresh preparations, bacteria frequently inhabit the slimy layers. The bacteria or even the slimy layers and algal cells themselves may be consumed by the plasmodia.

Lazo (1961) could show successful growth of plasmodia with green algae in agar culture. In spite of his attempt with litter myxomycetes (*Physarum*, *Fuligo* spp.) and freshwater algae (*Euglena*, *Chlorella* spp.), a combination probably not occurring regularly in nature, he was able to demonstrate the incorporation of algae into plasmodia, their much improved growth with algae compared to pure culture, and a higher resistance to acidity in the presence of algae. Especially the last finding seems to

Tab. 1. Algae, liverworts and musci from two collections of *Barbeyella minutissima* (5442, 5404) and one of *Colloderma oculatum* (5405); ++ forming extended, clearly visible layers up to 1 mm thick (or a ± dense network of shoots for mosses), + forming smaller and thinner layers not clearly visible (single shoots in mosses), - absent.

Taxa	5442	5404	5405
algae:			
Coccomyxa gloeobotrydiformis Reisigl (Chlorophyta)	++	-	-
Elliptochloris bilobata Tsch.-Woess (Chlorophyta)	+	-	+
Gloeobotrys gelatinosa Reisigl (Xantophyta)	-	++	-
Myrmecia bisecta Reisigl (Chlorophyta)	-	+	-
Pseudococcomyxa simplex (Mainx) Fott (Chlorophyta)	+	+	+
liverworts:			
Blepharostoma trichophyllum (L.) Dumort.	+	+	-
Cephalozia lacinulata J.B. Jack ex Spruce	+	-	+
Calypogeia spec.	+	++	-
Lophocolea heterophylla (Schrad.) Dumort.	+	-	-
Nowellia curvifolia (Dicks.) Mitt.	+	++	+
Plagiochila asplenioides ssp. *porelloides* (Nees) R.M. Schust.	-	++	-
Riccardia palmata (Hedw.) Carruth.			
Tritomaria exsecta (Schrad.) Loeske	+	++	-
	-	++	-
Musci:			
Herzogiella turfacea (Lindb.) Iwats.	-	+	-
Paraleucobryum sp.	-	+	-
Plagiothecium cf. *laetum* Schimp.	-	+	-

be noteworthy, because the decorticated logs in our survey were acidic (pH values between 3.8 and 4.1 measured on the log mentioned above).

Our observations suggest that the association of myxomycetes fruiting upon bryophytes is one of coincidence (Stephenson & Studlar 1985). *Licea pygmaea* and *Colloderma oculatum* grew almost always directly on the wood, *Barbeyella minutissima* was seen often but not always on the small leaf tips of the liverworts protruding above the water film.

An association with algae (*Barbeyella minutissima*: obvious in 70 %, *Colloderma oculatum*: 60 % of all observations) would explain the late fructification peak. Only the cool nights in late autumn guarantee extended dewfall that keeps the logs continuously wet for some weeks, thus allowing algal growth. The higher day-time temperatures allow the associated myxomycetes to develop.

In general, the richness of myxomycetes seen with fresh fructifications differs widely in the various valley sectors (Fig. 1A). With 39 species recorded in sector 1, it provided almost two thirds of all myxomycete colonies observed in fresh condition. In addition to the lower elevation the higher proportion of deciduous trees could be the reason. In the sectors 2 and 4 with a cold microclimate only

18 species occurred, 10 belonging to the late-autumn group. In spite of its higher elevation and small size, almost the same number of species were recorded in sector 3 as in 2 and 4, but with a different species composition. Sector 5 with an elevation above 1240 m and light and open woodland yielded only 5 species. Remarkable is the high degree of similarity between the two cold and rocky valley sectors (2 and 4).

Although represented by almost equal numbers of collections, deciduous wood (35) gave rise to more species than coniferous wood (26). About one half of all species were found on both substrate types (Coefficient of Community = 0.56). In correlation to their abundance, *Picea* and *Fagus* are the most important woody substrates, followed by *Alnus*, *Sorbus* and *Abies* (Fig. 1B).

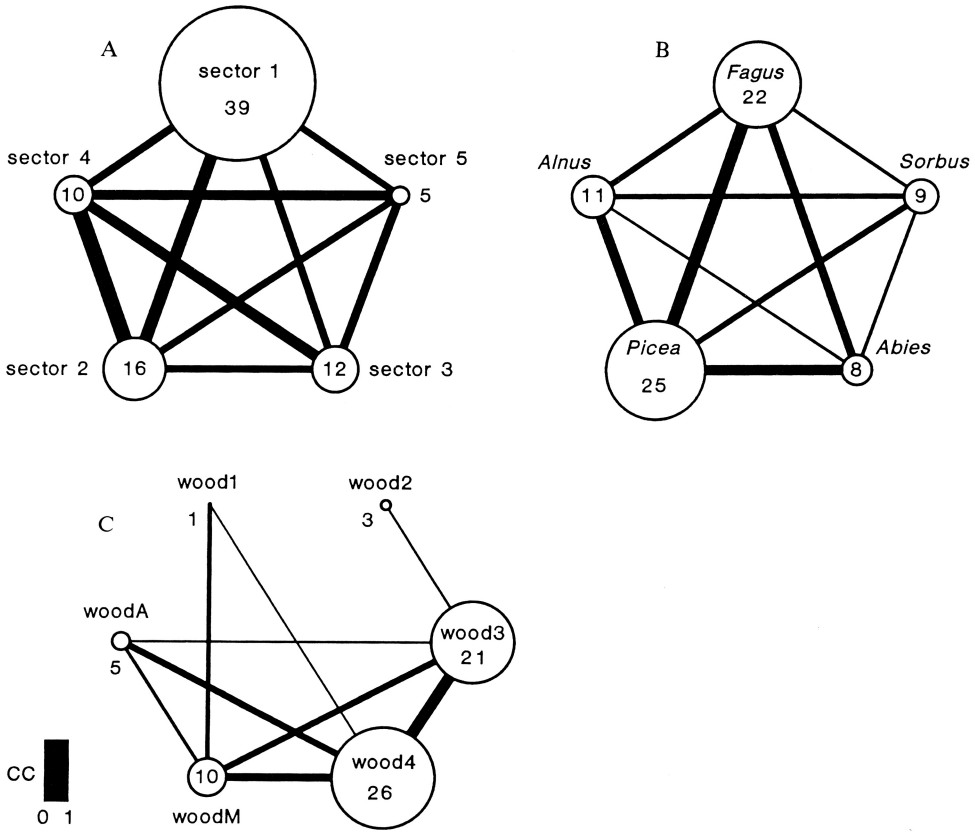

Fig. 1. Relationships of occurrence of myxomycetes within valley sectors (A), main tree species (B), and microhabitats (C). The sizes of the circles represents the numbers of species collected in the respective structure (numbers inside), the thickness of the connecting lines the degree of similarity (calculated as Coeffecient of Community, see Stephenson et al. 1993).

The main microhabitat was shaded wood in all stages of decay, preference being given to thoroughly rotted logs (Fig. 1C). Due to the absence of most Stemonitales, slightly decayed wood seldom harboured myxomycetes. Besides the open patch of grassland caused by man, litter on the ground had no fresh slime moulds. A comparison of microhabitat preferences between the late-autumn aspect (species found fresh grown only) and the remaining species (found weathered and fresh) indicates a preference of the former for substrates with algae and mosses (Fig 2). It can be speculated, that the late-autumn species live mainly on the surface of the wood, in contrast to other wood inhabitants (in particular Trichiales) with plasmodia hidden inside the wood. Therefore, these late-autumn species should suffer more from desiccation on warm days, resulting in a stronger dependance on dewfall and occurrence later in the year. On the other hand, smaller daily temperature fluctuations in the deep valleys, keeping off night frosts longer, allow a fructification period late in the autumn.

In attempts to reveal more of the total myxomycete diversity, samples for moist chambers were taken from liverwort layers (14), the main tree species (11 from deciduous, 9 from coniferous trees), dung of herbivorous animals (3, deer and chamois), decaying wood (3, wood3-4), slimy-algae-covered wood (4), and litter (2). The myxomycete yield was low; only bark (27%) and decayed wood (100%) gave positive results. None of the eight cultures with samples from the sectors 2 and 4 were successful. Also moist chambers from algae-covered wood, collected from logs with fresh myxomycete colonies, were negative. Even after $2^1/_2$ months no plasmodia were visible. Probably the cultures, set up at constant room temperature, could not induce fructification of these specialized myxomycetes. This may at least partly explain why we could not find *Licea* species in moist chambers, with exception of *Licea kleistobolus* known as having a short development time.

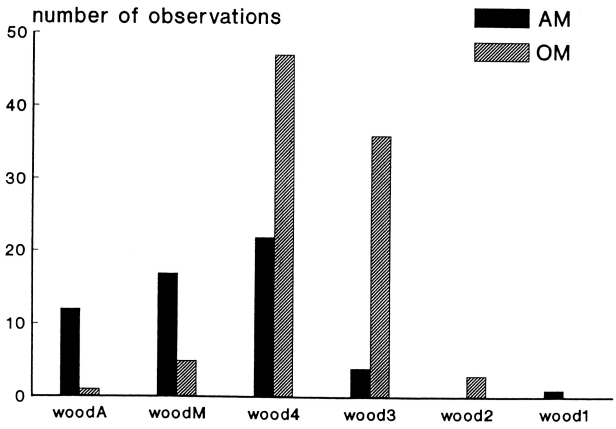

Fig. 2. Microhabitat spectrum of the late-autumn myxomycetes (AM - *Arcyria helvetica*, *Barbeyella minutissima*, *Calomyxa metallica*, *Clastoderma debaryanum*, *Colloderma oculatum*, *Diderma montanum*, *D. umbilicatum*, *Lamproderma columbinum*, *L.* cf. *sauteri*, *Lepidoderma tigrinum*, and *Licea pygmaea*), in contrast to that of the other species found with both fresh and weathered sporocarps (OM). Also fructifications observed in the field were included. Only *Arcyria helvetica* colonizes moderately decayed logs (wood3-1).

Localities investigated for myxomycetes within the Alps are still too scattered to draw conclusions regarding their distribution. But, there is at least some evidence for a distinct alpine myxomycete flora of non-nivicolous species. One example may be *Arcyria helvetica*, frequently recorded in the Swiss Jura by Meylan (1910) and in this study, furthermore in other pre-alpine mountains like the Black Forest (Neubert et al. 1993: 180). According to our present knowledge, it is almost confined to regions around the Alps, altough exceptions occur (records from Sussex, U.K., D.W. Mitchell pers. comm.). Another example is *Hemitrichia serpula*, frequently reported from Upper Austria (Neubert et al. 1993: 241) and in this study, but rare in the lowlands of central Europe. The distribution of *Barbeyella minutissima* is already roughly known, it seems to be common in montane areas with coniferous woodlands and higher precipitation (Kowalski & Hinchee 1972). As indicated by Meylan (1914) and in the present study, this species is probably common in the Alps, the Swiss Jura, perhaps in the Black Forest, but rare elsewhere in central Europe. More systematic surveys in limited areas, designed to record local species inventories as complete as possible, are necessary to elucidate exact distribution patterns of myxomycetes.

Acknowledgements

Field work was supported by a grant from the German Academic Exchange Service (DAAD) to the second author. We are indebted to Mrs. B. Piechotka for technical assistance, to Dr. V.M. Andreeva for determination of algae, to Dr. A. Potemkin (both St. Petersburg) for determination of liverworts, and to Dr J. Krug (Toronto) and D.W. Mitchell (Sussex, U.K.) for checking the English, and especially to Prof. J. Rammeloo for editorial assistance. In particular we are grateful to Mrs. M., E. and T. Mayer, for providing us accommodation in Garmisch-Partenkirchen.

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Received 10 March 1996, accepted in revised form 14 January 1997.

MYCOTAXON

Volume LXXIV (2), pp. 267-285 April-June 2000

Chapter 8

MYXOMYCETES OF THE WINTER-COLD DESERT IN WESTERN KAZAKHSTAN

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Abstract: During a four-week expedition in April and May 1995, the winter-cold desert of the Mangyschlak Peninsula (52°13' E, 44°01' N) was surveyed for myxomycetes. From about 1,000 substratum samples, 146 moist chamber cultures were prepared. With the intention to check all suitable microhabitats, bark of all common desert shrubs, the rarely occurring accumulations of litter, and dung of various herbivorous animals were collected. For each culture, 5-10 individual samples of 2-3 pieces each were pooled from one microhabitat type. Although only two species with 10 collections were found in the field, the moist chamber cultures revealed a whole flora of desert myxomycetes. Twenty-seven species of myxomycetes, two members of the Protosteliales, and various Myxobacteria were recorded, often with exceedingly high levels of abundance. Among these are numerous species previously considered as rare, including *Echinostelium arboreum*, *E. colliculosum*, and *Macbrideola oblonga*. For rare or taxonomically difficult species, brief taxonomic descriptions are given. Compared with surveys from other geographic regions, the desert flora encountered is rather poor but one of the most distinctive among myxomycetes. In addition to obvious features such as absence of trees and succulent plants or the harsh, arid conditions, the high (7.5-8.0) pH of almost all of the substrata present seems to be a limiting factor.

Key words: biodiversity, desert, myxomycetes, Kazakhstan, microhabitats

INTRODUCTION

The life cycle of Myxomycetes (plasmodial slime moulds) involves two trophic stages, one consisting of uninucleate amoebae and the other represented by a distinctive multinucleate structure, the plasmodium, surrounded by the cell membrane and a slime sheath only. Both feed phagotrophically on bacteria, yeasts, spores of filamentous fungi, algae, and other protists (Stephenson and Stempen 1994). Since both trophic stages require moist, humid conditions, deserts would seem to present an extreme habitat for myxomycetes. Due to the

apparent absence of fructifications in the field, desert myxomycetes are indeed poorly known. Nevertheless, some studies point towards a surprisingly rich and distinct myxomycete flora in arid regions (for example Arizona: Evenson 1961, Blackwell & Gilbertson 1980; Gobi desert: Novozhilov & Golubeva 1986).

The present study, made during a journey stretching about 1,500 km, adds a regional flora from one of the world's most extreme habitats - the winter-cold desert region east of the Caspian Sea. The region has a strong continental climate with extremely severe winters, and therefore even succulent plants are absent. Due to the rarity of myxomycete fructifications in the field, the survey presented herein focused almost exclusively on substratum sampling, including all frequently occurring substrata that appeared suitable for myxomycete growth. The region is seemingly not studied; a species account for Kazakhstan (Vasjagina et al. 1977) lists 111 species of myxomycetes, but these records are almost exclusively from montane areas of the country.

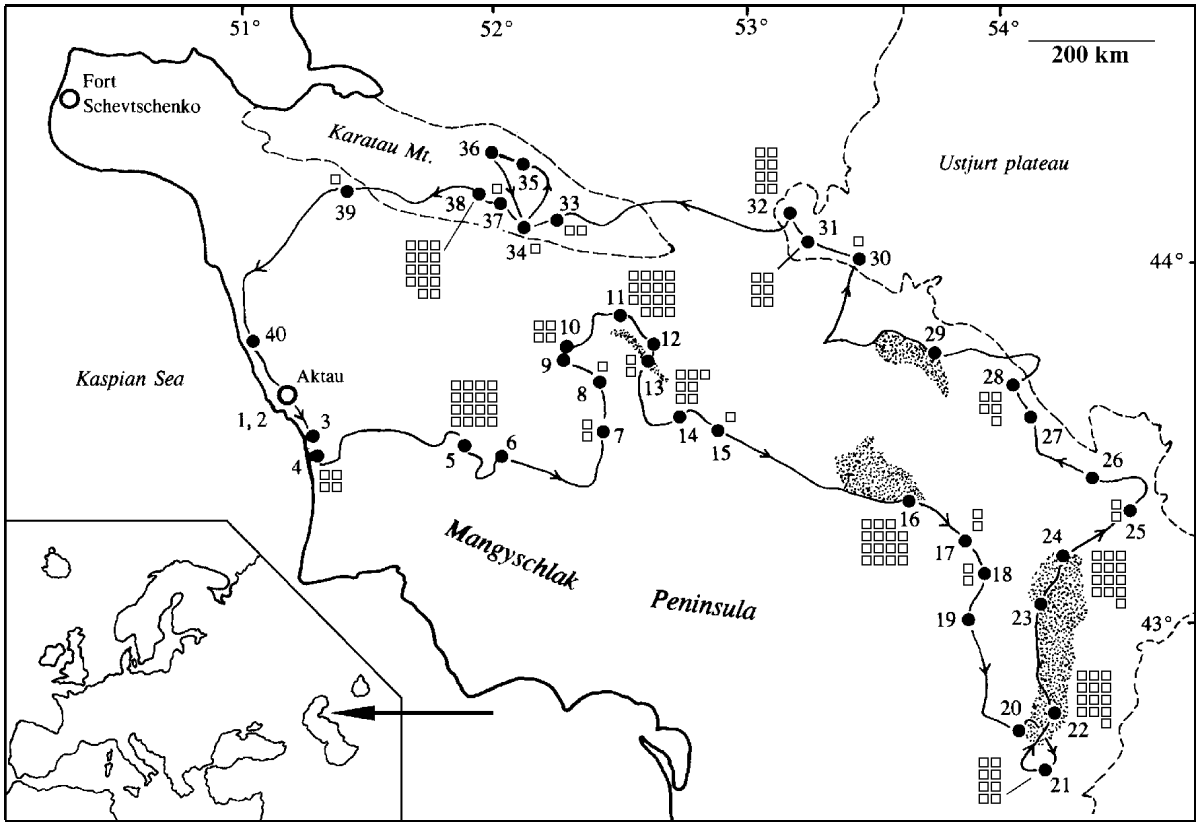


Fig. 1 Map of the Mangyschlak Peninsula, showing the journey (line with arrowheads) with collection points indicated. Dotted areas stand for larger sand dunes. Dotted lines mark the western boundary of the Ustjurt Plateau and the range of the Karatau Mountains. Numbers refer to the localities, with sets of quadrates indicating the number of collected substratum samples. Inset: Geographical position of the Mangyschlak region (arrow).

STUDY SITES

The Mangyschlak Peninsula, the area investigated, is naturally limited westwards by the shoreline of the Caspian Sea and eastward by the Ustjurt Plateau. In contrast to the very uniform sagebrush half desert of the Ustjurt Plateau, the desert of the Mangyschlak Peninsula is characterised by a more rugged relief, basically formed by a plateau furrowed by numerous deep depressions and canyons. Stony badlands dominate, harbouring a scanty vegetation of small shrubs and annual plants. With the exception of some planted individuals around artificial wells, larger trees are absent.

Our expedition was a four-week journey, describing a loop of about 1,500 km that began and ended at the town of Aktau (formerly named Schevtschenko). It extended from 51°18' E near Aktau in the west to 54°26' E in the east, touching the vegetation zones of southern feathergrass steppe in the Karatau Mountains, sagebrush desert in the central part, and southern desert dominated by *Chenopodiaceae* (Anonymous 1990). Fig. 1 shows the journey with the 40 localities investigated. The Mangyschlak Peninsula can be characterised as one of the harshest landscapes on Earth. Due to the extreme temperatures during the winter (up to -40 °C, with an average January temperature around -10 °C), no succulent or evergreen plants occur. The mean annual precipitation is 177 mm, with a monthly maximum of about 30 mm in August and September. Winter snowfalls are rare and are in some years absent. Considering the strong wind-chill, subterranean parts of wintering plants suffer from extremely low temperatures. Humid conditions with temperatures above 0 °C last for only about 1-2 weeks in spring and another 3-4 weeks in autumn. In spring, the temperature rises rapidly, soon changing into hot and very dry summer weather. Strong winds are typical, often producing dust storms at dawn, bringing hot air from Central Asia (Afghanistan). Remarkable were the high fluctuations in air humidity during our journey (which extended from the beginning to the end of spring), ranging from 100 % during nightly dew fall to less than 10 % around noon. In spite of the harsh conditions, the vascular plant flora is relatively rich (about 600 species). However, about 25 % of all plant species are annuals, living actively only during the short springtime (Safronova 1992). Only about 30 species of plants are higher shrubs (maximum height 1-2 m, in sand dune areas up to 3.5 m). The human influence on the vegetation is low, basically consisting of grazing by camels, horses and sheep. Small rodents occur with high population densities; among these are *Citellus citellus*, *C. fulvus* and mice of the genus *Meriones* (names after Gromova & Baranovoj [1981]). Due to hunting, the indigenous Saiga antelope (*Saiga tatarica*) is rare and often displaced by free roaming sheep.

Except for the Karatau Mountains, the whole region is derived from marine, basic sediment stones, mostly layers of dolomitic limestone, various kinds of calcareous marl, chalk and sandstone, often forming cliffs and rocky reefs. The soils are basic, with pH values mostly between 7.5 and 8.0. Huge areas are salt pans or are covered by sand dunes (Fig. 1). Only the Karatau Mountains are built from acidic slates. Due to the edaphic conditions often changing over short distances, various plant associations have been recognised (Safronova 1991a, b). As described below, five main habitats can be differentiated (nomenclature for vascular plants follows Czerepanov [1995]).

1. The **plateau**: The most uniform landscape, with elevations between 200 and 300 m. Loamy, very solidified soils support a poor vegetation of mainly sagebrush (*Artemisia* spp.), rarely intermixed with taller perennials such as *Rheum tataricum*. The investigated western part has slightly higher rainfall and harbours a flora richer in shrub-forming species. Shrubs are up to 70

cm tall and usually have a deeply furrowed, or less commonly a peeling bark. Of interest as myxomycete substrata are a number of common *Chenopodiaceae* (*Salsola* spp., *Haloxylon aphyllum*) as well as *Atraphaxis replicata*, *Convolvulus fruticosus*, or *Astragalus karakugensis*, the latter remarkable by possessing a fibrous bark with high water retention.

2. **Cliffs, gorges and rocky reefs**: Gigantic dry depressions and canyons interrupt the plateau, often with scenic cliffs dropping off 100-200 m. The deepest of these depressions (Karagia) lies 132 m below sea level. Exposed to the fogs from the Caspian Sea, the cliff edges house plant communities significantly richer in species. Here *Rhamnus sintenisii*, an endemic of the region, can be found, forming taller shrubs up to 3 m height. This is the only common plant providing noticeable amounts of leafy litter. Other shrubs have mostly tiny to scale-like leaves and green, assimilating twigs. The soils are stony, calcareous and not too salty.

3. **Salt swamps and pans**: At the bottom of the depressions, gypsum or very salty soils dominate; frequently, salt pans (solontschaks) without any vegetation occur. The prevailing shrubs are various species of *Tamarix*, more rarely *Halostachys caspica*. Exceptional was the Ukere salt spring in the southern desert; at this site a short salty rivulet drains into a salt swamp.

4. **Sand dunes**: Smaller and larger sand dune areas with a very different vegetation are scattered throughout the region. Shrubs, such as *Haloxylon aphyllum* and various species of *Calligonum*, accompanied by two larger species of *Astragalus*, dominate. Very conspicuous are the big umbrellas of *Ferula foetida*, a giant member of the Apiaceae family with a life history similar to the century plants (*Agave*) found in New World deserts. In general, the vegetation on sandy soils is richer and more dense, locally providing thin mats of twiglet litter under the shrubs.

5. **Karatau Mountains**: Shallow hills with moderate elevations between 350 and 450 m are interrupted by deep-cut valleys. The soils are rocky to stony, often with rubblefields of acidic slate. Only here fresh water was present in small rivulets, usually framed by dense thickets of *Mentha longifolia*. The northern valley slopes bear feathergrass steppes poor in shrubs, with the southern counterparts being dominated by sagebrush. In the valleys, larger shrubs and *Crataegus ambigua*, the only naturally occurring tree, can be found.

MATERIALS AND METHODS

Substratum samples were collected systematically from all major shrub species, plant refuse and animal dung - all organic matter considered suitable for myxomycetes - at 40 locations during the journey. The field work was carried out in late April and early May of 1995, which represented the end of the short spring season. The first days were still cold and cloudy, with occasional brief rainfalls; the last days were already very hot, often with dust storms in early morning.

For substratum sampling, within a sample plot typically covering 500-1,000 square meters, the vegetation was recorded (abundance and coverage of the dominant vascular plants, vegetation structure, and soil features). Substrata were collected in 2-3 pieces from 5-10 plant individuals or points within the plot that shared the same microhabitat features. These were pooled, yielding a total sample of 15-35 g weight. Sampling included (i) for all larger shrubs or trees, the non-living outer part of the bark as scales of 1-2 cm size, (ii) thin mats of litter at the base of trees or tussock-forming plants, and (iii) droppings of herbivorous animals, mostly rodents. For each sample, microclimatic conditions such as height, light, wind exposure as well as substratum features (texture, moisture, and degree of decay) were recorded for later ecological investigations (Schnittler, in prep.). A total of 146 samples was collected, including bark (81

samples), litter (35) and animal dung (30). The moist chamber cultures were prepared in the manner described by Härkönen (1977). For moist chambers, substratum pieces were placed on filter paper in Petri dishes, with the pieces touching but not overlapping each other and with the outer side of bark upside. Destilled water adjusted to pH 7.0 was added to each culture. All cultures were maintained 2 months under diffuse daylight and at room temperature (22-23 °C). On five occasions (days 2, 6, 11, 21 and 40 after start) the chambers were checked with a high-magnification dissecting microscope. Mature fructifications were mounted in small boxes, and sporocarps of minute species were immediately preserved in polyvinyl lactophenol or glycerol gelatine, when calcareous structures were present. From the 513 fructifications recorded, 169 specimens were collected and stored in the private collection of the first author at the Herbarium Haussknecht, Jena (JE). In addition, duplicates of some species were deposited at the Herbarium of the Komarov Botanical Institute, St. Petersburg (LE).
For comparison of myxomycete floras from different parts of the world, species lists of the respective papers were databased. From a synoptic table of all records, the coefficient of community indices (see Stephenson et al. 1993) were calculated. These have a value between 0 (nothing in common) and 1 (all species are members of both floras).

ANNOTATED SPECIES LIST

The following list includes all recorded species in alphabetical order. Nomenclature essentially follows Martin & Alexopoulos (1969), but for species not mentioned in this monograph, a reference to the protologue is given. Determinations considered as doubtful are given with the note 'cf.' (confer). Bold symbols in parentheses represent an abundance estimation of each species using the percentage scale of Stephenson et al. (1993), based on the proportion of a species in the total number of records (513): R - rare (<=0.5 %), recorded once or twice; O - occasional (0.5-1.5 %), 3-6 records; C - common (1.5-3 %), 7-11 records; A - abundant (>3 %), more than 11 records. After a comma, the number of collections follows, separated by a colon from the locality numbers as referred to in Fig. 1. Short comments on habitats and distribution are included; for rare and/or taxonomically difficult species, brief taxonomic descriptions are given. Colours are described as observed with a dissecting microscope and as seen by transmitted light. For the latter, the degree of transparency is described as: translucent - glass-clear; transparent - allowing milky light to come through, colours are visible; and opaque - impermeable to light, the structure appears black. Spore measurements are given for specimens mounted in polyvinyl lactophenol. Therefore, diameters can be slightly smaller (0-3 %) than for fresh material investigated in water. Terms for taxonomic descriptions are as used in Lado & Pando (1997), with colours described according to Kornerup & Wanscher (1981).
Although 40 localities where checked in the field for myxomycete fructifications, only for those mentioned in the following list were myxomycetes recorded. Except for the field collections obtained at localities 15 (*Physarum notabile*) and 33 (*Didymium squamulosum*), all records are from substratum samples cultivated in moist chambers. Locality numbers refer to Fig. 1.

4: sand dunes ca. 25 km SE Aktau, on the northern edge of the solontschak Karanol, near the Caspian Sea, 51°18'25" N 43°28'49" E ± 1 km
5: stony ground over limestone, near the upper edge of a cliff ca. 1 km NW of the well Sauttuy, E margin of the depression Karagije, elevation 110 ± 20 m, 51°52'37" N 43°31'23" E ± 1 km
7: sandy to loamy gypsum soils near the eastern margin of the depression Karagije, plateau on the NE edge of the depression Korganoi, 160 ± 20 m, 51°26'36" N 43°34'11" E ± 200 m
10: overgrazed and devastated sandy soil near the Karasasschokui Mt., next to the buildings of a Kazakh cemetery, 52°17'42" N 43°47'12" E ± 400 m
11: stony ground (limestone and chalk), plateau ca. 2 km N of the Baskuduk sand dunes, on the margin of giant chalk cliffs falling up to a depression, 52°28'51" N 43°52'39" E ± 200 m
13: loose, deep-grounded, sandy soil, at the NE margin of the Baskuduk sand dunes, 180 ± 20 m, 52°36'08" N 43°49'19" E ± 500 m
14: loose, deep-grounded, slightly overgrazed, sandy soil in a small valley between cliff edges, NW margin of the depression Usen, 240 ± 20 m, 52°44'09" N 43°33'46" E ± 600 m
15: stony soil between limestone plates, margin of the plateau to the depression Usen, NE-edge, 240 ± 20 m, 52°50'40" N 43°33'21" E ± 150 m
16: deep-grounded, loose soil, margin of the Tjuesu sand dunes, SE-edge, near the margin of a solontschak, ca. 2 km N of the well Besoktui, 80 ± 20 m, 52°36'53" N 43°21’07" E ± 500 m
17: solid, somewhat loamy soil between sandstone slates ca. 5 km N Mt. (cliffs) Kunabai, small sandstone hills, 120 ± 20 m, 52°48'49" N 43°13'53" E ± 100 m
18: solid, stony soil with marl, above limestone rocks, slightly overgrazed, ca. 10 km SSE Mt. Kunabai, on the plateau margin, 160 ± 20 m, 52°53'00" N 43°06'27" E ± 200 m
21: deep-grounded gypsum soil with earth lichens, small valley of the creek from the salt spring Ukere, SW-edge of the Ustjurt Plateau, 10 ± 20 m, 54°09'12" N 43°36'38" E ± 500 m
22: solid but sandy soil near a well, overgrazed, on the W margin of the Karünjarük sand dunes, SW-edge, ca. 5 km N of the well Seksorka, 90 ± 20 m, 54°08'50" N 43°46'25" E ± 5 km
24: loose sand dunes above red sandstone hills up to 50 m, Karaschek Mts. in the NW-part of the Karünjarük sand dunes, 140 ± 40 m, 54°11'23" N 43°10'37" E ± 1 km
25: solid, sandy soil on the bottom of a depression at the northernmost margin of the Karünjarük sand dunes under the cliffs to the plateau, 40 ± 20 m, 54°26'14" N 43°20’06" E ± 500 m
28: loose, sandy soil between sandstone boulders, terasses of a cliff slope forming the Kolbai Mts., W margin of the Ustjurt Plateau, 140 ± 40 m, 53°59'18" N 43°41'23" E ± 400 m
30: stony soils above chalk rocks, cliff valley in the Ustjurt Plateau at the NE edge of the Tusbair salt lake ca. 1 km SSE of the well Sandui, 53°27'39" N 44°01'22" E ± 600 m
31: stony soil above limestone rocks, near a cliff delimiting the Ustjurt Plateau, near the well Monata, 250 ± 20 m, 53°12'32" N 44°06'11" E ± 600 m
32: stony soil above limestone, cliffs delimiting the Ustjurt Plateau, falling down to the Kaidak salt lake, ca. 2 km NE of the spring Okbai, 240 ± 20 m, 53°3'35" N 44°10'25" E ± 1 km
33: stony soil above Devonian slate, ca. 12 km E Schetpe, hills on the N margin of the eastern Karatau Mts., 260 ± 40 m, 52°16'28" N 44°08'41" E ± 2 km
34: stony ground on the bottom of a deep-cut rivulet canyon ca. 4 km SW Scharmüsch, N margin of the eastern Karatau Mts., 160 ± 40 m, 52°25'19" N 44°07'59" E ± 1 km
37: sandy, overgrazed soil ca. 5.5 km NW Schetpe, foothills at the E margin of the Karatau Mts., near a well, 200 ± 50 m, 52°04'58" N 44°10'45" E ± 400 m
38: shallow, somewhat sandy soil above Devonian slate, deep-cut rivulet valley ca. 16 km NW Schetpe, western Karatau Mts., 180 ± 40 m, 51°57'31" N 44°14'20" E ± 1 km
39: stony soil between plates of limestone rocks, cliff edge ca. 7 km SW Danüspan Mt., southern foothills of the Karatau Mts., 160 ± 20 m, 51°21'57" N 44°15'19" E ± 100 m

Arcyria minuta Buchet (**R**, 1: loc. 4). Once on bark of *Tamarix*, sand dunes near the Caspian Sea.

Comatricha laxa Rostaf. (**O**, 4: loc. 4, 38). Four records, bark of *Tamarix* and *Crataegus* in areas with higher moisture (coast and Karatau Mountains).
Small groups of always single, scattered sporocarps (0.35)-0.5-0.8-(1) mm tall, relatively long stalked, stalks reaching one to one and a half times the sporotheca diameter. Sporotheca globose to weakly ovoid in larger sporocarps, (0.15)-0.2-0.3-(0.35) mm in diameter, dark blackish brown (6F8). Stalk fibrous, especially at the base, with an inconspicuous hypothallus lacking any reddish tints, under the microscope opaque, black, turning to olivaceous-yellow (4B6) 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 (6F8-6D6), outer threads pale brown (6D6-6C5), forming in most except very small sporocarps an incomplete surface net with meshes of (6)-10-30-(50) µm, mostly between 10 and 15 µm diameter. Peridium absent, no conspicuous collar. Spores dull olivaceous brown (5E8) in mass, lacking reddish tints, globose, olivaceous brown (5D5) under transmitted light, with regularly arranged warts up to 0.2 mm high, (10)-11-12.7-(13) µm in diameter. Seemingly a common species in arid regions (unpublished observations from Big Bend, Texas, and the Caspian basin around Astrachan) with a habit as pictured in Mitchell (1999, specimens DWM 5423, Tanzania), whereas the drawing in Nannenga-Bremekamp (1991) seems to depict the wood-inhabiting form with larger, ovoid sporocarps and a more lax capillitium.

Comatricha pulchella (C. Bab.) Rostaf. (**C**, 6: loc. 4, 16, 21, 24, 34, 38). Preferentially on bark of *Tamarix* (3 of 6 records) but occasionally on litter; scattered over the whole area investigated.

Didymium anellus agg. (**A**, 25: loc. 4, 5, 7, 10, 11, 14, 16, 17, 21, 22, 24, 31, 32, 38). Common throughout the journey on all kinds of substrata, including the dung of various animals. All fructifications are sessile on a broad or constricted base, ranging from half-globose to flattened sporocarps and plasmodiocarps. Three forms, one regarded as an separate species, could be differentiated.
Didymium anellus Morgan, a form with small lime crystals. Small, scattered sporocarps of 0.25-0.4 mm diameter and up to 0.2 mm high, less commonly short plasmodiocarps, sessile on a dark, sharply constricted base, globose to depressed-globose. Hypothallus a small, brownish disk under the sporocarp, inconspicuous. Peridium black to dull brown (4F7) at the base, here often without lime, in the upper part densely sprinkled with isolated lime crystals, these easily differentiated under a dissecting microscope but relatively small, one half or equal the spore size. Peridium translucent, colourless to pale brownish (4A2-4B2) under transmitted light. Capillitium consisting of colourless to pale brownish (5A2-5D5) threads, 1-2-(2.5) µm wide, often branching and anastomosing to form an incomplete network, sometimes with flattened and darker coloured sections on the branches. Spores dull brown (5F6) in mass, under the microscope olive brown (7D4), globose, regularly covered with warts up to 0.5 µm high, (9.2)-9.6-10.5-(11.5) µm. This form best fits the description of *Didymium anellus*, except for the slightly larger spores (described as 7-10 µm in diameter).

Didymium anellus, a form with large lime crystals. Differing by the mostly short plasmodiocarps, sessile on a constricted base; lime crystals on the peridium very scattered, large and well developed, mostly 2-3 times larger than spores; the spores larger and slightly paler, (9.5)-10.5-11.5-(12.5) µm in diameter, warts smaller, and more densely arranged.
Didymium inconspicuum Nann.-Bremek. & D.W. Mitch. (Nannenga-Bremekamp, 1989). Small and inconspicuous, scattered sporocarps and short plasmodiocarps of 0.25-0.4 mm diameter, up to 0.1 mm high, less commonly short plasmodiocarps, flattened and sessile on a broad base. Hypothallus not detectable. Sporocarps grey to ochraceous (5B2-5B3), evenly sprinkled with very small, coalescing lime crystals, these much smaller than the spores, 3-6 µm in diameter and difficult to differentiate under a dissecting microscope, often forming a thin crust. Peridium translucent and pale colourless to yellowish-brown (4A2-4B3) under transmitted light. Capillitium formed by colourless to pale brown (5A2-5D5) threads, 1-2-(2.5) µm wide, often branching and anastomosing to an incomplete network, sometimes with flattened and darker coloured sections on the branches. Spores dull brown (5F6) in mass, under the microscope pale olive brown (7C3-7D4), globose, regularly covered with very fine and dense warts up to 0.3 µm high, (9.5)-10.5-11.5-(12.5) µm in diameter. As compared with isotype material (coll. Mitchell, DWM 4430), the Kazakh specimens seem to be identical with *D. inconspicuum*, described from one moist chamber culture prepared with bark from an unidentified desert shrub in Arizona.

Didymium annulisporum H.W. Keller & Schokn. 1989 (**R**, 1: loc. 24) Once on sheep dung, pH 8.2.
Very small, scattered globose sporocarps of (0.1)-0.15-0.2-(0.25) mm, sessile on a slightly constricted base. Hypothallus pale white to straw-coloured (4B4-4B7), limeless except for some lime granules in the centre. Sporothecae ash-grey (4B1) to white, densely covered with fine, star-like lime crystals touching each other with their tips. In contrast to *Didymium difforme*, individual lime crystals are still recognisable under a dissecting microscope; the crystals forming a brittle crust. Peridium colourless under transmitted light, smooth or minutely roughened. Capillitium consisting of colourless and slender threads arising from the base of the sporocarp, rarely branching and anastomosing, mostly with free ends, some reaching the peridium and connected with it, 1-1.2 µm wide. Spores dark brown (7F8 and darker) to almost black in mass, globose to slightly lemon-shaped under the microscope, pale violet grey (8D3) with conspicuous, scattered blunt and very dark spines up to 1.2 mm in length, with a darker, thin but conspicuous germination slit surrounding the spore like a belt, 12-13-(13.5) µm in diameter. Our specimen fits the excellent original description perfectly, except for the larger spores, which are described as 10-11 µm in size.

Didymium difforme (Pers.) S.F. Gray (**C**, 12: loc. 5, 7, 11, 14, 18, 22, 25, 28, 31, 32, 38). Surprising was the occurrence of this usually litter-inhabiting species on bark, especially *Rhamnus* (4 records). Localities are scattered over the whole region, except near the coast.

Didymium squamulosum (Alb. & Schwein.) Fr. (**R**, 3 + 8 field collections: loc. 25, 38). Except for two records on dung, the usually common species was found only in the Karatau Mountains within dense thickets of *Mentha longifolia* in a creek. Fresh sporocarps were abundant on dead stems protruding the water. Perhaps due to the extremely dry air, only a small zone of about 2 cm above the water surface was suitable for myxomycete growth. As indicated also by other

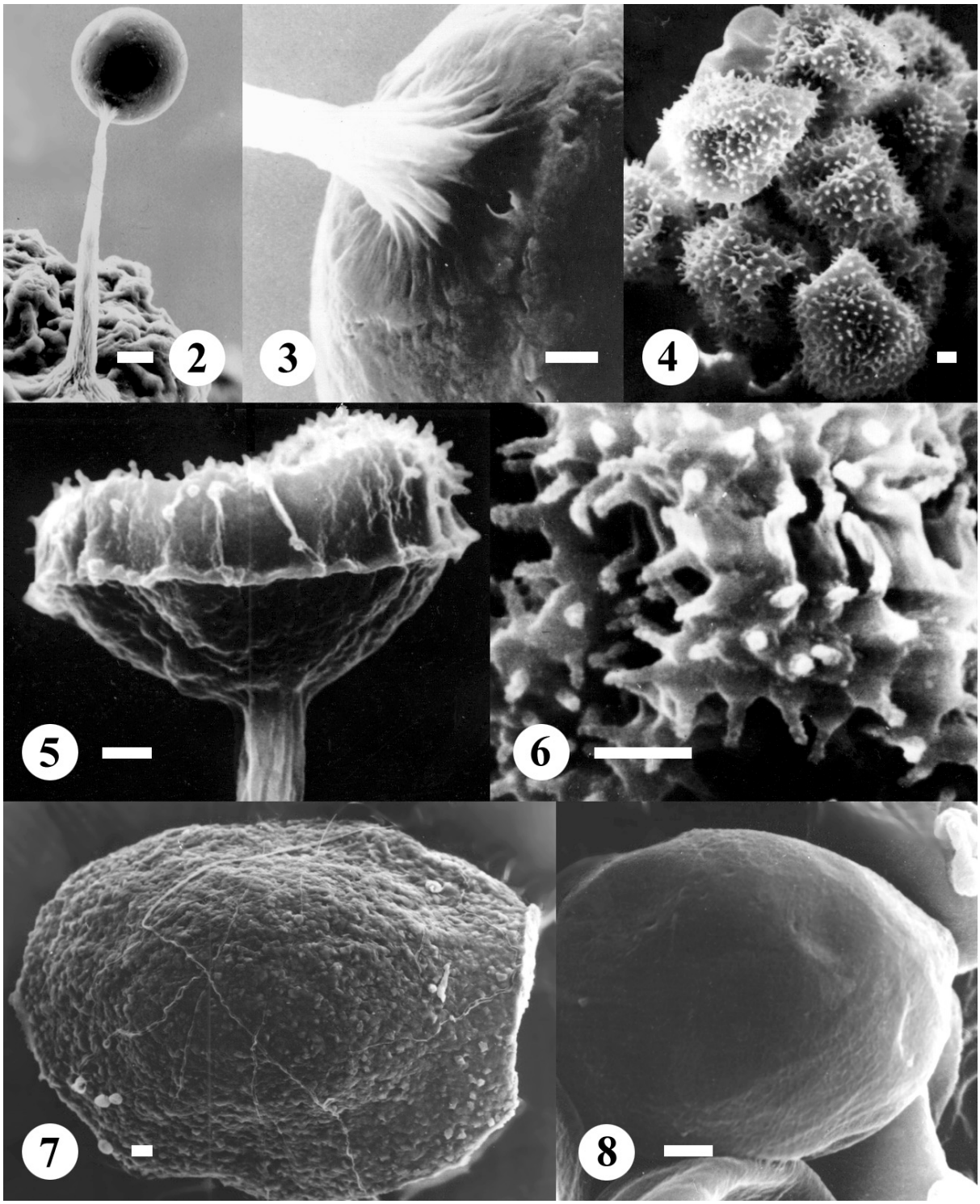
findings (Kappel 1992), this species seems to be able to develop in water, thus not requiring extensive amounts of moist substratum.

Echinostelium arboreum H.W. Keller & T.E. Brooks, 1976 (**A**, 16: loc. 5, 11, 14, 16, 17, 22, 24, 32, 38)
Exclusively on the bark of various desert shrubs; throughout the region except near the coast.
Small to large colonies of single sporocarps, stout in habit, stalked, yellow-brown (4B4-4B5). Sporothecae urn-shaped, 30-50 µm in diameter. Stalk 120-150 µm long, in transmitted light yellow (4A4) to pale ochraceous (4B4) in the lower section, about two thirds of length filled with darker granules, diameter 10-15 µm on base, tapering to 2.5-3.5 µm on top. Peridium often persistent, smooth and colourless in transmitted light, leaving at least a conspicuous collar. 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 ends about 1 µm in diameter. Spores in mass rose (4B4) to olivaceous (5B4) brown, very pale olivaceous (4A3) under the microscope, globose, ornamented with flat, patchy, slightly darker warts of 1-1.2 µm diameter, (5.5)-6.5-8-(9) µm in size.

Echinostelium colliculosum K.D. Whitney & H.W. Keller, 1980 (**A**, 45: loc. 4, 5, 10, 11, 13, 14, 16, 17, 18, 21, 22, 24, 28, 37, 38), Figs. 2-6. With high preference for bark, only exceptionally occurring on litter.
Large colonies of single but gregarious sporocarps, pink (7B2) to colourless, fresh shining like a small brilliant brooch, (50)-60-100 µm in height, each with 40-100 spores. Stalk white, colourless and translucent under the microscope, filled with a few dirt granules in the lower third, (40)-50-70 µm in height, diameter about 10 µm at the base, 2-2.5 µm on top. Peridium fugacious, collar absent. Columella consisting of a single, spore-like cell attached on the top of the stalk, with the same diameter and ornamentation as the spores. Spores white in mass, seldom very pale pink (7A2), colourless under the light microscope, globose, almost smooth but with large, thickened patches (articular surfaces) of unequal size, spore wall often shrinking on the smaller, thinner areas, (7)-8-9.5-(10.5) µm in size. Astonishingly, the spores appearing smooth under the compound microscope show small spines when viewed by SEM (Figs. 4, 6). The solid clusters of spores with not sharply separated articular surfaces very different in size within a spore as well as the longer stalks exclude the similar *E. coelocephalum* T.E. Brooks & H.W. Keller (Keller & Brooks 1976).

Echinostelium minutum de Bary (**O**, 3: loc. 4, 22, 38). Probably not belonging to the regular desert flora. The single record consisting of a large colony was from the bark of *Salix alba* planted around an artificial well.

Fuligo cinerea (Schwein.) Morgan (**R**, 2: loc. 5, 11).
Fructifications arranged in colonies of heaped plasmodiocarps, bent brain-like and coalescing into an aethalium of irregular shape and (3)-5-10 mm size, sessile on a broad base and a white hypothallus containing lime granules. Peridium persistent, white to pale lilac (18A2-18A4)



Figs. 2-8 SEM photographs of *Echinostelium colliculosum* (2-6, Schnittler 6791) and *Licea* spec. (7-8, 6856). 2 Developing sporocarp, still with a closed peridium; bar = 10 µm. 3 Detail of a later developmental phase, showing the columella as a ring differentiated from the still homogenous plasma mass. 4 Mature spores. 5 Tip of stalk with a spore-like columella; the horizontal ring marks the position of the peridium present in early development. 6 Detail of spore ornamentation; all bars = 1 µm. 7 Closed sporocarp of *Licea* spec.; the lines crossing the sporocarp are contaminant fungal hyphae; bar = 10 µm. 8 Completely smooth spore; bar = 1 µm. Photos Y. Novozhilov.

when fresh, densely covered with coalescing, thick lime patches, translucent and colourless under the microscope, smooth. Capillitium a network of translucent, colourless threads of 1-4 µm width, with irregular to elongate white lime nodes of 30-80(-100) µm size, filled with amorphous, conglomerated and colourless granula. Spores in mass dark-brown (7F8), ellipsoid to subglobose, pale brown (6C4-6D5) under transmitted light, ornamented with regular distributed to scattered spine-like warts up to 0.8 µm height, (10)-10.5-11.2-(12) µm. Our taxon is probably the small form with a gyrose cortex (approaching *Physarum gyrosum* Rostaf. in shape), as mentioned for 'warm regions' in Martin & Alexopoulos (1969: 264).

Licea biforis Morgan (**R**, 1: loc. 21). Occurring once on *Tamarix* bark from the southernmost locality of the journey.

Licea denudescens H.W. Keller & T.E. Brooks, 1977 (**R**, 2: loc. 13, 38). On leaves and twiglets of *Crataegus* and the bark of *Calligonum*.

Licea kleistobolus G.W. Martin (**A**, 21: loc. 4, 5, 10, 11, 14, 21, 22, 24, 32). The only abundant *Licea*, inhabiting bark of a wide range of desert scrubs.

Licea spec. (**R**, 1: loc. 24), Figs. 7-8. One specimen obtained in culture from rodent droppings (*Citellus* spec.).
Small, densely arranged fructifications of irregular shape, developing from the segregation of one larger plasmodium, of all sizes ranging from *Licea*-like sporocarps of 0.1 mm diameter to short, angular plasmodiocarps up to 0.5 mm size, flattened to half-ovoid, sessile on a broad base. Hypothallus separate for each fructification, slightly broader than these, with the same features as the peridium. Peridium olivaceous brown (5E6-5E7) due to the colour of spore mass, in transmitted light translucent to bright amber (4A6), densely encrusted with small granules and angular crystals of 2.5-5 µm length, densely and very fine warted. Capillitium absent, but very rare short, irregular winded golden yellow (4B8) threads were seen in the microscope, these 2.5-4 µm in diameter, 10-20 µm in length, free, evenly covered with fine warts. Spores in mass pale chestnut brown (5D6), amber (4A6-4B6) in transmitted light, smooth, globose, (9.2)-9.6-10-(10.5) µm, not conspicuous thick-walled.
Licea retiformis Nawawi (1973) fits our specimen except the presence of small capillitium pieces and the non-reticulate shape of the plasmodiocarps. *Perichaena brevifila* H.W. Keller & T.E. Brooks (1971) differs by having very large, conspicuously spiny spores. *Arcyodes luteola* (Kowalski) Nann.-Bremek. (1985) has similar, slightly larger spores, but is described as having a non-ornamented capillitium; *Arcyodes incarnata* (Alb. & Schwein.) Cooke usually has an abundant capillitium and forms crowded to heaped sporocarps without yellowish tints. *Perichaena liceoides* Rostaf., as redescribed in Gilert (1990), differs in having densely ornamented spores and smooth capillitium threads. From habit, *Licea tenera* Jahn (1919) comes closest to our specimen, but differs by having spinulose spores.

Macbrideola oblonga Pando & Lado, 1988 (**A**, 25: loc. 4, 5, 11, 16, 17, 18, 22, 24, 28, 32, 38). Found throughout the journey, occurring exclusively on bark.
Small groups of always single, scattered sporocarps, relatively short stalked, (0.4)-0.5-0.75-(1) mm tall, stalks reaching one fifth to one third the size of the reddish-brown, (8E7) ovoid, seldom globose sporotheca that is (0.35)-0.4.-0.65-(0.7) mm in height. Stalk hollow, not fibrous

at the base, emerging from a membranous, discoid hypothallus, translucent pale to dull reddish brown (8C6-8E8) under the microscope, stalk itself dull reddish brown (8E8), transparent, (0.08)-0.1-0.12-(0.2) mm high, thick and stout, on the base 50-100 µm in diameter, often still 30 µm in the centre of the sporotheca. Capillitium stiff and coarse, main branches mostly perpendicular, arising over the whole length of columella, dull reddish brown (8E8), outer threads paler (8B5), branching especially near the surface and ending with pointed spines. Surface net absent. Peridium absent, also no conspicuous collar. Spores reddish brown (8E8) in mass, globose, pale reddish olivaceous brown (8D4) under transmitted light, with very fine, regularly arranged warts up to 0.2 µm high, (8.5)-9.2-10.5-(11.5) µm in diameter.
This taxon matches a description given by Nannenga-Bremekamp & Yamamoto (1983) for a *Macbrideola*, described also by Eliasson et al. (1988) as a *Comatricha*. Comparison with material obtained from Spain (D. Wrigley de Basanta, Madrid, DWB 1372) led to a clear assignment of the Kazakh specimens to *M. oblonga*, previously known only from the Mediterranean area.

Perichaena liceoides Rostaf. emend Gilert, 1990 (**R**, 1: loc. 16). One, larger collection from the bark of *Calligonum densum*, pH 7.6.
Very small, scattered sporocarps without a common hypothallus, globose in shape, (0.1)-0.2-0.4-(0.6) mm in size, sessile on a restricted base and without a visible hypothallus, up to 0.3 mm tall, always rounded in outline. Peridium yellow (4A8) to olivaceous (4B8), with irregularly distributed large black areas, dehiscence line invisible. The membranous layer under transmitted light pale yellow (4A5-4A6), almost smooth, sometimes with paler strips, the duller, opaque patches covered with dull-brown (4C7), rounded inclusions, these 2.5-4 µm in size and densely baked together. Capillitium absent except a few, short outgrowths from the peridium, these wrinkled, 2-3-(3.5) µm wide threads, irregular in shape, pale yellow (4A5) to ochraceous (4B5) and up to 25 µm long. Spores in mass bright golden yellow (4A8), pale yellow (4A5) to ochraceous (4B5) under the microscope, globose, ornamented with conspicuous, scattered and blunt to capitate conspicuous spines up to 1.5 µm in height, (10.5)-11-13.5-(16) µm in diameter. The small, yellow sporocarps lying on the substratum like small eggs are very distinctive.

Perichaena corticalis (Batsch) Rostaf. (**A**, 15: loc. 4, 5, 10, 16, 22, 24, 28, 31, 32, 38). Throughout the region on bark of various desert scrubs, only occasionally found on litter.

Perichaena depressa Libert (**C**, 6: loc. 11, 37, 38). Rarer than the previous species, only recorded from the Karatau Mountains and one locality nearby.

Perichaena vermicularis (Schwein.) Rostaf. (**A**, 42: loc. 4, 5, 10, 11, 13, 14, 15, 16, 17, 18, 21, 22, 24, 31, 32, 33, 38). In spite of the regular occurrence of this species on both bark and litter, only the litter form with a membranous, thin peridium and abundant capillitium was seen.

Physarum cinereum (Batsch) Pers. (**R**, 1: loc. 38). Only once in the Karatau Mountains, on litter of *Mentha longifolia*.

Physarum cf. *confertum* T. Macbr. (**C**, 6: loc. 5, 7, 18, 22). On the bark of various shrubs; found only in the southern part of the journey.
Fructifications in small colonies of scattered, short plasmodiocarps, sometimes coalescing, all sessile on a inconspicuous hypothallus. Plasmodiocarps worm-like, often forming annulate rings, globose in cross-section and ca. 0.3 mm high, ranging from small and round sporocarp-like fructifications up to plasmodiocarps of 3 mm length. Hypothallus inconspicuous, cream to straw-coloured (4B4-4B7), separate for each fructification. Peridium persistent, opening irregular, regularly sprinkled with separated, white patches of ash-grey (4B2) granular lime, these 30-50 µm in size, under the microscope translucent and colourless, with small warts and ridges to almost smooth. Capillitium a dense network of translucent, colourless threads 1-3 µm wide, bearing long and often confluent, sometimes branched nodes of granular lime, 50-100 µm, often attached to the peridium and of badhamioid habit. Spores in mass dark-brown (5F8 and darker) to black, globose, pale brown under transmitted light, ornamented with regular distributed, fine warts up to 0.3 µm in height, (10.5)-10.8-11.5-(12) µm.
With very small, distinct and never coalescing lime nodes, this taxon fits into the concept of *Physarum confertum*. However, the latter species is described as forming heaped fructifications with a peridium almost free of lime, and spores 10-14 µm in size.

Physarum decipiens M.A. Curtis (**R**, 2: loc. 38). Karatau Mountains, on bark of *Rhamnus*.
All characters of our specimen are typical, with greenish-yellow plasmodiocarps during development as described by Jahn (1919) and the distinctive, rugulose surface. However, our collection differs by having curious spores (10.5)-11-12-(12.5) µm in diameter which are dark brown under transmitted light and ornamented with irregularly distributed, very conspicuous baculate spines up to 1.2 µm height, these often arranged in rows but leaving larger parts of the spore smooth.

Physarum didermoides (Pers.) Rostaf. (**R**, 1: loc. 18). Collected once from the bark of *Atraphaxis*.

Physarum notabile T. Macbr. (**A**, 82 + 2 field collections: loc. 4, 5, 7, 10, 11, 13, 14, 15, 16, 17, 18, 21, 22, 24, 28, 30, 31, 32, 33, 34, 37, 38) This species, usually regarded as rare in the Old World, was the most abundant myxomycete, inhabiting all types of substrata. Two destroyed and obviously wintered specimens were found in the field, both preserved in dense, up to 15 cm thick mats of the previous year stems of *Capparis spinosa*. Three forms, often with intermediate sporocarps in a given colony, could be recognised (Table 1). The most common form 1 fits best the description and the photograph given by Neubert et al. (1995: 283). However, spore colour is described as dark olive brown, more pronounced in Nannenga-Bremekamp (1991: 195) as very dark like in *P. didermoides*. Our form 1 differs in having pale spores like most of the *Physarum*-species, which is also the case in a specimen of Jaaps exsiccate series (No. 85). A specimen from Colorado (Larimer Co., cow dung, TRTC) determined by Sturgis is identical with form 2, whereas form 3 approaches somewhat *Physarum compressum* Alb. & Schwein. in habit.

Table 1. Morphological differentiation between forms of *Physarum notabile*.

character	form 1	form 2	form 3
sporotheca shape	globose-depressed to umbilicoid	globose	compressed to weakly reniform
diameter	0.5-0.7 mm	0.4-0.6 mm	0.2-0.3 x 0.5-0.8 mm
base	reddish (5B8-5D8)	dull grey (5D4-5B4)	reddish (5B8-5D8)
stalk	dark brown (5E8), solid	black	dirty brown (5F8) - black
lime nodes	40-80 µm, mostly separate	50-100 µm, sometimes coalescing	100 µm and more, coa-lescing to badhamioid
spore colour	violet brown (8C3-8E4) with a paler side, often a germination visible	dark violet brown (8E4) with a paler side	dark olive brown (5D4-5E5), no conspicuous paler area
diameter	(9.7)-10-10.8-(11.5) µm	(11)-11.6-12-(12.5) µm	(10.5)-11-11.5-(12) µm
ornamentation	warts < 0.4 µm high	spines 0.4-0.8 µm high	spines 0.8-1 µm high
habitat	litter and dung	preferentially dung	litter and dung

Protophysarum phloiogenum M. Blackw. & Alexop., 1975 (**O**, 3: loc. 16, 21, 24). This species was only found in the south-eastern loop of the journey, the true desert region. One of the Kazakh specimens is described and figured in Castillo et al. (1998).

Stemonitis virginiensis Rex (**R**, 1: loc. 38). Collected once on the bark of *Crataegus* from the Karatau Mountains. A small group of sporocarps matching the redescription of the species by Castillo et al. (1997) except for slightly larger spores (6.5-7.2 µm in diameter).

In addition, two forms of the Protosteliales and five forms of myxobacteria were common throughout the survey.

Protosteliales, sp. I (**A**, 42: loc. 4, 5, 10, 13, 14, 16, 17, 18, 21, 22, 24, 31, 32, 33, 37, 38). Very common on all kind of bark throughout the region, occurring rarely on litter.
Large colonies of gregarious, single, stalked but deciduous, globose, colourless and smooth spores (6.7-)7.2-8(-8.6) µm on slender, short stalks of one to two-fold spore diameter; very probably *Protostelium mycophaga* Olive & Stoianovitch.

Protosteliales, sp. II (**C**, 11: loc. 5, 11, 13, 24, 37, 38). As for the previous species, with a strong preference for bark.
An unidentified species with smaller colonies of scattered, single and stalked, deciduous thick-walled spores having a roughened surface, (7.8-)8.2-10.2(-10.8) µm in diameter, stalk not observed under the light microscope.

Myxobacterium div. spec. (**A**, 132: loc. 4, 5, 10, 11, 13, 14, 15, 16, 17, 18, 21, 22, 24, 25, 28, 31, 32, 33, 34, 38, 39). With 132 records, myxobacteria were exceedingly abundant on all substratum types throughout the region.

RESULTS AND DISCUSSION

The 146 moist chamber cultures yielded a total of 513 records, with 328 of these belonging to the myxomycetes. In the field, only 10 fructifications were collected, all under exceptional situations and representing only two species (*Didymium squamulosum* and *Physarum notabile*). Altogether, 27 species of myxomycetes, two members of the Protosteliales, and five forms of Myxobacteria (not differentiated) were registered. The average yield of the moist chambers was about 2.2 myxomycete species per culture. Only six of the cultures gave no results; fifteen others produced only myxobacteria.

It seems to be a common biological rule that extreme environments have impoverished floras, albeit with a few, extremely abundant species. The results of the study presented here confirm this. Compared with surveys from wooded areas (Stephenson et al. 1993, Schnittler & Novozhilov 1996), the desert investigated harbours a rather poor myxomycete flora. If only species regularly (more than two records) occurring in true desert habitats and outside the Karatau Mountains are regarded, the species list declines from 27 to 15, but these are species often found with exceedingly high frequencies (*Echinostelium colliculosum*: 43 of 81 cultures with bark; *Physarum notabile*: 82 of 146 cultures). These and other species previously regarded as rare (e.g. *Echinostelium arboreum* and *Macbrideola oblonga*) underline the distinctiveness of this desert myxomycete flora. From a number of substrata, especially bark of desert shrubs (e.g., *Atraphaxis replicata* and *Calligonum densum*), all cultures yielded myxomycetes. Under favourable weather conditions, literally each square centimetre of bark must be covered with myxomycetes.

Bark yielded most of the species, as well as most of the records, followed by litter and dung. Only two species occurred exclusively on animal droppings (*Didymium annulisporum* and *Licea* spec., both recorded only once), although dung is well known as an occasional substratum for many species (Eliasson & Lundquvist 1979). Of particular interest is the abundance of myxomycete taxa forms often regarded as ancient, such as *Echinostelium*, *Protophysarum* or the *Protosteliales* in comparison to the poor total myxomycete flora. The extremely high abundance of corticolous myxomycetes stands in contrast to the purity and scarcity of the epiphytic lichen flora (about 10 species only); 26 bark moist chambers were from taller shrubs almost free of epiphytic lichens, and 21 (81%) of these yielded myxomycetes. From the 46 moist chambers of shrubs with epiphytic lichen coverage exceeding 5%, 43 (93%) yielded myxomycetes.

What are the limiting factors for myxomycete diversity in such extreme environments? One obvious and striking factor is the very harsh climate, with only two short time windows (spring and autumn) available for myxomycete development. An indirect confirmation for this assumption is the appearance of additional species (*Perichaena depressa*, *Physarum cinereum*, *P. decipiens*, and *Stemonitis virginiensis*) in the Karatau Mountains, characterised by a more steppe-like vegetation and a slightly more humid climate. The extreme fluctuations in air humidity favour species with a short development time or those able to survive repeated desiccation during development. The rarity of decaying wood is a further limitation; dead branches remain over a long time on the shrubs, and those on the ground dry out quickly due to their small diameter. Due to the extremely cold winters, the region lacks any succulent plants, thus excluding species such as *Badhamia gracilis* (T. Macbr.) T. Macbr., known from arid regions but with a strong preference for decaying succulents (Blackwell & Gilbertson 1980, Eliasson 1991). Thin litter mats were observed only under the rare denser shrubs with well-developed foliage (e.g., *Rhamnus sintenisii*, *Ammodendron eichwaldii*) or as heaps of dead

branches like in *Capparis spinosa*, thus limiting the number of litter species. A less obvious factor is the high pH of all substrata, usually ranging from 7.4-8.2. The reasons are the often salty soils as well as the actual plant substrata; especially the abundant *Chenopodiaceae* with high Na^+ and ash contents. These high pH values may be a reason for absence of most members of the Stemonitales, Liceales and Trichales except *Perichaena*. The only exception, bark of *Tamarix* (pH 4.6-7.2, n=5), harboured a different myxomycete flora (e.g., *Comatricha laxa*, *C. pulchella*, *Arcyria minuta*, and *Licea biforis*).

Table 2. Comparison of regional myxomycete floras with the results of the present survey. T = total number of species recorded, S = species shared, and CC = coefficient of community. For data sets from the boreal zone, compare Schnittler & Novozhilov (1996).

climate	T	S	CC	region and source
boreal	90	9	0.15	Russian Karelia (Schnittler & Novozhilov 1996)
boreal	125	10	0.13	boreal Finland (Härkönen 1979a, b, 1981, 1989)
boreal	101	8	0.12	boreal Sweden (Eliasson 1975, 1977, Eliasson & Lundqvist 1979, Eliasson & Strid 1976, Eliasson & Sunhede 1972, Fries 1899, 1906, 1910, 1912, Harling 1952, Santesson 1948, 1964)
temparate	106	5	0.07	(Stephenson et. al. 1993)
montane	56	-	0.00	(Stephenson et. al. 1993)
subtropical	77	7	0.13	(Stephenson et. al. 1993)
tropical	101	11	0.17	(Stephenson et. al. 1993)
tropical	94	10	0.16	Hawaii (Eliasson 1991)
mediterranean	93	10	0.17	Israel (Ramon 1968, Binyamini 1986, 1987, 1991)
desert	39	9	0.27	Arizona (near Tucson, Chaparral and desert records only: Evenson 1961; Sonora: Blackwell & Gilbertson 1980)

Compared to surveys in temperate and tropical regions having a humid climate, the myxomycete species list obtained in the present study is short, but it comprises one of the most distinct myxomycete floras on Earth. Expressed in terms of similarity (coefficient of community, compare Stephenson et al. [1993]) the species inventory shows very low degrees of similarity (0.07-0.15) with all temperate regions and only slightly higher ones (0.13-0.17) with tropical and subtropical regions (Tab. 2). Surprisingly, the Mediterranean region also is very different (0.17 for myxomycetes from Israel). Only the flora of a hot desert (Arizona) shows a higher degree of similarity (0.27). Consequently, it can be expected that the most similar flora in the New World should occur in a winter-cold desert such as the Mojave region.
The area investigated in the present study is still too small to reveal differences in geographical distribution. Among the five main habitat types, sand dune areas showed the highest richness of

species, correlating with a richer and more abundant shrub flora. Some shrubs, such as the *Calligonum* species, are limited to sand dunes. Obvious differences in the species inventory existed only for the Karatau Mountains, which have more rainfall, non-calcareous soils and with *Crataegus ambigua* the only true tree of the region. In terms of vegetation, this region can be regarded as the southernmost steppe peninsula.
At the present level of knowledge, further comparative investigations in other arid regions are necessary to explore the whole richness of desert myxomycetes and reveal their world-wide distribution patterns.

ACKNOWLEDGEMENTS

Field work of the first author was supported by a travel grant (40095/705.6.168) from the Stifterverband für die Deutsche Wissenschaft. For confirming determinations or loan of authentic or type material, we are indebted to D.W. Mitchell, G. Moreno, D. Wrigley de Basanta and Y. Yamamoto. Thanks are also due to D.W. Mitchell for revising the determination of *Comatricha laxa* and S.L. Stephenson for discussing and proof-reading the manuscript.

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Chapter 9. Myxomycetes of the Maquipucuna Cloud Forest Reserve, Ecuador

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Abstract: The assemblage of myxomycetes associated with cloud forests of the western Andes was investigated in the Maquipucuna Cloud Forest Reserve, located *ca* 40 km W of Quito, Ecuador. From more than 1000 myxomycete records (roughly half of these originated from substratum cultures) 77 taxa were identified with certainty; 30 of these are new for the country. Within three study sites situated along an elevational gradient that extends from 1200 to 2700 m above sea level a clear pattern of decreasing myxomycete diversity and abundance with increasing elevation was found. The frequency distribution of the 68 species identified from field records follows a log normal model. Using Preston's octave scale method for the field records as well as a bootstrap procedure for records from moist chamber cultures, it can be assumed that the survey revealed about 75% of all species potentially occurring in the general study area. A comparison of our data with comparable data reported for two similar comprehensive surveys carried out in temperate and boreal regions suggests that Neotropical cloud forests have a lower myxomycete diversity than temperate forests, but the assemblage of myxomycetes present displays a number of distinctive characteristics. Among these are a shift from wood to litter as the substratum most important for myxomycetes, a very low diversity of bark-inhabiting myxomycetes, a higher productivity of aerial versus ground substrata, a higher proportion of myxomycete species (especially members of the order Physarales) possessing phaneroplasmodia, a higher proportion of species of myxomycetes with stalked sporocarps and longer stipes for stalked species occurring in both temperate and tropical zones. These characteristics can be explained by three factors, all of which are unfavourable for myxomycete growth and development. These are an excess of rainfall, a lower chance for most substrata to dry out and allow myxomycetes to disperse their spores and a higher probability of sporocarps becoming colonized by fungi.

Keywords: western Andes, cloud forest, biodiversity, ecology, distribution

Much of what is known about the distribution and ecology of plasmodial slime moulds (myxomycetes) has been derived from field surveys undertaken to collect and study various groups of fungi, with collections of myxomycetes being produced as a by-product. This is particularly true for the Neotropics, as reflected by the collection records cited in *Flora Neotropica* (Farr, 1976). For many of the apparently uncommon species of myxomycetes, often only a few specimens are available. In numerous cases, this limited material does not allow the taxonomic status of a particular species to be clarified. Abundance data relating to myxomycetes in Neotropical forests are not available at all.

The Galapagos Islands represent one notable exception for the Neotropical region. Earlier studies by Bonar (1939) and Martin (1948), Eliasson (1971) and Eliasson & Nannenga-Bremekamp (1983) reported the results of surveys for myxomycetes carried out on the islands. Reid, Pegler & Spooner (1981) listed 18 species of myxomycetes for the Galapagos Islands. When the records from all of the literature sources cited above are combined, this number increases to 96 species. This total is more than the number of species (87) known for the mainland of Ecuador, as derived from records reported in *Flora Neotropica* (Farr, 1976) as well as in papers by Farr (1974), Farr, Eliasson & Dumont (1979), Harling (1967) and Stephenson & Mitchell (1994). However, none of these studies provides abundance data that can be used to estimate the degree of completeness of the surveys.

Carried out in the context of a project with the objective of studying the biodiversity and ecology of Neotropical myxomycetes, the present paper adds data obtained from a survey along an elevational gradient in the western Andean cloud forests, situated *ca* 40 km W of Quito, Ecuador (Pichincha Province, 00° 07' N, 78° 38' W). During three weeks of field work carried out in November and December 1998, an effort was made to record or collect every myxomycete fructification in selected study sites and to obtain samples of a number of different substratum types for moist chamber cultures. Overall objectives of the present study were (i) to obtain additional baseline data on myxomycete biodiversity in Neotropical forests, (ii) to characterize the assemblage of commonly occurring species by assessing their abundances, (iii) to use these abundance data to estimate the degree of completeness that can be achieved in this type of survey, (iv) to obtain data relating to the elevational distribution of myxomycetes within the cloud forests of the western Andes and (v) to compare and contrast the characteristic features of the assemblage of myxomycetes associated with these forests with the assemblages associated with temperate and boreal forests.

MATERIALS AND METHODS

Sampling and species identification

Specimens of myxomycetes as well as substratum samples for moist chamber cultures were collected almost exclusively from the three study sites described below. All microhabitats suitable for myxomycete growth were subjected to careful examination. Fruitings of common and easily recognizable species of myxomycetes were only occasionally collected but always recorded. Rare species and those not easily identified in the field were always collected. For the purposes of this study, all sporocarps that could have arisen from one plasmodium were defined as one specimen. In practice, it was assumed that sporocarps that share the same substratum and are separated by a distance that could be overcome by a migrating plasmodium were derived from the same plasmodium. Mature sporocarps were air-dried and mounted in small boxes. In addition, permanent slides were prepared using polyvinyl lactophenol, polyvinyl alcohol or Hoyer's medium. Due to the lack of colour, sporocarps of *Arcyria* were mounted in polyvinyl lactophenol mixed with methylene blue, to stain the capillitium and spores. Descriptions of specimens follow the terminology of Lado & Pando (1997), with colours described according to Kornerup & Wanscher (1981). Collections reported herein were deposited either in the Royal Botanical Garden, Madrid (MA-Fungi), with duplicates in the collection of the first author stored at the Herbarium Haussknecht, Jena (JE) or in the herbarium of Fairmont State College (FWVA).

Substratum samples for moist chamber cultures were collected along a transect of *ca* 200 m length that was established at each study site. Within a distance of 10 m, several substratum pieces of one type were collected and pooled to produce a sample of 15–25 g weight. Sampling was repeated over the transect, to obtain a series of substratum samples of each type. For each series of samples, the number of samples (equal to the number of cultures prepared) as well as the substratum type, according to the following classification, is given. All myxomycete substrata were classified as following: *b* – bark of living trees; *w* – decaying, formerly solid wood in various stages of decay; *lw* – decaying woody but soft plant parts of a small diameter (e.g. lianas and shoots of climbing members of the family Araceae); *li* – decaying corolla parts and bracts of inflorescences of giant herbs, all belonging to the order Zingiberales, with all samples obtained from living plants above ground; *ll* – leafy litter, aerial (dead but still attached plant parts) or from the forest floor; *lh* – litter of fleshy herbaceous plant parts such as shoots from members of the family Heliconiaceae; and *ep* – epiphyllic liverworts on living, mostly leathery leaves of understorey shrubs and trees. Dung of herbivorous animals, which represents a potential microhabitat for myxomycetes in temperate and boreal forests (Eliasson & Keller, 1999), was never encountered in the present study.

Moist chamber cultures

All moist chamber cultures were prepared within a week after returning from the field survey, using disposable plastic Petri dishes lined with filter paper. Cultures were moistened with distilled water adjusted to pH 7.0. After 24 h, excess water was poured off and the pH of the wet substratum was measured with a flat surface electrode, using an Orion model 610 pH meter. For each culture, pH was determined for three randomly chosen substratum

pieces. Cultures were maintained in a greenhouse up to four months under diffuse light and at a temperature of 22–25° and checked on five occasions (days 6, 17, 47, 81 and 109 after excess water was poured off).

Data analysis

Two different approaches, a bootstrap analysis and Preston's octave scale method, were used to estimate the completeness of the survey in terms of the species recorded, both of which are explained in detail in Schnittler & Stephenson (2000). In brief, for the bootstrap analysis, the sequence of samples (moist chambers) was permutated randomly and the number of recorded species was plotted against the number of moist chambers (samples). The mean of 100 plots of species versus samples was then subjected to a regression analysis, using a saturation formula $y = ax / (b+x)$, with the parameter a giving an estimate for the total number of species to be expected. Preston's octave scale method (Preston, 1948) assumes a log normal frequency distribution of the species present in a given community. When classifying the numbers of records for each species in a geometric sequence of octaves ranging from 0–1 records, 1–2, 2–4, 4–8 and so on, the resulting curve can be fitted with a bell-shaped Gaussian function $y = a\ e^{(-b * b * x * x)}$, with the area under the curve providing an estimate for the total number of species to be expected. For comparison of myxomycete biodiversity within forest types, Shannon's formula $H' = \sum (p_i \ln p_i)$, which is based on the proportion p_i of the records belonging to one species to the total number of records made for all species, was used (Shannon and Weaver, 1963). To be considered as sampled above the ground, myxomycete substrata had to be above ground level. For records from litter, the fructifications had to be recorded from a height of more than 5 cm above ground level. For records from wood, the respective log or branch had additionally not to be in contact with the ground for most (>75%) of its entire length. For the analysis of sporocarp features, stalked sporocarps were defined as those with a stipe which was developed well enough to elevate the sporotheca above a water film covering the substratum. Stipe length was measured under low magnification with a light microscope from slides prepared with five sporocarps of the respective collection, with stipe length defined as the distance from the bottom of the basal disc (hypothallus) to the point where the stipe widens again to merge into the sporotheca.

Study sites

The Maquipucuna Cloud Forest Reserve, located *ca* 40 km W of Quito, Ecuador (Pichincha Province), is a 4500 ha nature reserve, surrounded by 14000 ha of protected forest. The reserve is located adjacent to the Choco bioregion of northwestern Ecuador and ranges in elevation from 1200 to 2720 m above sea level. Tropical Andean rain and cloud forests intergrade with each other on the mostly west-exposed slopes of the reserve. The closest town is Calacalí; two villages, Nanegal and Nanegalito, are the nearest settlements. For the three study sites selected within the reserve, forest type and structure of the vegetation are briefly described, with emphasis on those features that might influence myxomycete diversity. All localities represent primary forests, with no or only a limited degree of human disturbance at the lowermost site.

Site 1 (Moist Forest; abbreviation *MF*) is in a small valley of a tributary of the Rio Tulambi, where it extends along the Palmitos Trail *ca* 2.5 km SE of the village of Marianitas and *ca* 1.15 km SW of the Maquipucuna Foundation Lodge, elev. 1300 ± 100 m (00º07'15" N, 78º38'05" W ± 250 m). The annual rainfall is approximately 2500 mm (2453 mm registered at the village of Nanegalito, *ca* 5 km SW of this study site and situated at approximately the same elevation). In spite of this rather high value, the influence of a dry season is still remarkable, with less than 100 mm average monthly rainfall from May to November. Leaves of understorey shrubs, as well as the litter layer, can dry out almost completely during a week without rain. Nevertheless, the continuously humid atmosphere in the river valley supports leaves with dense but not totally closed covers of epiphyllic liverworts, more rarely lichens. The forest canopy, formed by evergreen trees with medium to large leaves, is closed except for treefall gaps and stream valleys. The bark of the trees present at this study site ranges from very smooth to deeply furrowed or flaky but is mostly soft and noticeably hydrophilic. It is covered by thin mats of leafy liverworts in sheltered places but also frequently occurs free of epiphytes. Lianas as well as climbing plants belonging to the family Araceae are very frequent, whereas other epiphytes are rather rare. Along small streams and in slightly disturbed areas near the Lodge, tall herbs of the order Zingiberales were locally abundant, particularly *Costus guanaiensis* Rusby and *Heliconia griggsiana* L.B. Sm. (names after Jørgensen & León-Yánez, 1989), with their decaying floral parts providing a hitherto unknown microhabitat for myxomycetes. The forest at this site can be assigned to the Tropical Moist Forest in the classification of Holdridge *et al.* (1971). The following substrata were sampled at this site (number of samples and substratum type in parentheses): tree bark in a height of 1.0–2.0 m (33, *b*); leafy litter from the forest floor (44, *ll*); aerial leafy litter, such as fallen leaves trapped in dense understorey vegetation or dead but still attached leaves (21, *ll*); pieces of living leaves of understorey plants covered with foliicolous liverworts and located 0.5–2.5 m above the ground (21, *ep*); dead, soft and thin shoots of lianas hanging from trees in 1.5–2.5 m height (21, *lw*); and dead rachis and leaf parts of palm fronds at a height of 0.5–1.5 m above the ground (20, *lh*). In addition, decaying floral parts were collected from living individuals of the following plants, with each inflorescence constituting one sample: *Heliconia griggsiana* (11, *li*, from a height of 3.0–6.0 m), *Calathea plurispicata* H. Kenn. (16, *li*, height of 1.5–2.5 m) and *Costus guanaiensis* (13, *li*, height of 1.5–3.0 m).

Site 2 (Wet Forest – *WF*) is a middle elevation cloud forest, located near the NNW-exposed first summit of the Cerro de Sosa massive, *ca* 6 km SE of Marianitas (*ca* 3.5 km S of the Maquipucuna Foundation Lodge), elev. 1900 ± 150 m (00°05'40" N, 78°37'00" W ± 1 km). Annual rainfall is probably between 3300 and 3700 mm and daily cloud exposure is also common during the dry season. The almost closed forest canopy is formed by tall evergreen trees; members of the Clusiaceae, Cunoniaceae and Lauraceae are the most abundant. The influence of the dry season is much less apparent than in site 1, with rainfall common also during the months of May to November. Leafy litter on the forest floor stays continuously wet in deeper layers and leaves of understorey plants are covered with thin but nearly closed mats of epiphyllic liverworts, sometimes mosses. The bark surface of most trees is covered with a thick, almost closed mat of mosses and liverworts. Bark texture is mostly smooth or slowly peeling, with large but smooth flakes. Members of the Araceae are the predominant epiphytic plants; lianas are considerably less common than in site 1. In the Holdridge classification, this site would be assigned to the Tropical Premontane Wet Forest. Samples were collected from the following series of substrata: tree bark

(24, *b*), leafy litter on the forest floor (42, *ll*), aerial leafy litter (21, *ll*), leaves with foliicolous liverworts (20, *ep*), decaying liana shoots (21, *lw*) and the decaying inflorescences (12–17 cm in length and collected at a height of 1.0–1.5 m) of the Andean endemic *Calathea ischnosiphonoides* H. Kenn. (21, *li*), a member of the Marantaceae that is abundant at this elevation.

Site 3 (Rain Forest – *RF*) is a high elevation cloud forest located near the highest summit of the Maquipucuna Reserve, Cerro Montechristi, *ca* 20 m below the top of a ridge extending SW to NE, *ca* 5.7 km NW of the village of Yunguillas (*ca* 2 km NW of 'Rolandos Finca'), elev. 2700 ± 75 m, (00°03'15" N 78°35'55" W ± 500 m). Annual rainfall is probably between 3500 and 4000 mm, with daily, long periods of cloud exposure also occurring during the dry season. At this elevation, no effective dry season occurs. Long curtains of epiphytic mosses, together with a lush epiphyte cover of bromelids, ferns and members of the Cyclanthaceae are characteristic features of this cloud forest. However, true lianas are absent. Leafy litter on the forest floor stays continuously wet throughout and is often covered by a film of water. Leaf surfaces of understorey plants dry out for only a short period during the day or stay continuously wet. Relatively strong winds allow epiphyllic liverworts to grow only in sheltered sites, but then with closed mats. Trees are small, 10–20 m tall and the canopy is only about 70% closed. The bark of trees is almost completely covered with lush, 2–5 cm thick mats of mostly mosses and hymenophyllaceous ferns. In the Holdridge system, this study site would be assigned to the Tropical Lower Montane Rain Forest. Substratum samples collected included tree bark (19, *b*), leafy litter on the forest floor (41, *ll*), aerial leafy litter (20, *ll*) and leaves with epiphyllic liverworts (20, *ep*). A small number (26) of miscellaneous substratum samples was collected throughout the three study sites, but these did not yield any additional species of myxomycetes.

ANNOTATED SPECIES LIST

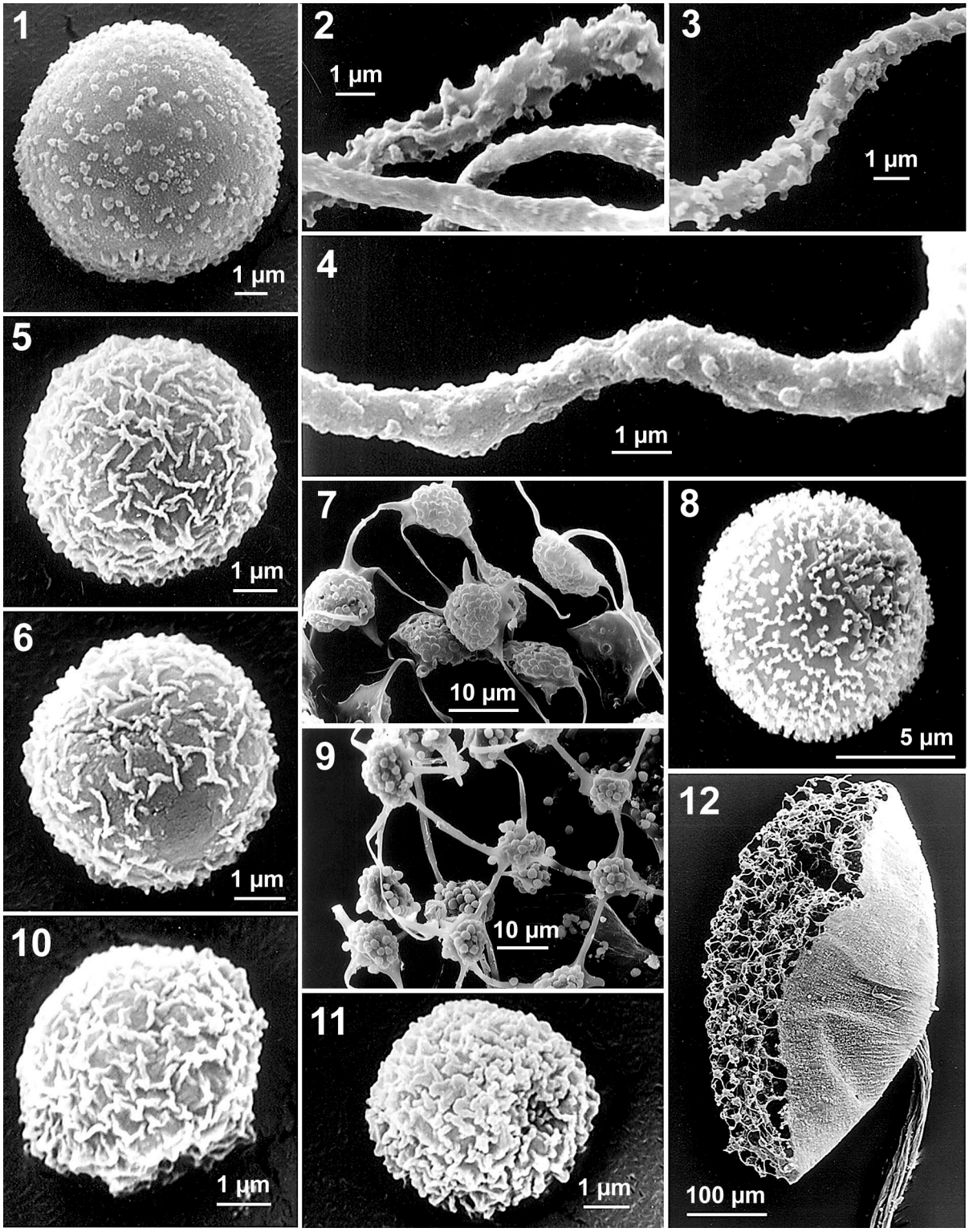
All species recorded are arranged alphabetically, with the nomenclature essentially following Martin & Alexopoulos (1969). For species not included in this monograph, a reference to the protolog is cited. The abbreviation 'cf.' in the name of a taxon indicates that it could not be assigned to this name without remaining doubts, whereas a '?' stands for taxa represented by scanty and/or poorly developed collections only. After each species name, an estimate of abundance as described by Stephenson, Kalyanasundaram & Lakhanpal (1993) is given in brackets. This estimate is based on the proportion of a particular species to the total number of records (936 myxomycete specimens that could be identified): R – rare (<0.5%, in this study fewer than 5 records), O – occasional (0.5–1.5%, 5–14 records), C – common (>1.5–3%, 15–28 records) and A – abundant (>3% or more than 28 records). For rare and/or taxonomically difficult species, vouchers are cited, referring to the collection numbers of the first author. The last number in brackets is the total number of records for each taxon. One asterisk indicates a species recorded as new for the mainland of Ecuador, whereas two indicate a new record for the entire country. For each of the three study sites, the number of specimens recorded

is provided, according to the substratum types mentioned above, with collections made in the field preceding a slash and specimens obtained in moist chamber following the slash. For records of doubtful identity, as well as for rare species, taxonomic descriptions are provided.

Arcyria afroalpina Rammeloo Bull. Jard. Bot. Belg. 51: 229. 1981 [R, 17322, 1 record **] *RF*: ep -/1.
This collection is described in detail by Schnittler (2000). Comparisons with the excellent description given by Rammeloo (1981 *a*, 1981 *b*) as well as his specimen 4997 (isotypus) leave no doubt that the Ecuadorian specimen represents *A. afroalpina*, the third record of this species outside the East African Mountains (Spain: Lado & Pando, 1997: 165; Japan: Yamamoto, 1998: 166) and the first for the New World. All characters match the original description, except for the slightly thinner capillitium (described as 1.8–3.0–4.5 µm wide). The SEM micrographs (Figs 1–4) show that considerable variation exists in the ornamentation of the capillitium, with the basal threads having a less pronounced ornamentation than the thinner ones near the apex of the sporotheca. This and the diminutive forms of *A. cinerea* may represent a complex of apomictic biotypes, as demonstrated for *Didymium iridis* by Clark & Mires (1999).

Arcyria cinerea (Bull.) Pers. [A, 108 records] *MF*: ep -/20, li -/4, ll 3/15, lw 0/3, w 21/0; *WF*: b -/1, ep -/17, li -/7, ll -/5, lw 0/1, w 1/0; *RF*: ep -/4, ll -/5, w 1/-.
This species is very variable in sporocarp size and colour. From the field collections on wood, the single stalked var. *cinerea* (12 records) was slightly more common than the var. *digitata* (8 records), in which several sporothecae share a common stalk. The latter variety was observed only on wood. Differences between the varieties are relatively minor, with var. *digitata* having larger, cylindrical sporothecae typically 4–6 mm in length, whereas typical specimens of var. *cinerea* are characterized by ellipsoid sporothecae 2–4 mm in length.
Specimens from epiphyllic liverworts and most of the fructifications from inflorescences, all obtained in moist chamber cultures, constitute a diminutive form that may represent a distinct taxon (see description in Schnittler, 2000). However, specimen 13043 from forest floor litter displays characters that are intermediate with *A. afroalpina*: the sporothecae are ochraceous (4B4) and the spores are with (7.8–)8–9(–9.7) µm diam. larger than usual for *A. cinerea*. On the other hand, the spore-like cells in the stalk are smaller than those in *A. afroalpina* (13–17 µm diam.), the spore ornamentation consists of fewer, scattered warts and the sporothecae are ellipsoid in well-developed sporocarps, being 0.6–0.8 x 0.2–0.4 mm in extent. Specimens morphologically intermediate between *A. afroalpina* and *A. cinerea* were mentioned also by Rammeloo (1981 *b*) for the East African mountains.

Arcyria denudata (L.) Wettst. [C, 24 records] *MF*: ll 1/-, w 21/-; *WF*: w 1/-; *RF*: w 1/-.
Specimens 13054, 13056 and 13129 deviate from typical specimens of *A. denudata* in having fresh brick red (7A8) sporocarps on stalks 1.5–2.5 mm long and with capillitial plumes expanding up to 10 mm in length. The capillitium is ornamented with relatively distant (4–6 per 20 µm) half-rings and rings. This form tends to appear in large colonies; specimen 13129 was estimated to consist of more than 5000 sporocarps.



Figs 1–4. *Arcyria afroalpina* (Schnittler 13722). **Fig. 1.** Spore. **Figs 2–4.** Variation in the ornamentation of the capillitial threads. **Figs 5, 6.** *Cribraria intricata*, spores (Lado 9778). **Figs 7, 8.** *Cribraria languescens* (Lado 9825). **Fig. 7.** Peridial nodes. **Fig. 8.** Spore. **Figs 9–12.** *Cribraria tenella* (Lado 9798). **Fig. 9.** Peridial nodes. **Figs 10, 11.** Spores. **Fig. 12.** Sporocarp, showing the calyculus and the peridial net.

Arcyria globosa Schwein. [O, 12819, 12995, 13045, 10 records **] *MF*: ll 9/1.
All collections are very homogenous in their characters. Features distinguishing this species from the closely related *A. cinerea* complex are the cream to light grey, globose, rather short-stalked sporocarps; a very deep calyculus having concentric shrinkage lines; and the tendency to occur in small colonies of scattered sporocarps.

Arcyria major (G. Lister) Ing [R, 13166, 1 record **] *MF*: w 1/-.
One small colony of gregarious, stalked sporocarps on well-decayed white-rotten wood. Sporothecae obviously already faded in colour, reddish grey brown (10D5), which suggests a pink or scarlet red colour when fresh. Hypothallus common to the whole group; stalks 0.3–0.5 mm in length, 100–140 µm diam. and gradually merging into the calyculus, the latter concolorous with the sporotheca colour, densely stuffed with spore-like cells 10–13 µm diam. Calyculus plicately folded, with a rather conspicuous pattern of evenly distributed warts on the inner surface, small but deep, funnel-shaped, 0.3–0.4 mm wide and 0.3–0.5(–0.6) mm long. Capillitium a dense network of strongly coiled threads with meshes approximately 50–120 µm wide, readily separating from the calyculus and extending into a 0.6–0.8 mm long plume, threads 5.0–5.5 µm wide (including ornamentation), very evenly adorned with short, blunt, conical spines or cogs (9–12 per 20 µm), by transmitted light pale red brown (10B3). Spore-mass coloured as the sporotheca, by transmitted light concolorous with the capillitium (10B3–10B2), globose, (6.5–)7.2–7.8(–8.1) µm diam., with a few scattered warts.
These characters match those of authentic material from Nannenga-Bremekamp (specimen NENB 8990, Doorwerth, dead hardwood), except for the more regular capillitial ornamentation and a larger calyculus with a more pronounced ornamentation (D.W. Mitchell, pers. comm.).

Ceratiomyxa fruticulosa (Müll.) T. Macbr. [A, 37 records] *MF*: lh 3/-, w 22/-; *WF*: lh 1/-, w 9/-; *RF*: w 2/-.
Whereas the var. *arbuscula* (Berk & Broome) Nann.-Bremek. (Nederlandse Myxomyc. 55. 1975) with its arborescent, solitary sporophores was observed on wood in 8 out of 10 instances, the more caespitose var. *fruticulosa* was also common on litter, where it formed smaller sporocarps that were pale yellow (1A3–1A5) when fresh.

Ceratiomyxa morchella Welden [R, 12997, 2 records **] *MF*: w 1/-; *WF*: w 1/-.
Observed twice as large fructifications (*ca* 700 and 1000 sporophores, respectively) on acidic, decorticated logs.

Comatricha ? *lurida* Lister [R, 13612, 1 record **] *MF*: li -/1.
Represented by a single sporocarp obtained from a moist chamber culture.

Comatricha pulchella (C. Bab. & Berk.) Rostaf. [O, 6 records **] *MF*: ep -/1, ll 4/-, lw -/1.

Comatricha tenerrima (M.A. Curtis) G. Lister [R, 12934, 1 record **] *MF*: lh 1/-.

Craterium aureum (Schum.) Rostaf. [O, 12982, 13090, 13093, 7 records] *MF*: ll 6/-; *WF*: 1/-.

Found repeatedly on forest floor litter, always with bright yellow (3A8) to chrome yellow (4A8) sporocarps. In three cases, this species was associated with the more common *C. leucocephalum*.

Craterium concinnum Rex [R, 13046, 2 records **] *MF*: ll 2/-.
Sporothecae on stalks 0.15–0.25 mm long, obconical, 0.25–0.3 mm diam. and light brown (5C4–5C3). The lid is concolorous, sunken and separated by a distinct rim. The closely related *C. minutum* was not encountered in this study.

Craterium leucocephalum (Pers.) Ditmar [C, 26 records] *MF*: lh 1/-, ll 25/-.

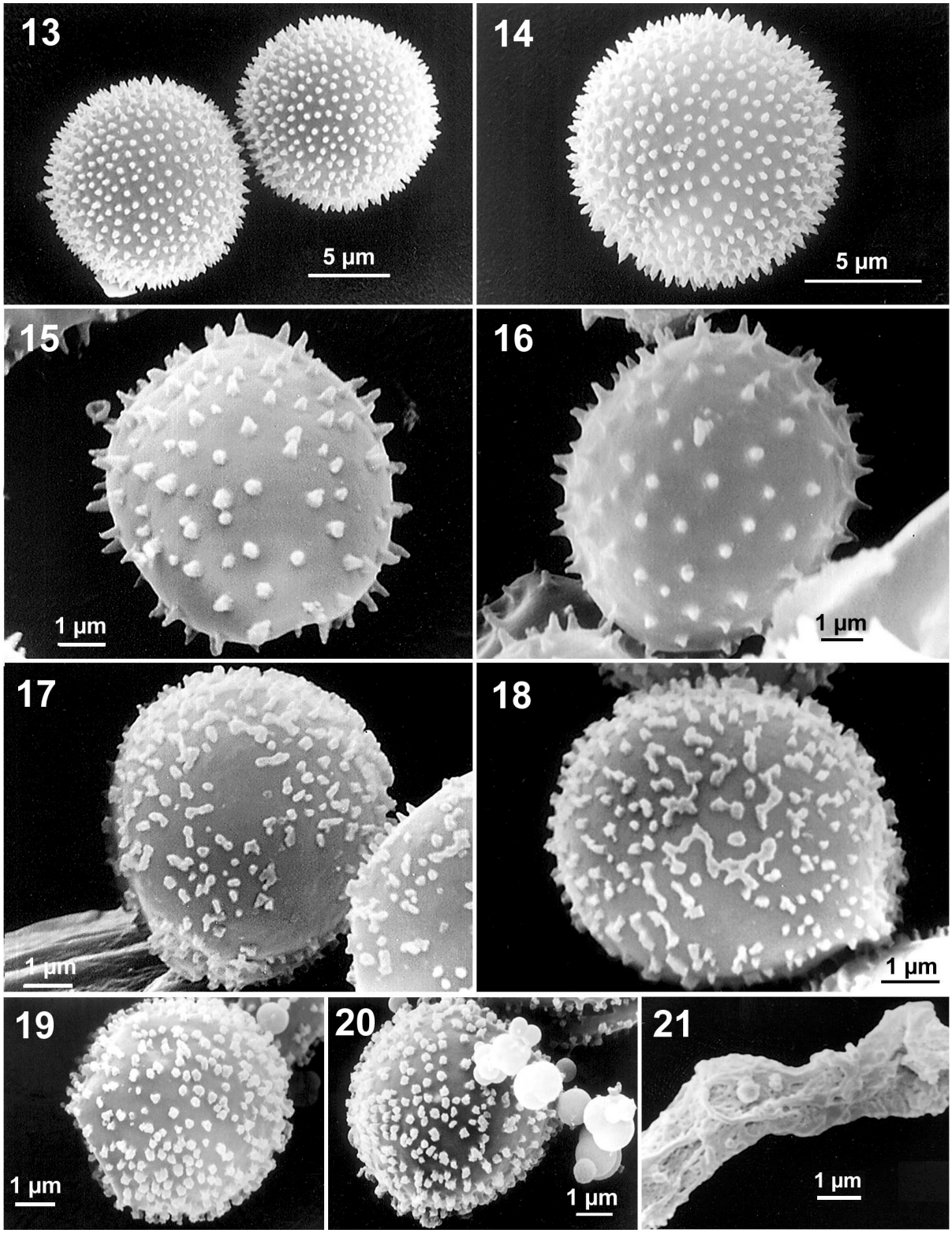
Cribraria cancellata (Batsch) Nann.-Bremek. [C, 15 records] *MF*: w 13/-; *WF*: w 1/-; *RF*: w 1/-.
The less common var. *fusca* was recognized by the presence a small but distinct calyculus. Both varieties were usually observed to possess very long (up to 4 mm) stalks.

Cribraria confusa Nann.-Bremek. & Y. Yamam. Proc. Kon. Ned. Akad. Wet. C86: 212. 1983 [R, 13604, 1 record **] *MF*: b -/1.
A new record for Ecuador, but also known from the Amazonian part of the country and Puerto Rico (Schnittler & Stephenson, unpubl. data).

Cribraria intricata Schrad. [O, 12887, 5 records **] *MF*: ll 1/-, w 4/-.
Hazel-brown (4B7–4C8) sporothecae 0.5–0.7 mm diam., with no distinct calyculus and a peridial net with numerous free ends and rather irregularly spaced, thickened nodes 8–15 µm wide were considered as the typical characters for this species. It is closely related to *C. tenella*, which possesses a very similar spore ornamentation (Figs 5, 6 and 10, 11).

Cribraria languescens Rex [R, 13077, 1 record *] *MF*: lh 1/-.
Differing from the closely related *C. tenella* by having more coppery brown (5C8–5C7) sporothecae with a deeper, more urn-shaped calyculus comprising half of the height of the sporothecae and relatively longer stalks. In the SEM micrograph (Fig. 7), the peridial nodes clearly differ from those of *C. tenella* by their larger size and almost pillow-shaped habit. Also, the spores deviate by having an ornamentation consisting of subreticulate warts (Fig. 8).

Cribraria tenella Schrad. [C, 12832, 12881, 13014, 15 records] *MF*: ll 1/-, w 13/-; *WF*: w 1/-.
Characters distinguishing this species from *C. intricate*, with which it is often confused, were the smaller size (sporotheca 0.2–0.4 mm diam.), an always present calyculus which is 40–60% of the total height of the sporotheca (Fig. 12), the darker brown colour (4E8–4D7) and a peridial net that is much more regular in appearance, having larger (15–20 µm in extent), more thickened nodes and almost no free ends (Fig. 9). The spores are very similar to those of C. *intricata* (Figs 10, 11).



Figs 13, 14. *Diderma corrugatum* (Schnittler 13126), spores. **Fig. 15.** *Lamproderma muscorum* (Lado 9856), spore. **Fig. 16.** *Lamproderma muscorum* (Lado 9688), spore. **Figs 17, 18.** *Lamproderma* sp. (Schnittler 13036), spores. **Figs 19, 20.** *Physarum* sp. (Lado 9961), spores. **Fig. 21.** *Perichaena quadrata* (G.W. Martin 176, USA, Iowa, Johnson Co., oak bark in moist chamber, 9 Dec. 1959), capillitial thread.

Cribraria violacea Rex [R, 14008, 2 records *] *MF*: ll 1/1.

Diachea leucopodia (Bull.) Rostaf. [R, 2 records] *MF*: ll 2/-

Diderma corrugatum T.E. Brooks & H.W. Keller apud Brooks Mycologia 69: 180. 1977 [R, 13126, 1 record **] *MF*: b 1/-.
One field collection from the bark of a living tree covered with algae and liverworts. Figs 13, 14 show the spore ornamentation, which consists of very regularly arranged short spines.

Diderma effusum (Schwein.) Morgan [C, 15 records] *MF*: lh 1/-, ll 12/-; *WF*: ep -/2.

Diderma hemisphaericum (Bull.) Hornem. [C, 22 records] *MF*: ep -/1, lh 1/-, ll 15/2; *WF*: ll -/2; *RF*: ll -/1.

Didymium anellus Morgan [O, 13047, 9 records **] *MF*: lh 2/-, ll 4/1; *WF*: ll 1/-; *RF*: ll -/1.
Grey (6D1), flattened plasmodiocarps 0.15–0.25 mm thick. Hypothallus inconspicuous, peridium membranous and sprinkled evenly with lime crystals, these in some specimens forming an almost shell-like crust but still recognisable as being distinct under a dissecting microscope. Peridium itself pale grey brown (6B2) to almost colourless by transmitted light, smooth. Capillitium a flexuous network of anastomosing threads 0.7–1 µm in diam., extending from the bottom to the top of the plasmodiocarp, mostly perpendicular in orientation and attached to the peridium with their very fine, almost colourless outermost ends, the central part of the capillitial threads often with dark, nodular swellings, dull to light brown (6F6–6D4). Spore-mass coffee brown (6E6), pale brown (6C3) by transmitted light, globose to subglobose, (7.2–)7.8–9.0(–9.3) µm in diam., ornamentation consisting of very fine warts and groups of darker warts.
Specimens 12828 and 12994 differ from the description given above by having extensive plasmodiocarps and smaller, paler (6C2) spores (6.0–)6.2–7.2(–7.5) µm in diam. The first was found as a giant plasmodiocarp, covering a total area of approximately 50 cm^2 on the stem of a living understorey palm, *ca* 40 cm above ground; the second (12994) developed only about 1 cm^2 of mature plasmodiocarp from a much larger plasmodium found in the field. The large and extremely flat plasmodiocarps match the habit of *Didymium flexuosum* Yamash., *D. serpula* Fr. or *D. perforatum* Yamash. However, *D. flexuosum* has a columella and vesicular bodies in the capillitium, *D. serpula* also possesses vesicular bodies and *D. perforatum* is distinguished by its larger, more spiny spores and its labyrinthiform habit. In spite of their habit, specimens 12828 and 12994 appear closest to *D. anellus* and are therefore placed under this name.

Didymium bahiense Gottsb. Nova Hedwigia 15: 365. 1968 [O, 13173, 12 records **] *MF*: b 2/-, li 4/-, lh 1/-, ll 4/-, lw 1/-.
Because the conspicuously flattened, white pseudocolumella permits a separation of *D. bahiense* from *D. iridis* on the basis of an easily accessible morphological character, in spite of the proposal of Clark & Mires (1999) to merge this taxon with *D. iridis*, it is here treated separately to maintain comparability with earlier works. This taxon was not obtained in moist chamber cultures.

Didymium clavus (Alb. & Schwein.) Rabenh. [C, 16 records] *MF*: lh 2/-, ll 12/2.

Didymium difforme (Pers.) S.F. Gray [R, 13691, 2 records] *MF*: li -/1; *WF*: ep -/1.

Didymium floccosum G.W. Martin, K.S. Thind & Rehill [R, 13288, 1 record *] *MF*: ll 1/-.
A single, large colony from the densely moss-covered bark of a living tree, located among mosses and small amounts of leafy debris. All characters agree with the isotypus (K.S. Thind 250, in BPI), although the spore diameter is at the upper end of the range (9.1–9.4 µm versus 8–10 µm reported in the original description). Distinguishing features of this species are the rather long, ochraceous but internally limy stalks combined with an aerolate peridium resembling that of *D. nigripes* (Link) Fr., as illustrated in Matsumoto & Deguchi (1994). For South America, the species is also reported from the Galapagos Islands (Eliasson & Nannenga-Bremekamp, 1983) and Venezuela (Farr, 1974).

Didymium iridis (Ditmar) Fr. [A, 111 records] *MF*: -/14, li 3/7, ll 13/20, lw -/1; *WF*: ep -/16, li -/1, ll -/10, lw -/13; *RF*: ep -/13.

Didymium leoninum Berk. & Broome [R, 13289, 13290, 2 records] *MF*: ll 2/-.
Although it seems to be more common in tropical Asia, this species also is known from Jamaica (Farr, 1974) and Ecuador (Farr *et al.*, 1979).

Didymium nigripes (Link) Fr. [C, 13187, 15 records] *MF*: lh 5/-, ll 9/-, lw 1/-.
Distinguished here from the closely related *D. iridis* by the areolate peridium with brown patches 50–100 µm wide that are separated by colourless bands, as described in Neubert, Nowotny & Baumann (1995: 122). In the experience of the authors, this species does not appear in moist chambers and has never completed its life cycle in pure culture.

Didymium squamulosum (Alb. & Schwein.) Fr. [A, 80 records] *MF*: b 1/-, ep -/14, li 7/-, lh 7/-, ll 9/6, lw 1/-; *WF*: ep -/19, ll 1/2; *RF*: ep -/9, ll -/3.

Echinostelium minutum de Bary [R, 13525, 13725, 2 records, *] *MF*: ll -/1, *RF*: b -/1.

Enerthenema papillatum (Pers.) Rostaf. [R, 13940, 1 record, **] *MF*: b -/1.

Fuligo septica (L.) F.H. Wigg. [R, 1 record] *RF*: w 1/-.
One, large fructification was observed in development.

Hemitrichia calyculata (Speg.) M.L. Farr [A, 38 records] *MF*: lw 1/-, w 34/-; *WF*: w 2/-; *RF*: w 1/-.

Hemitrichia serpula (Scop.) Rostaf. [C, 19 records] *MF*: lh 8/-, ll 2/-, w 9/-.

Lamproderma arcyrionema Rostaf. [R, 7 records] *MF*: ll 2/2, w 2/-; *WF*: lh 1/-.

Lamproderma cf. *muscorum* (Lév.) Hagelst. [R, 12941, 13112, 2 records **] *MF*: lh 1/-, b 1/-.
Gregarious sporocarps appearing in large to very large colonies on a red brown (8D8–8E8) hypothallus, stalk black, 0.5–0.6 mm in length, as long or only slightly longer than the sporotheca, opaque black by transmitted light, 60–100 µm wide at the base, 20–40 µm wide at the apex. Sporotheca with a silvery, rarely blue, iridescent peridium, 0.35–0.5 mm diam., subglobose with a flattened base. Stalk continuing into a short, slightly clavate and blunt columella one 20–40% of the diameter of the sporotheca. Peridium concolorous by transmitted light, slightly paler (7C4–7A2), smooth, darker and thicker around the stalk. Capillitial threads (0.8–)1.2–1.8 µm wide, arising mostly from the upper part of the columella, pale red brown (7D5–7B3), with a tendency to become paler towards their tips, flexible, slender and anastomosing; with their tips attached to the peridium. Spore-mass dark chocolate brown (7E7), pale brown (7C5) by transmitted light, globose, (8.4–)8.6–9.2–(9.6) µm diam., evenly covered with somewhat distant, darker, spines, 10–14 spines per hemisphere (Figs 15, 16).
Specimen 13112 has a very flexible and finely branched capillitium, which is very pale by transmitted light and causes empty sporocarps to appear almost colourless. The spore ornamentation and size of both specimens matches *L. muscorum* as described by Martin & Alexopoulos (1969), with spores (6.5–)8–10(–14) µm in diam., but Farr (1976) gives the spore diameter as (8–)10–12(–14) µm. The spore ornamentation, with distant, prominent spines excludes *L. arcyrioides* (Sommerf.) Rostaf., which is known as a variety with a very pale capillitium (var. *leucofilum* Neubert, Nowotny & Baumann, 1989). However, *L. muscorum* is described with a purple-brown and fairly rigid capillitium, which leaves some doubt as to the placement of the Ecuadorian specimens in this taxon.

Lamproderma scintillans (Berk. & Broome) Morgan [C, 19 records] *MF*: b 1/-, ep -/1, ll 2/9; *WF*: ll -/4; *RF*: ll -/2.

Lamproderma sp. [R, 13036, 1 record **] *MF*: ll 1/-.
A small colony of scattered sporocarps, shining, appearing black, on long, slender, black stalks 0.8–1.1 mm long and with sporothecae 0.3–0.45 mm diam. Stalk arising from a discoid, red brown (9E8–9D7) hypothallus, by transmitted light opaque black, *ca* 60 µm diam. at the base and tapering to *ca* 25 µm diam. at the apex, protruding in a blunt, clavate columella. Peridium by transmitted light clearly areolate, with brown (7D6) fields 40–50 µm in extent separated by 5–8(–10) µm broad, almost colourless bands. Capillitial threads arising all from the upper, thickened part of the columella, which is about 35 µm in diam., colour ranging from dull brown (8F8) at the base to pale brown (8C3) at the tips, radiating and rarely anastomosing, 2–2.5 µm wide near the base and connected to the peridium by the much thinner tips. Spores very dull brown (darker than 8F8) in mass, pale brown (7C3) by transmitted light, globose, (7.5–)7.7–8.0(–8.2) µm diam., covered with small, blunt verrucae <0.3 µm in height (Figs 17, 18), with a prominent paler germination slit. The warts are blunt to slightly bacculate, sometimes leaving areas of a spore smooth.

Only *L. gulielmae* Meyl., also with sunken areas at the peridium, shows some resemblance to this specimen but differs by having considerably larger, spinulose spores (described as 12–15 µm diam.) and a paler capillitium.

Licea operculata (Wingate) G.W. Martin [R, 13587, 13913, 2 records] *WF*: b -/1, lw -/1.

Licea cf. *perexigua* T.E. Brooks & H.W. Keller apud Keller & Brooks Mycologia 69: 674. 1977 [R, 13886, 1 record **] *MF*: b -/1.
Scattered sporocarps, almost black (8F8 and darker) when wet but becoming iridescent when dry, on a short, paler brown (5C6–5B5) stalk-like elevation of the hypothallus which reaches two-thirds to slightly more than the whole sporotheca diameter. Sporothecae (40–)60–80 µm diam., almost globose, sessile on the stalk-like, stout extension of the hypothallus, which is 40–45 µm wide at the base and 35–40 µm wide above; pale amber (5A4–5B4) by transmitted light, sometimes darker due to the presence of substratum particles. Peridium translucent chestnut brown (5C5) by transmitted light, with an inconspicuous ornamentation of consisting of faint, regularly distributed warts on the inner surface, dehiscing irregularly without an operculum or along preformed lines. Spores globose, thick-walled, chestnut brown (5D6), smooth, (13–)13.5–14.5(–15.2) µm diam.
Although the spores are larger (8.5–10.5 µm is given in the original description) and darker than described originally, the overall habit fits *L. perexigua* more closely than the similar *L. scyphoides* T.E. Brooks & H.W. Keller apud Keller & Brooks (Mycologia 69: 679. 1977), which is described as having a circumsessile dehiscence and granular deposits on the peridium.

Lycogala epidendrum (L.) Fr. [O, 6 records] *MF*: w 6/-.

Macbrideola decapillata H.C. Gilbert [R, 13889, 1 record **] *MF*: ll -/1.
Very small, solitary sporocarps on a stalk 0.25–0.35 mm long, with a chestnut brown (6E8), globose sporotheca 70–90 µm diam. Stalk arising from a small, discoid hypothallus, almost black under the dissecting microscope, red-brown (6C8) by transmitted light, 15–25 µm wide at the base, tapering towards the tip and then dark red-brown (6F8), 5–6 µm wide, appearing solid. Peridium evanescent except for a 20–25 µm wide collar, smooth, pale red brown (6B4). Columella developed as a rapidly tapering extension of the stalk, reaching about two-thirds of the sporotheca diameter, with a few, pale red brown (6B4–6B3) capillitial threads 1–1.2 µm wide that branch off the columella; the branches are almost perpendicular and have free ends. Spore mass having the same colour as the sporotheca, spores very pale red brown (6B2) by transmitted light, globose, (6–)6.4–7.5(–7.9) µm diam., thin-walled and ornamented with much darker, sharp spines up to 1 µm long (15–20 per hemisphere).
The overall habit best fits that of *M. decapillata*, whereas the spore ornamentation appears to be closest to that of *M. ovoidea* Nann.-Bremek. & Y. Yamam. (Proc. Kon. Ned. Akad. Wet. C86: 231. 1983), which is described as having ovoid, more robust sporocarps.

Metatrichia floriformis (Schwein.) Nann.-Bremek. [O, 12899, 5 records **] *MF*: w 1/-.

Metatrichia vesparium (Batsch) Nann.-Bremek. [R, 12911, 1 record] *MF*: lh 1/-.

Paradiacheopsis cf. *fimbriata* var. *penicillata* (Nann.-Bremek. & Y. Yamam.) Y. Yamam. Myxomycete Biota Japan 583. 1998 [R, 13724, 1 record **] *RF*: b -/1.
Only two but well-matured sporocarps from moist chamber culture constitute the single record of this taxon, originally decribed as *Comatricha penicillata* Nann.-Bremek. & Y. Yamam. Proc. Kon. Ned. Akad. Wet. C86: 223. 1983.

Perichaena chrysosperma (Currey) Lister [R, 12877, 13911, 2 records] MF: lw -/1, w 1/-.

Perichaena pedata (Lister & G. Lister) G. Lister [R, 13899, 13964, 13484, 14020, 4 records **] *MF*: li -/1, ll -/1; *WF*: ll -/1; *RF*: ll -/1.
Small sporocarps with a spherical sporotheca 0.15–0.25 mm in diameter on a stalk 1.5–2.5 times longer than the sporotheca. Capillitium sparingly branched, consisting of thin (2.5–3.5 µm wide) threads. The four collections display considerable variation in the appearance of the peridium, capillitium ornamentation and spore size. Specimen 13484 has smooth, globose sporothecae without any dehiscence lines or warts and the capillitium is wrinkled and ornamented with ridges and short spines, very similar to that of *P. chrysosperma*. Specimen 14020 (Figs 22–25) has many small warts on the sporotheca, as in *Perichaena minor* var. *pardina* (Minakata) Hagelst. and a capillitium with faint ridges that are densely covered with needle-like spines up to 2 µm in length (10–15 per 20 µm, Figs 23, 24) and spores (9–)9.5–10.8(–11.5) µm diam. Collection 13964 has again a smooth sporotheca, but possesses an areolate peridium resembling a miniature *Trichia erecta* Rex, thus matching the description of *P. areolata* Rammeloo in this character. The capillitium has prominent spiral lines but lacks spines. The spores are, with a diameter of (12.2–)12.7–14.0(–14.5) µm, larger than usual for *P. pedata*. Specimen 13899 (Figs 36, 37) has again the habit of *P. minor* var. *pardina*, with small, globose, short-stalked sporothecae possessing distant, dark and elongated warts. However, the capillitium is ornamented with rather distant (3–5 per 20 µm) spines up to 6 µm long and very faint longitudinal ridges (Fig. 36). The spores are (9.5–)9.8–10.6(–11.0) µm in diam.
Having only four collections, all of them scanty, we tentatively assign them to *P. pedata*. It should be noted, that three of the four specimens came from different sampling plots, having only the substratum type (litter) in common.

Perichaena cf. *dictyonema* Rammeloo Bull. Jard. Bot. Belg. 51: 230. 1981 [O, 13602, 13942, 13949, 14 records **] *MF*: li -/13, l -/1.
Gregarious to scattered sporocarps, sessile with a constricted base and almost globose in shape, 0.4–0.55 mm diam. Peridium in the lower part simple, shining, membranous, the sporocarp thus appearing bright ochraceous yellow (4A6) in the colour of the spore mass, but in the upper part two-layered and dark chestnut brown (5F8), giving the sporocarp the appearance of a head with an irregularly lobed hat. The lower, membranous peridium is translucent pale yellow (3A6) by transmitted light, smooth; in the upper part with an additional, firmly attached layer of round granular deposits 3–5 µm in diam., opaque amber (5C8). Under SEM, the inner surface of the peridium has wrinkled ridges (Figs 29, 32). The capillitium is a rather abundant network of rigid, profusely branched threads 1.8–3.0 µm diam., appearing under the light microscope as if composed of transversel

segments (like a limb of the popular Michelin-man used for advertisements). However, SEM micrographs reveal a network of mostly longitudinal ridges (Figs 30, 31, 33–34). Spores are pale golden yellow by transmitted light, globose to subglobose, (13.1–)14–15.2(–15.8) µm diam., ornamented with regularly distributed fine spines up to 0.8 µm length (Figs 26–28, 35).

All specimens except 13696 (from banana litter) came from decayed parts of living inflorescences cultivated in moist chamber. Comparison with American material of *P. quadrata*, as described in Keller & Eliasson (1992), revealed a number of deviating features. Here, spores are smaller (10–11 µm diam.), more faintly warted and have a thinner wall than those of the Ecuadorian collections. In addition, in the American material the sporocarps are more closely packed and pulvinate. As observed with the light microscope, the capillitium has a less pronounced annulate appearance; viewed with SEM (Fig. 21) the network of ridges is much less pronounced than in our specimens. Since Rammeloo (1981 *b*) stresses the network of ridges on the capillitium as well as the darker peridium in the upper part of the sporotheca in his description of *P. dictyonema*, the Ecuadorian specimens are best accommodated under this name.

Perichaena vermicularis (Schwein.) Rostaf. [C, 19 records] *MF*: li 3/1, lh 1/-, ll -/5; *WF*: li -/9.

Physarella oblonga (Berk. & M.A. Curtis) Morgan [R, 13201, 1 record] *MF*: w 1/-.

Physarum bogoriense Racib. [R, 12977, 13075, 3 records] *MF*: lh 1/-, ll 2/-.

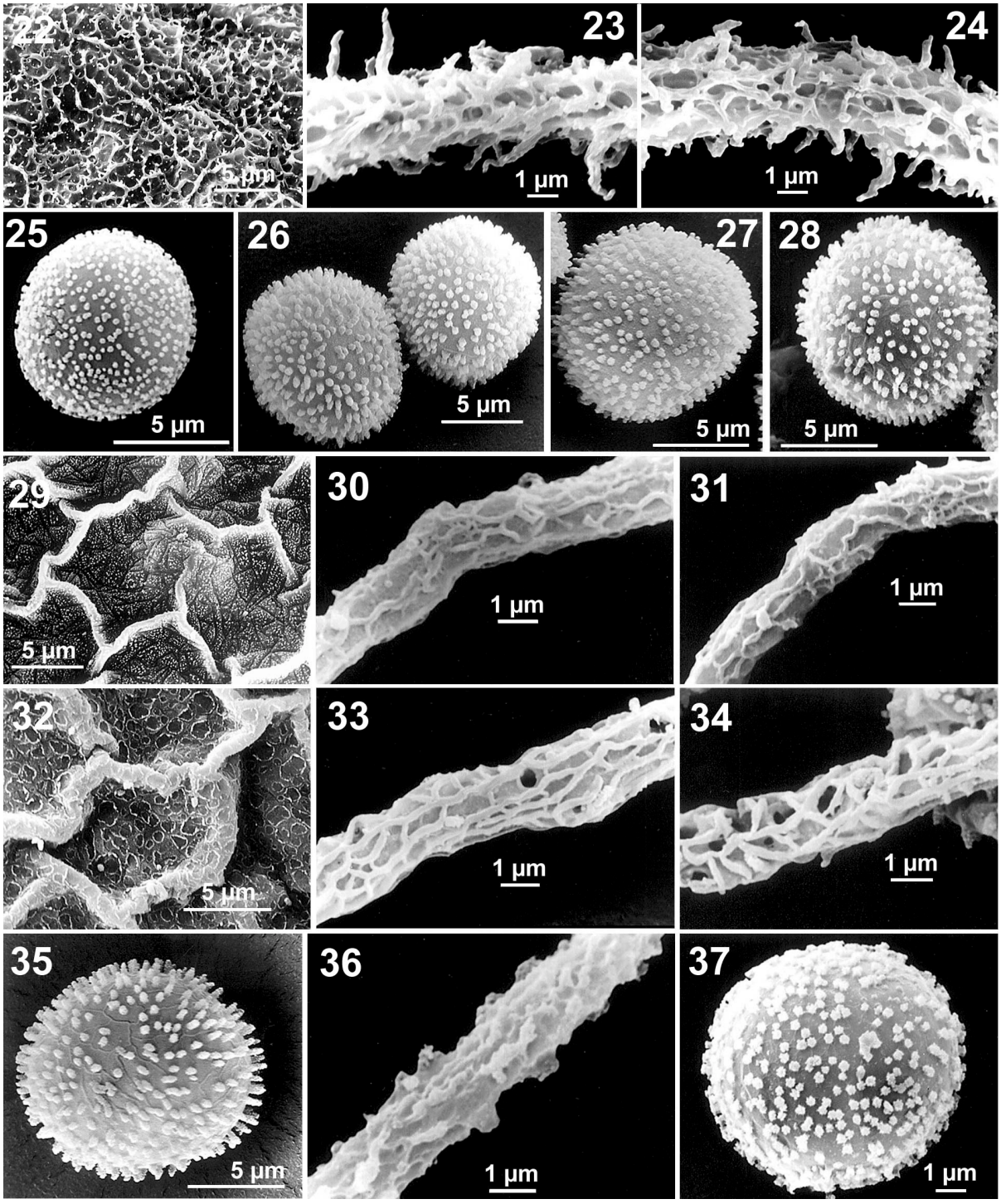
Physarum cinereum (Batsch) Pers. [O, 13041, 5 records] *MF*: li 1/-, ll 4/-.

Physarum compressum Alb. & Schwein. [A, 84 records] *MF*: li 11/14, lh 19/-, ll 11/6, lw 3/2, w 1/-; *WF*: ep -/1, li 1/6, ll -/1, lw -/3; *RF*: ep -/5.

Physarum didermoides (Pers.) Rostaf. [C, 22 records] *MF*: li 17/5.

Physarum cf. *galbeum* Wingate [R, 12894, 12945, 2 records **] *MF*: b 1/-, lw 1/-.

Small colonies of gregarious, long-stalked sporocarps with urn-shaped, subglobose sporothecae 0.2–0.35(–0.4) mm diam., the whole sporocarp reaching a height of 1.0–1.5 mm. Stalk arising from an inconspicuous discoid hypothallus, striate, dull orange (5B8) in the lower half, becoming more yellow (4A7) towards the upper half, bright orange (5A8) by transmitted light, limeless, *ca* 80 µm wide at the base and *ca* 60 µm wide at the apex, 1.5–1.7 times longer than the diameter of the sporotheca. Sporotheca with relatively little lime, in the lower part almost limeless and dull yellow (3B8), the upper part with a thin, evenly distributed lime layer, appearing sulphur yellow (3A8). Peridium transparent bright yellow (3A7) by transmitted light, smooth, membranous. Capillitium a dense isodiametric network of thin threads almost free of lime nodules, colourless to very pale yellow (3A4) under the compound microscope, almost white when observed with a dissecting microscope. Spore-mass pale violet brown (7D5), very pale brown (7B2) by transmitted light, globose, (7.1–)7.6–7.9(–8.3)



Figs 22–25. *Perichaena pedata* (Schnittler 14020). **Fig. 22.** Inner surface of the peridium. **Figs 23, 24.** Capillitial threads. **Fig. 25.** Spore. **Fig. 26.** *Perichaena* cf. *dictyonema* (Schnittler 13949), spore. **Figs 27–31.** *Perichaena* cf. *dictyonema* (Schnittler 13602). **Figs 27, 28.** Spores. **Fig. 29.** Inner surface of the peridium. **Figs 30, 31.** Capillitial threads. **Figs 32–35.** *Perichaena* cf. *dictyonema* (Schnittler 13694). **Fig. 32.** Inner surface of the peridium. **Figs 33, 34.** Capillitial threads. **Fig. 35.** Spore. **Figs 36, 37.** *Perichaena pedata* (Schnittler 13899). **Fig. 36.** Capillitial thread. **Fig. 37.** Spore.

µm diam., very faintly verrucose (verrucae only visible under oil immersion), often with an even paler, colourless germination slit extending over almost a whole hemisphere and then appearing as a pale band.
Applying the currently used generic delimitation of *Craterium*, the Ecuadorian specimens have to be accommodated in the genus *Physarum* due to the lack of lime nodes and the absence of dehiscence lines. However, the urn-shaped sporothecae as well as the same substratum (forest floor litter) as *Craterium aureum*, a species found to be rather frequent throughout this study, suggest a close relationship between the two taxa. It is possible that *P. galbeum*, *C. aureum* and *P. flavidum* (Peck) Peck (said to differ from the latter species only by larger spores and a double peridium richer in lime, Nannenga-Bremekamp, 1991) are forms of a single polymorphic species.

Physarum globuliferum (Bull.) Pers. [R, 13035, 4 records **] *MF*: ll 4/-.

Physarum javanicum Racib. [R, 13611, 1 record **] *MF*: li 1/-.

Physarum ? *leucophaeum* Fr. [R, 13062, 1 record] *MF*: ll 1/-.

Physarum melleum (Berk. & Broome) Massee [O, 13 records] *MF*: ll 12/-, w 1/-.

Physarum nutans Pers. [O, 12 records] *MF*: lw 1/-, w 11/-.

Physarum oblatum T. Macbr. [R, 3 records **] *MF*: li -/1, ll -/2.
Although *P. oblatum* is described as being more common on wood, the Ecuadorian specimens conform very closely to the description given in Martin & Alexopoulos (1969: 318) for that species, with a habit similar to that of specimen M 5466a pictured in Neubert *et al.* (1995: 288). On the other hand, a comparison of the circumscriptions for *P. oblatum* and *P. pusillum* reveals no substantial differences except for the sporocarp colour and the ultimate taxonomic value of that character has been questioned for the Physarales (Aldrich, 1982).

Physarum ? penetrale Rex [R, 13219, 1 record **] *MF*: w 1/-.

Physarum pusillum (Berk. & M.A. Curtis) G. Lister [A, form I: 12849, 13018, 13071, form II: 12993, 13138, 13930, 35 records] form I *MF*: lh 1/-, ll 1/-, w 1/-; form II *MF*: li 15/-, ll -/1; *WF*: li 6/8, ll -/1, lw -/1.
Two forms of this species were distinguishable. Form I is the typical form of *P. pusillum*, with slender stalks 0.5–0.7 mm long that are orange-brown (6B8–6C8) under the dissecting microscope, translucent bright yellow orange (5A8) by transmitted light, 120–140 µm wide at the base, tapering to 50–70 µm at the apex, fibrous and free of dirt granula. The capillitium is physaroid, with small (20–30 µm in extent), angular lime nodes.
Form II has much stouter stalks. These are 0.3–0.5(–0.6) µm long and 180–240 µm wide at the base, tapering to 100–120 µm at the apex, dull orange brown (6E8 and darker) to almost black under the dissecting microscope, opaque orange brown (6B8–6C8) and heavily incrusted with darker granula probably taken up from the

substratum. The capillitium is a badhamioid, very rigid network of tubulae 8–12(–20) µm wide, which gives the sporocarps the appearance of a stalked *Badhamia*. Both forms have the same spore diameter of (10–)10.6–11.4(–12.0) µm, the spores are thin-walled, globose, pale violet brown (8B2–8C3) and minutely warted. Following the comments given by Martin & Alexopoulos (1969: 325), who mention a capillitium 'sometimes approaching badhamioid', both forms are herein assigned to *P. pusillum*.

Physarum serpula Morgan [R, 13024, 13088, 2 records] *MF*: ll 1/-, w 1/-.
Two small collections of short to elongated plasmodiocarps, sulphur-yellow (3A5) to grey-yellow (3B4) are assigned to this species, following the species circumscription as given by Farr (1961) and emended by Martin & Alexopoulos (1969: 329).

Physarum stellatum (Massee) G.W. Martin [R, 12845, 3 records] *MF*: ll 1/-, w 2/-.

Physarum superbum Hagelst. [R 13121, 1 record **] *MF*: lh 1/-.
Plasmodiocarps that are usually laterally compressed and bright orange (5A8) separate this species from the closely related *P. serpula*.

Physarum ? tenerum Rex [R, 12905, 13113, 4 records **] *MF*: lh 2/-, w 1/-; *WF*: lw -/1.

Physarum viride (Bull.) Pers. [R, 13005, 1 record] *MF*: w 1/-.

Physarum sp. [O, 13037, 13223, 13232, 7 records **] *MF*: ll 7/-.
Small colonies of gregarious sporocarps on slender stalks, with a globose sporotheca (0.15–)0.25–0.35 mm diam. Stalk arising from a very small, discoid hypothallus, thin and slender but straight, 0.4–0.6 mm long and of uniform thickness (45–55 µm) over the whole length, straw-coloured (4A5–4B6), by transmitted light paler but concolorous (4A6–4B7), fibrous, limeless and with a few dirt granula. Sporotheca in the lower part (*ca* one-eighth of the total height), limeless and dirty yellow (4C8), this area sharply separated from the upper part that is sprinkled with rather coarse lime flakes, very pale yellow (3A3–3A4), apparently fading with age. By transmitted light, the peridium itself is almost colourless to pale straw-coloured (4A4 and paler) in the lower part. Capillitium an isodiametric network with evenly distributed, rounded lime nodes 20–40 µm in extent, with the same colour as the peridial lime, somewhat resembling that of the genus *Craterium*. Spore-mass chestnut brown (5E7), pale brown (5C5) by transmitted light, globose, (7.2–)7.6–8.2(–8.4) µm diam., minutely warted with inconspicuous groups of darker warts (Figs 19, 20).
This taxon is represented by several small but well-matured collections from forest floor litter. All are very similar to each other and clearly recognizable in habit by the pale yellow (fading to cream white) sporothecae, with rather coarse, flaky lime on long but straight, pale yellow stalk. *Physarum limonium* Nann.-Bremek. (Proc. Kon. Ned. Akad. Wet. C69: 357. 1966) appears closest to our specimens, but the spores of the latter are described as 10–13 µm in diam.

Stemonitis axifera (Bull.) T. Macbr. [O, 7 records] *MF*: ll 1/-, w 6/-.

Stemonitis fusca Roth [O, 8 records] *MF*: lh 1/-, ll 1/-, w 5/-; *WF*: w 1/-.

Stemonitis ? *pallida* Wingate [R, 12836, 1 record] *MF*: lh 1/-.

Stemonitis smithii T. Macbr. [R, 13198, 13285, 2 records **] *MF*: w 2/-.

Stemonitis splendens Rostaf. [R, 13211, 1 record] *MF*: w 1/-.
The only record represents var. *splendens*, with a sturdy capillitial surface net having large rounded meshes.

Stemonitopsis typhina (F.H. Wigg.) Nann.-Bremek. Nederlandse Myxom. 209. 1975 [R, 2 records] *MF*: w 2/-.

Trichia affinis de Bary [R, 12883, 12924, 12953, 3 records **] *MF*: ll 1/-, w 2/-.
According to Farr (1958), both *T. persimilis* Karst. and *T. affinis* should be united with *T. favoginea* (Batsch) Pers., giving the latter species a wider concept. However, this and other specimens collected by the authors in the Neotropics would match the description of *T. affinis*, whereas typical *T. favoginea* seems to be very rare in the region.

Trichia decipiens (Pers.) T. Macbr. [R 12927, 1 record] *MF*: w 1/-.

Trichia varia (Pers. ex J.F. Gmel.) Pers. [R, 13307, 1 record] *RF*: w 1/-.

Tubifera microsperma (Berk. & M.A. Curtis) G.W. Martin [O, 5 records] *MF*: w 5/-.

RESULTS

Species diversity

Of the 1033 records of myxomycetes generated in the present study, 590 were from the field, including five collected plasmodia that failed to form fructifications and 21 indeterminable collections (leaving 564 records that could be determined). The other 443 records were obtained from the 475 moist chamber cultures prepared during the course of the study. In 70 moist chambers plasmodia were observed that could not be induced to fruit and one record was immature (leaving 372 records that could be determined). All together, 936 myxomycete records were considered for the annotated species list presented above. From these, 77 taxa were identified with certainty, with another six represented by scanty or damaged specimens that did not allow a save determination. Among the 77 taxa were seven that could not be clearly assigned to any described species. Including those, the

present study adds 30 taxa as new to the myxomycete flora of Ecuador. When all of the taxa known from the literature are included, 111 myxomycete taxa have now been recorded from Ecuador, with 84 of these collected in mainland Ecuador.

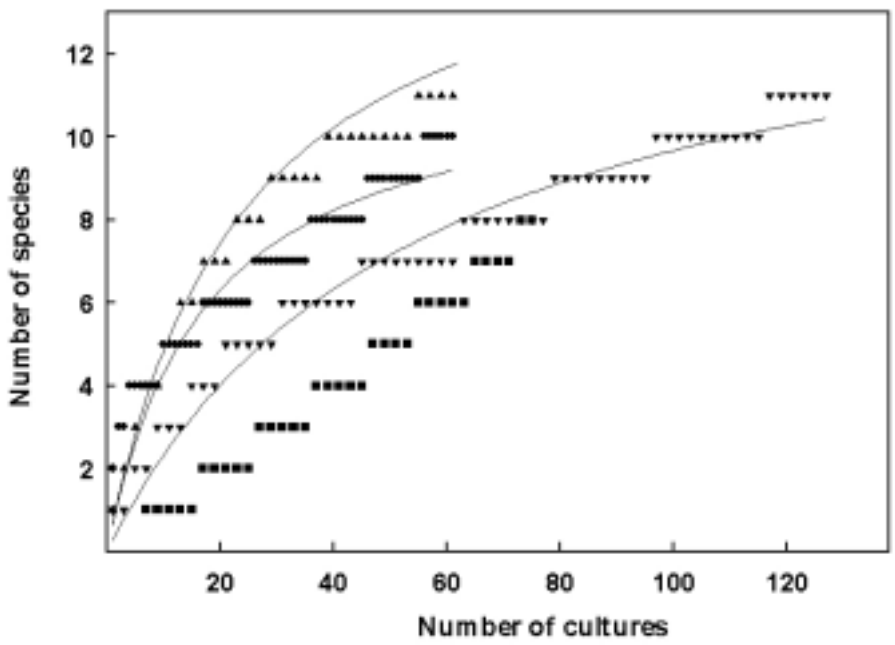


Fig. 38. Bootstrap analysis of the randomly permutated sequence of samples (moist chambers) versus mean cumulative species numbers for series of moist chamber cultures prepared with bark (rectangles), leaf litter from the forest floor (inverted triangles), covers of epiphyllic liverworts (circles), and aerial leaf litter (triangles). Except for bark samples, where no converging fit was obtained, solid lines show the results of a regression analysis with a saturation function $y = a * x /(b + x)$. Parameter values for the best fit were found to be $a = 14.9$, $b = 54.2$, mean square error 0.22 for myxomycete records from ground litter; $a = 11.8$, $b = 17.4$, mean square error 0.44 for epiphyllic myxomycetes; and $a = 16.3$, $b = 23.7$, mean square error 0.03 for myxomycete records from aerial litter.

If moist chamber cultures are considered to represent discrete sampling units, the completeness of the survey in terms of the species recovered can be estimated using the bootstrap procedure (Fig. 38). From the four types of substrata sampled from all three study sites, 76 cultures prepared with the bark of living trees (*b*) produced only 8 species, each with a single record and two plasmodia that did not develop into fructifications. Since the resulting bootstrap curve is a linear one, a fit with a saturation function did not converge to a minimum sum of squares. As such, the survey for this group is far from being complete. For leafy litter from the forest floor (*ll*), 11 species were recovered from 127 cultures, with the survey estimated by the bootstrap method to be 74% complete for this group of myxomycetes. Aerial leafy litter (*ll*) produced 11 species from 62 cultures, a total that was estimated to represent 68% of the potential number of species present. Covers of foliicolous liverworts resulted in 10 species from 62 cultures, seemingly representing 85% of all species potentially occurring on this substratum.

For field collections of myxomycetes not originating from discrete sampling units, data on frequency distribution (Fig. 39) can be used to estimate the completeness of the survey, using Preston's octave scale method. According to this method of analysis, the survey is 64% complete for myxomycetes collected from the field. The frequency distribution of the entire assemblage of myxomycetes (Fig. 40) shows a few exceedingly common species, a large number of fairly common ones and also a high number of 'tail' species. Adding the records from the field and from moist chamber cultures, the four most common species – *Didymium iridis* (111 records), *Arcyria cinerea* (108 records), *Physarum compressum* (84 records) and *D. squamulosum* (80 records) – account for 41% of all 936 myxomycete records. On the other hand, from the 82 taxa observed in total, 40 (50%) were collected only once or twice.

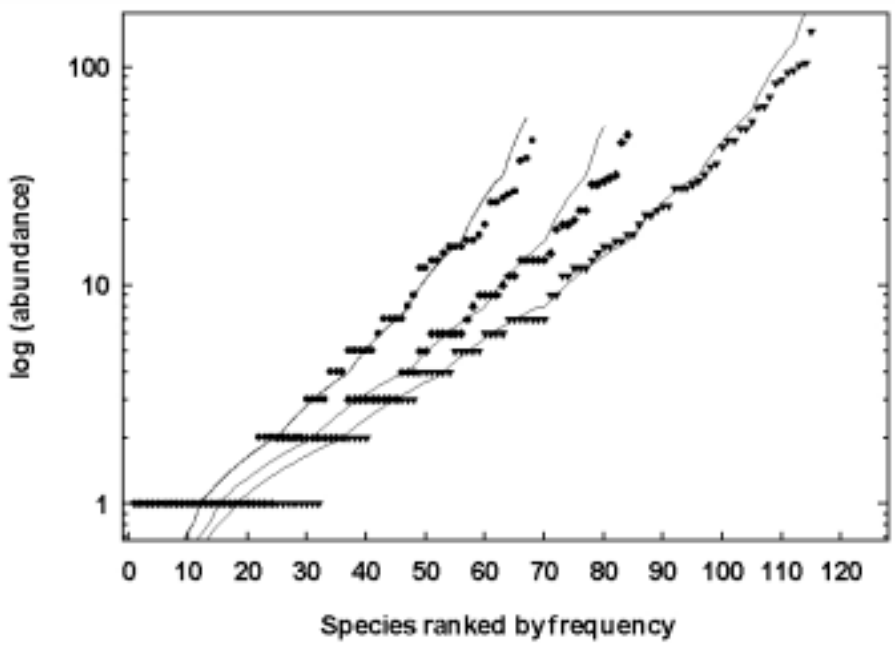


Fig. 39. Frequency distribution for field records of myxomycetes from Maquipucuna (circles), the Russian Karelia (diamonds) and southwestern Virginia (triangles). Solid lines show the recalculated frequency distributions according to a log normal model, resulting from the best fit of an analysis with Preston's octave scale method.

Myxomycete distribution in the three forest types

Although the initial sampling effort was essentially the same for each of the three study sites, remarkable differences were apparent with respect to the relative abundance of fructifications in the field (Table 1). With the hours spent by the first two authors for field collecting tallied, the number of fructifications observed per hour was calculated. If the value for site 1 (Moist Forest, 6.9) is considered as 100%, myxomycete abundance for sites 2 (Wet Forest) and 3 (Rain Forest) reached only 37% and 21%, respectively. The overall productivity of the moist chamber cultures showed a

Table 1. Numbers of myxomycete fructifications recorded in the field and from moist chamber cultures for the three study sites. According to the Holdridge classification, abbreviations for the study sites are: *MF* – Tropical Moist Forest, *WF* – Tropical Premontane Wet Forest, *RF* – Lower Premontane Rain Forest.

Site	*MF*	*WF*	*RF*
Field records	549	32	9
Collecting hours	80	12	6
Records per hour	6.9	2.6	1.5
Number of species	66	14	5
Number of moist chamber cultures	220	155	100
Records from moist chamber cultures	230	152	61
Records per culture	1.05	0.98	0.61
number of species	28	13	12

similar pattern (Table 1). With a mean of 1.05 records per moist chamber culture for site 1 considered as 100%, productivity values for site 2 and 3 were 93% and 58%, respectively. Not all types of substrata were available in each study site. Consequently, only a comparison of myxomycete productivity for the same substratum type can reflect the true abundance relationships. Table 2 and Fig. 41 show the results for the four types of substrata (bark of living trees, forest floor litter, aerial leafy litter and leaves overgrown with epiphyllic liverworts) available at all three study sites. Although productivity varies widely among the substratum types, all show a pattern of decreasing productivity with increasing elevation. When reviewing absolute numbers of records for the three sites (Table 3), the two high-elevation sites produced only 18 and 9% of the total records for litter- and wood-inhabiting myxomycetes, respectively.

A similar pattern holds true for species diversity (Table 1). At site 1 (Moist Forest), situated at the lowest elevation, all but two (*Fuligo septica* and *Trichia varia*) of the species recorded from the field were present. With 14 versus 66 taxa, the Wet Forest (site 2) had a significantly lower myxomycete diversity. Records obtained from moist chambers also conform to the same pattern, with less than half the number of species (13) recorded from site 2 as compared with site 1 (28). When comparing the results for series of moist chambers prepared with samples from comparable substratum types (Table 2), all types showed lower diversity values at higher elevations. This trend is strongest for litter substrata and least pronounced for covers of epiphyllic liverworts on living leaves.

Myxomycete-substratum relationships

From all substratum groups, litter (comprising the substratum types *ll*, *lh* and *lw*, as defined under materials and methods) was most productive both in terms of records as well as in terms of species, with 56 species recovered from 485 records (284 from the field, including 5 plasmodia and 8 indeterminable collections; 201 from moist chamber cultures, including 57 plasmodia). Decaying wood was the substratum for 34 species from 222 records (all from the field, including 4 indeterminable collections). An unexpected result of the present study was the discovery of two

substratum types as new for myxomycetes. The first of these is represented by the covers of foliicolous liverworts that occur on living leaves (10 species from 141 records, all from moist chamber, including 2 plasmodia). The second consists of the decaying corolla and other flower parts on otherwise living (seed-producing) inflorescences of living plants (14 species from 166 records, 76 observed in the field, including 8 indeterminable collections and 90 from moist chamber cultures, including 10 plasmodia). Myxomycetes associated with these substratum types will be the subject of two separate papers (Schnittler 2000; Schnittler & Stephenson, in prep.). Bark of living trees was rather unproductive (14 species from 18 records, 8 from the field, 10 from moist chambers, including 2 plasmodia).

Table 2. Productivity of moist chamber cultures for the four substratum types available in all three study sites. Abbreviations for study sites are the same as those used in Table 1.

Site	*MF*	*WF*	*RF*
Bark of living trees			
cultures prepared	33	24	19
number of records	6	2	2
records per culture	0.18	0.08	0.10
number of species	4	2	2
Forest floor litter			
cultures prepared	44	42	41
number of records	53	20	16
records per culture	1.20	0.48	0.39
number of species	9	4	5
Aerial leafy litter			
cultures prepared	21	21	20
number of records	29	16	6
records per culture	1.38	0.76	0.30
number of species	10	6	3
Foliicolous liverworts	21	20	20
cultures prepared			
number of records	52	51	33
records per culture	2.47	2.55	1.65
number of species	5	6	5

As shown in Fig 40, field collections and records from moist chambers compliment each other. When excluding those species collected only from decaying wood (a substratum not studied with moist chamber cultures), 15 of 22 (68%) of the more common species (> 5 records) were observed in the field as well as in moist chamber cultures. Examples of common species recorded only from the field include *Craterium leucocephalum* (26 records, all from litter), *Didymium nigripes* (15 records, all litter) and *Physarum melleum* (13 records, all litter). Among the more common species, only *Perichaena* cf. *dictyonema* (14 records, all from inflorescences) was observed exclusively in moist chamber cultures. However, moist chambers yielded fewer species (33) than the number of species observed in the field (68). On the other hand, 15 taxa (18% of the total number) were observed exclusively in moist chamber cultures.

Of the 34 species inhabiting wood (substratum type *w*), 30 were found exclusively on this substratum and the average specificity of a wood-inhabiting species was 75%. Average specificity values were slightly lower for leafy litter (*ll*, 43 species, 61%), followed by bark (*b*, 14, 59%), inflorescences (*in*, 14, 53%), herbaceous litter (*lh*, 25, 35%), epiphyllic liverworts (*ep*, 10, 33%) and woody litter (*lw*, 15,

17%). A rather high proportion of all myxomycete records originated from substrata above the ground. For litter (substratum types *ll*, *lh* and *lw*) as well as for wood, about one-third (94 from 284 collections, 32.8%; and 75 from 230 collections, 32.6%) of all field collections came from aerial substrata that did not touch the ground directly. In addition, living inflorescences as well as leaves covered with epiphyllic liverworts are two substratum types found only above the ground.

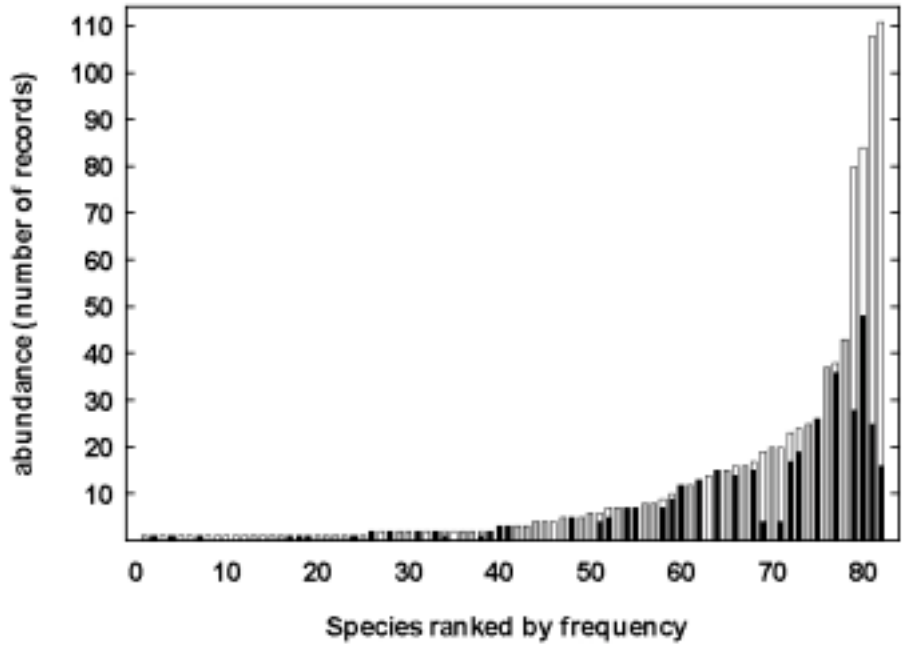


Fig. 40. Frequency distribution of all 936 records of myxomycetes (records from the field and from moist chamber cultures) for Maquipucuna. Grey bars represent species found exclusively on decaying wood in the field. For the other species, dark sectors of the bars represent field records, whereas white sections indicate records from moist chamber cultures.

Comparisons with myxomycete assemblages from temperate and boreal regions

The data obtained from two surveys undertaken with an approach similar to that of the present study were used to compare features of myxomycete assemblages in tropical, temperate and boreal forests. Both were carried out in a limited area with fairly undisturbed woodlands and targeted to record all myxomycete fructifications visible in the field. The first study was conducted in a boreal, mostly coniferous forest of the the Russian Karelia (two subsequent years, three field surveys involving two persons, each lasting about 14 days, Schnittler & Novozhilov, 1996). The second study took place in a temperate, mostly deciduous upland forest in southwestern Virginia in the eastern United States (five subsequent years, one person, repeated visits, each lasting one to several days, Stephenson 1988, 1989). The numbers of species of myxomycetes recorded from the three areas are significantly different. Maquipucuna yielded 82 species (6 not identified with certainty, 7 unidentified taxa). From these, 68 taxa were observed in the field and 33 developed in moist chamber cultures. For the Russian

Karelia, 95 species were recorded (2 not identified with certainty, 1 unidentified taxon), with 84 species observed in the field and 25 obtained from moist chamber cultures. The study in southwestern Virginia yielded 144 species (4 not identified with certainty, 5 unidentified taxa); 115 species were recorded in the field and 60 appeared in moist chamber cultures. The respective Shannon diversity indices are more similar to each other (Maquipucuna: 3.43, the Russian Karelia: 3.97, southwestern Virginia: 3.91).

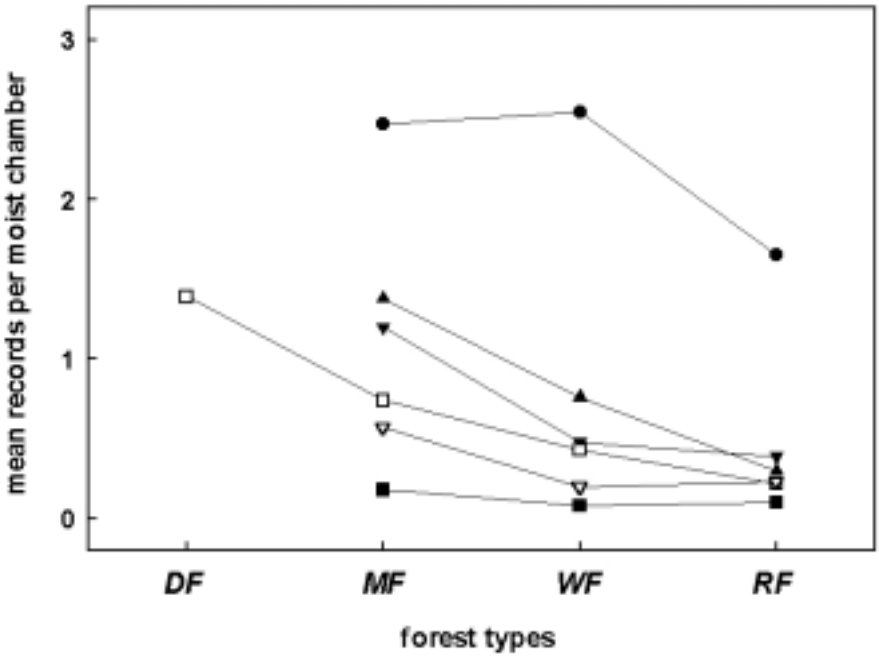


Fig. 41. Productivity of moist chamber cultures prepared with samples from Maquipucuna (bark of living trees, solid rectangles; leaf litter from the forest floor, solid inverted triangles; aerial leaf litter, solid triangles, covers of epiphyllic liverworts on living leaves, solid circles) and Costa Rica, Area de Conservación de Guanacaste (bark, open rectangles; leaf litter from the forest floor, open inverted triangles). Except for leaf litter from the forest floor (40 cultures), each dot represents the mean number of records per culture from a series of 20 ± 2 cultures with material from the forest types Tropical Dry Forest (*DF*), Moist Forest (*MF*), Wet Forest (*WF*), and Lower Premontane Rain Forest (*RF*).

A comparison of the frequency distributions from the field component of these three surveys reveals that the patterns are very similar. All correspond roughly to a log normal distribution model (Fig. 39), with a proportion of rare ‘tail’ species corresponding roughly with the overall species diversity. An estimate of the completeness of this component of each survey, calculated using Preston's octave scale method, reveals a degree of completeness ranging from 59% for southwestern Virginia and 64% for Maquipucuna to 67% for the Russian Karelia. An examination of the proportions of the six orders of myxomycetes for each of the three study areas (Fig. 42) reveals a much higher proportion of members of the Physarales at Maquipucuna, whereas members of the Stemonitales, but especially members of the Liceales, have lower proportions. This tendency is even more pronounced when comparing

numbers of records instead of species. At Maquipucuna, 56.5% of all myxomycete records were members of the Physarales, compared with 18.4% in southwestern Virginia and 28.2% in the Russian Karelia, respectively.

Table 3. Proportions of stalked and sessile taxa and records for the myxomycete assemblages (field collections only) of Maquipucuna (*Ec* – tropical forest), southwestern Virginia (*Va* – temperate forest) and the Russian Karelia (*Rs* – boreal forest).

Study area	*Ec*		*Va*		*Rs*	
Number of taxa						
stalked	54	(79.4%)	77	(67.0%)	46	(54.8%)
sessile	14	(20.6%)	38	(33.0%)	38	(45.2%)
total	68		115		84	
Number of records						
stalked	481	(85.3%)	1668	(76.2%)	415	(62.9%)
sessile	83	(14.7%)	522	(23.8%)	245	(37.1%)
total	564		2190		660	

Table 4. Comparisons of stipe length for four wood-inhabiting species of myxomycetes common in both southwestern Virginia (*Va* – temperate forest) and Maquipucuna (*Ec* – tropical forest). For each species and study area, 10 collections were randomly selected, and five sporocarps per collection were measured. Significant differences in stipe length are indicated by asterisks (* t-Test: $p<0.01$, ** t-Test: $p<0.001$, $^{+}$ normality test failed, the Mann-Whitney rank sum test was applied).

Species	Area	Stipe length (mm) mean ± S.D.	Range (mm)
Arcyria cinerea **	*Va*	0.61 ± 0.25	0.23 – 1.01
	Ec	1.55 ± 0.59	0.97 – 2.61
Arcyria denudata *	*Va*	0.84 ± 0.14	0.64 – 1.02
	Ec	1.29 ± 0.37	0.66 – 1.91
Cribraria cancellata **$^{+}$	*Va*	1.55 ± 0.19	1.33 – 1.91
	Ec	2.84 ± 0.73	1.62 – 4.05
Hemitrichia calyculata **	*Va*	1.03 ± 0.22	0.69 – 1.55
	Ec	2.03 ± 0.36	1.37 – 2.61

Among the substratum types present in all three study areas, wood yielded 34 species (41% of all field records at Maquipucuna). In southwestern Virginia, more than 90% of the species reported were found on wood, with 74.6% of all collections coming from decorticated logs and other coarse woody debris. In the Russian Karelia, wood was of similar importance, accounting for 68 species (73.8% of all field records). Litter (substratum types *ll*, *lh* and *lw*) was of much higher importance at Maquipucuna (49 species, 46.6% of all field records) than in temperate (> 15 species, 6.1% of all field records) or boreal (10 species, 14.2% of all field records) regions. In the Neotropics, two aerial substratum types (inflorescences of living herbs and leaves with a cover of epiphyllic liverworts), both

absent in the other study areas, were found to support myxomycetes, especially when studied with the moist chamber culture method. The only major substratum type present in one of the other study areas but absent in Maquipucuna was the substratum represented by rocks provided with trickling water, which yielded 10 species (14.2% of all field collections) in the Russian Karelia. Bark, when studied with the moist chamber method, revealed dramatic differences among the three study sites. At Maquipucuna, corticolous myxomycetes seem to be nearly absent (8 species identified from 76 cultures, 11% positive cultures, 0.13 species per culture). Southwestern Virginia has an exceedingly rich flora of corticolous myxomycetes (47 species from 632 cultures, 90% positive cultures, >1.75 species per culture). For the Russian Karelia, 18 species were recorded in 75 moist chambers prepared with bark of living trees and shrubs (68% positive cultures, 1.32 species per culture).

Table 5. Proportions of taxa and records with aethalia or pseudoaethalia, plasmodiocarps, and sporocarps for the myxomycete assemblages (field collections only) of Maquipucuna (*Ec* – tropical forest), southwestern Virginia (*Va* – temperate forest) and the Russian Karelia (*Rs* – boreal forest).

Study area	*Ec*		*Va*		*Rs*	
Number of taxa						
aethalium	3	(4.5%)	10	(8.7%)	9	(10.7%)
plasmodiocarp	9	(13.4%)	6	(5.2%)	7	(8.3%)
sporocarp	55	(82.1%)	99	(86.1%)	68	(81.0%)
total	67		115		84	
Number of records						
aethalium	12	(2.1%)	209	(9.5%)	55	(8.3%)
plasmodiocarp	55	(9.8%)	28	(1.3%)	27	(4.1%)
sporocarp	497	(88.1%)	1952	(89.2%)	578	(87.6%)
total	564		2189		660	

Table 6. Proportions of taxa and records with proto-, phanero- and aphaneroplasmodia for the myxomycete assemblages (field collections only) of Maquipucuna (*Ec* – tropical forest), southwestern Virginia (*Va* – temperate forest) and the Russian Karelia (*Rs* – boreal forest). Records for the Ceratiomyxales were omitted from this analysis.

Study area	*Ec*		*Va*		*Rs*	
Number of taxa						
protopl.	-		4	(3.5%)	3	(3.6%)
phaneropl.	54	(81.8%)	84	(73.7%)	62	(74.7%)
aphaneropl.	12	(18.2%)	26	(22.8%)	18	(21.7%)
total	66		114		83	
Number of records						
protopl.	-		107	(5.1%)	53	(8.2%)
phaneropl.	488	(93.0%)	1449	(68.4%)	409	(63.2%)
aphaneropl.	37	(7.0%)	561	(26.5%)	185	(28.6%)
total	525		2117		647	

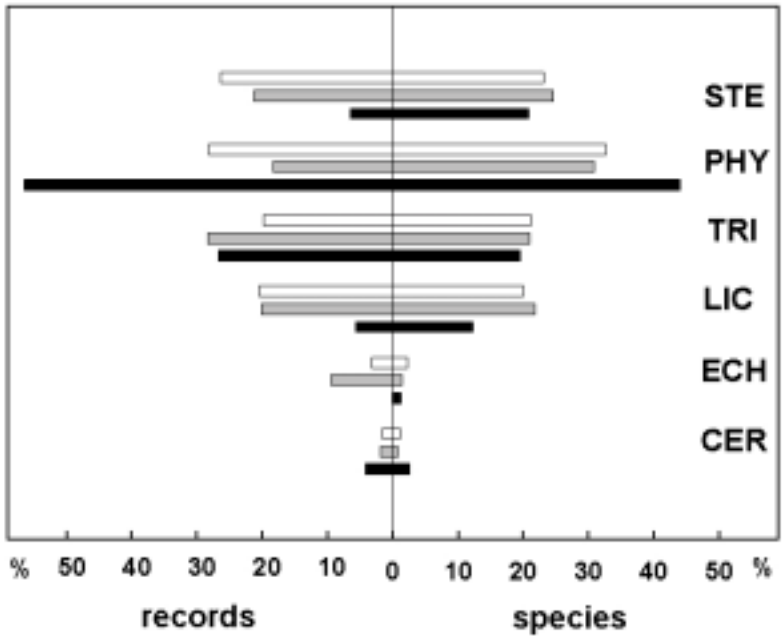


Fig. 42. Percentage proportions of members of the Ceratiomyxales and the five orders of myxomycetes to the total number of species (right) and number of records (left) for Maquipucuna (black bars), southwestern Virginia (grey bars) and the Russian Karelia (white bars).

A comparison of morphological features of the myxomycete assemblages among the three study areas revealed a number of conspicuous differences. (To avoid introducing the biases associated with the choice of substrata for moist chamber cultures, only field collections were compared.) A comparison of species producing sessile sporocarps versus those producing stalked sporocarps revealed that the latter type was represented by the majority of species as well as records in all three areas (Table 3). However, the percentage of sessile species as well as the percentage of their records decreased steadily from the Russian Karelia to southwestern Virginia to Maquipucuna (Table 3). This seems to correlate with a longer stipe for the same taxon in tropical forests. When comparing four wood-inhabiting species of myxomycetes common in southwestern Virginia as well as at Maquipucuna, sporocarps of tropical specimens were found to possess consistently longer stipes (Table 4). When considering the type of fructification, most taxa form single sporocarps in all three areas. However, in the Neotropics, the proportion of taxa forming aethalia or pseudoaethalia is lower than in temperate regions, whereas the proportion of plasmodiocarp-forming taxa is higher (Table 5). When the type of plasmodium (here excluding the genus *Ceratiomyxa*, which is classified within the Protostelids) is considered, species with phaneroplasmodia make up the highest proportion of the myxomycete assemblages in all three study areas (Table 6). In the Neotropics, no species possessing protoplasmodia was encountered in the field and the proportion of taxa, but especially records, for species with aphaneroplasmodia is lower than in the two other study areas. Taxa with

phaneroplasmodia appear to represent a very high percentage of the myxomycetes present in Neotropical forests, accounting for 82% of all species observed in the field and 93% of all field records for Maquipucuna.

DISCUSSION

Species diversity

The study reported herein is one of the very few in which an effort was made to record every myxomycete fructification observed in field or obtained in moist chamber cultures. Since all of our data are derived from a single area limited in size, in accordance with Schnittler & Mitchell (2000) we do not formally describe these apparently new taxa (*Lamproderma* sp. and *Physarum* sp.). More collections from different locations would be necessary to justify this.

Since the primary objective of the present study was to characterize the assemblages of myxomycetes associated with undisturbed forests, the survey carried out is in no way complete for the western Andes. Disturbed ecosystems occurring in the region, such as cattle pastures, plantations or single, free-standing trees in settlements provide additional microhabitats (e.g., herbivore dung, solid accumulations of herbaceous litter such as decaying banana plants or dry, sun-exposed bark covered with lichens) for myxomycetes. An examination of these microhabitats would undoubtedly yield at least some species not encountered in the present study. As such, the estimates for completeness given herein refer only to forested areas. The two methods used to generate these estimates, Preston's octave scales and the bootstrap method, are independent of each other and require different assumptions about the species data subjected to the analyses. The bootstrap method is appropriate for use only with a series of randomly prepared samples of one and the same substratum type, such as a series of moist chamber cultures. Except for cultures prepared from bark, the analyses predicted a fairly high degree of completeness for all the substratum types present in all three study sites (leaf litter, forest floor: 74%; leaf litter, aerial: 68%; covers of foliicolous liverworts: 85%; Fig. 38). For litter, these values are comparable to those reported for a study in Costa Rica (84%, Schnittler & Stephenson, 2000). In contrast to the Costa Rican study, which included examples of Tropical Dry Forest with its higher diversity of corticolous myxomycetes, the results obtained from moist chamber cultures prepared with bark in the present study seem to indicate that members of this ecological group are too rare in tropical cloud forests to be exhaustively surveyed without considerable additional sampling.

Preston's octave scale method can be used for myxomycete surveys in the field, but only if two preconditions are fulfilled. First, every fructification observed in the field has to be recorded. Second, the resulting frequency distribution has to approach a log normal one (Preston, 1948). If the frequency

distribution is recalculated from the best fit with a Gaussian function according to Preston's octave scale method (Fig. 39), it is obvious that the frequency distribution of records roughly follows the log normal model for the Maquipucuna area as well as for the temperate and the boreal study areas. However, a small systematic deviation of the model calculated after the best fit of the Gaussian function is apparent when the very abundant species at the upper end of the frequency distribution are considered. Almost certainly, this deviation is caused by the fact that the resolution of the frequency data is very low at the lower end of the distribution curve, since species can only be recorded as discrete units. Because of this systematic deviation, the resulting estimates for completeness of the surveys are rather conservative. In each instance, a somewhat higher percentage of the species potentially observed was recorded than the estimate predicts. As such, it can be assumed that all three surveys are about 75% complete. In view of the sampling intensity and the total number of records that could be identified to species (936 for Maquipucuna, 3684 for southwestern Virginia and 773 for the Russian Karelia), this estimate is still rather low. However, it certainly conforms with the experience of the authors that new species can still turn up even in well-studied areas. There are three possible explanations for this phenomenon. First, long-distance dispersal can result in myxomycete spores occurring, at least theoretically, around the globe. As such, this spore fallout (for which the density and percentage of viable spores is still completely unknown) could produce exceptional and very rare records of species that usually not occur in a particular area. Second, exceptional climatic conditions (such as unusually warm and humid summers in temperate regions) can produce records of species that usually cannot develop in the area. Third, as suggested by the unexpected discovery of two new microhabitats in the Maquipucuna study, it cannot be ruled out that types of microhabitats previously unknown as suitable for myxomycete growth and development may yield new species or will be identified as the primary microhabitat for a species thought to be very rare in the area in question.

Myxomycete distribution in the investigated forest types

When comparing both the frequency of field records encountered per hour as well as the productivity of moist chamber cultures, species diversity – but especially the relative abundance of myxomycetes – decreases dramatically with increasing elevation and annual precipitation. This trend holds true for all substratum types, with covers of epiphyllic liverwort as the only possible exception. As discussed in detail by Schnittler (2000), this substratum type supports a limited assemblage of myxomycetes. Most species seem to appear upon other litter substrata as well, although the existence of biotypes specialized for covers of epiphyllic liverwort is possible. It can be speculated that this microhabitat works as a reservoir for some species of litter-inhabiting myxomycetes. The leaves, with their often

wet covers of liverworts, receive the spore fallout from the air and provide conditions that allow small populations of myxamoebae to exist. These populations may form fructifications in the field or, what is more likely, are washed off the leaf by rain and fall to the layer of litter on the forest floor litter, where the myxamoebae would encounter a much higher diversity of invertebrate predators. Especially in cloud forests, the probability that ground litter dries out and allows the proper development of fructifications of myxomycetes is likely to be much lower than for leaves with covers of epiphyllic liverworts. However, the much higher levels of nutrients available in litter eventually allow the development of larger bacterial populations and, in turn, larger myxomycete fructifications that are capable of producing significant numbers of spores to eventually become air-borne.

As indicated by the data presented in Fig. 41, which includes the results of a study carried out in Costa Rica (Schnittler & Stephenson, 2000), the pattern of decreasing myxomycete abundance and diversity with increasing elevation seems to be consistent for Neotropical forests. These results are also supported by data from studies carried out in the Luquillo Mountains of Puerto Rico (Stephenson, Landolt & Moore, 1999; Novozhilov *et al.*, 2000).

Interestingly, cloud forests at higher elevations seem to harbour some species of myxomycetes with a mainly temperate distribution that are absent or very rare in lowland forests. Prominent examples are *Fuligo septica* and *Trichia varia*, each with a single record from the high-elevation site (*WF*). Observations from studies carried out near the summit of the volcano Cacao (Area de Conservación de Guanacaste, Costa Rica, unpubl. data) seem to confirm this pattern. Here, the two species mentioned above as well as *Tubifera ferruginosa* occur occasionally. All three species are known to be common in temperate regions. These observations can be considered as indirect evidence for long-term dispersal of airborne spores, even if they do not allow any conclusions about the efficiency of this method of dispersal.

Myxomycete-substratum relationships

In accordance with the Costa Rican study (Schnittler & Stephenson, 2000), also at Maquipucuna, litter (substratum groups *ll*, *lh* and *lw*) was the most productive substratum both in terms of records and numbers of species. It seems to be a general trend in the tropics that litter substrata are richer in species than wood (compare Stephenson *et al.*, 1993), whereas decaying wood and the bark of living trees are the two most diverse substratum types in temperate zones (Stephenson, 1988, 1989). However, decaying wood shows the highest substratum specificity (75%) and litter substrata have a clearly lower degree of specificity (61–35%). At least when sampled in breast height, the bark surface of living trees was found to be very poor in the present study; again in accordance with the Costa

Rican study. The most likely reasons for this phenomenon are an excess in rainfall, connected with the fact that the bark surface of tree trunks in closed-canopy cloud forests rarely dries out and is mostly carpeted with liverworts and mosses (Schnittler & Stephenson, 2000). For bark-inhabiting myxomycetes, possible consequences are leaching of nutrients and a lesser probability that fructifications dry out and release spores. It can be expected, that substratum samples from the tree canopy, where the bark is exposed to direct sunlight and dries out much faster, yield a more diverse assemblage of corticolous myxomycetes.

Moist chamber cultures were found to be an essential technique to survey the whole myxomycete diversity of tropical forests. The 475 cultures prepared as one component of the present study added roughly half of all myxomycete records and increased the number of taxa by 20 per cent. Some substratum types, such as inflorescences, were far more productive in moist chambers than in the field. The tiny myxomycete fructifications associated with the epiphyll covers of living leaves were observed only in moist chamber cultures. Many species, especially most of the common litter-inhabiting species, were found in both moist chambers and in the field, providing evidence that moist chamber cultures do reflect the myxomycete assemblage actually occurring in a region. However, a number of species common on leafy litter were never appeared in culture and moist chambers prepared with litter had a high proportion (75 of 201 records or 36%) of plasmodia that could not be induced to develop fructifications during the four months of culture.

Comparisons with myxomycete assemblages from temperate and boreal regions

A comparison of the data obtained in this survey with data from two similar comprehensive studies carried out in temperate and boreal regions was undertaken to reveal further characteristics of tropical myxomycete assemblages. Interestingly, species richness was found to be highest in the temperate zone (southwestern Virginia, 144 taxa), followed by the boreal zone (the Russian Karelia, 95 taxa), whereas only 82 taxa were recorded from Maquipucuna. Comparing the numbers of records made in the field (2190, 660 and 590, respectively) as well as from moist chambers (1494, 113 and 443), it can be assumed that the higher diversity reported in the study in southwestern Virginia was caused by the higher number of records made during that study. However, this is not the case, as the comparison of the frequency distributions (Fig. 39) reveals. All curves have roughly the same slope, which indicates a comparable survey intensity. In accordance with this are the results for estimates of the completeness of the various surveys, calculated using Preston's octave scale method (surveys complete to 59, 67 and 64%, respectively). Comparing the numbers of taxa recorded in the field (115, 84 and 67) with the number of records, these figures suggest that an almost fourfold increase in extent of sampling is necessary when the number of species theoretically to be expected in an area doubles.

The number of very rare (‘tail’) species, here defined as these represented by a single record, corresponds roughly with the number of taxa recorded from the field (southwestern Virginia: 115 taxa, 32 rare; the Russian Karelia: 84 taxa, 24 rare; Maquipucuna: 67 taxa, 21 rare). Results from a study of vascular plants carried out in Australia indicated that more than 90% of these tail species are significantly more abundant in other areas (Murray *et al.*, 1999). If judged from the collective experience of the three authors, a much larger proportion of the tail species found in the three myxomycete surveys would be considered rare in every other survey of which we are aware (13 of 32, 11 of 24 and 6 of 21). These high percentages (41, 46 and 29%, respectively) reflect the difficulties in determining myxomycetes reliably, as well as the fact that a number of described species may be nothing more than aberrant forms of more common species. Examples for such taxa might very well be found among some the rare forms classified in the genera *Calonema* and *Cornuvia*. A study of the genesis of the spiral capillitial elements (taenia) by McHugh, Reid & Ronan (2000) suggests the possibility that some of these species could belong to much more common species within the genera *Trichia* or *Hemitrichia*. In some instances, the superficially striking differences in capillitial ornamentation could be the result of nothing more than a disruption in the formation of the taenia, which develop relatively late in sporocarp formation.

The assemblage of myxomycetes at Maquipucuna deviates in several features from the two assemblages reported for areas with well-pronounced seasons. In addition to the much lower diversity of corticolous myxomycetes (mentioned above), these are the higher diversity and productivity of aerial litter compared with ground litter; a higher percentage of species, but especially records, with a phaneroplasmodium; a longer stalk in specimens from Neotropical forests compared to the same species from temperate zones; and a higher proportion of stalked species as well as records when compared with sessile ones. One possible explanation for these features is the much higher rainfall in tropical forests in connection with a lower probability that the respective substrata dry out and herefore allow myxomycete fructifications to disperse their spores. Many species with a protoplasmodium, especially members of the genera *Echinostelium* and *Licea*, are well known to be corticolous, developing rapidly on bark that dries out soon after a period of moist weather. Members of these genera were exceedingly rare in the Maquipucuna study (*Echinostelium*: 1 taxon, *Licea*: 2 taxa, each represented by one or two records only). Very probably, the almost continuously wet bark of tree trunks in tropical cloud forests with a closed canopy does not allow such species to disperse their spores, since the tiny fructifications rarely exceed the water film covering the substratum. Coincidentally, *Echinostelium minutum* is the largest species of the genus (having the longest stalk) and both species of *Licea* found in the survey were stalked. Similarly, the higher percentage of stalked species in the Maquipucuna survey can be explained by the assumption that a stalked sporocarp can elevate the spore mass above a water film, which results in a higher probability that the spores can dry

out, a precondition for them becoming released into the air. According to this hypothesis, stalked myxomycete species in the wet tropics should face a higher evolutionary pressure to develop longer stipes, as indicated by comparative measurements of the stipe length for species occurring in both temperate and tropical zones. This explanation is further supported by the fact that substrata on the ground are often less productive than aerial ones, since the latter dry out faster, which allows myxomycete fructifications to develop. Very probably, species with a phaneroplasmodium, the most robust plasmodium type, can survive best (and probably the longest time) in a very moist environment. In addition, the fructifications produced by many members of the Physarales possess a thick covering of lime, which enhances the chance that a substratum bearing a fructification dries out before the sporocarps are colonized by fungi. Mouldy fructifications were observed much more often during the Maquipucuna survey than is usually the case in temperate or boreal regions. It has been hypothesized (Alexopoulos, 1970) that one of the limiting factors for myxomycetes in tropical forests is the constant high humidity, which promotes the colonization of their fructifications by filamentous fungi. Such fungi tend to ‘smother’ a given fructification, producing a mycelium over the entire surface. Fungal hyphae also rapidly penetrate the spore-mass of the fructification, where they invade the protoplasts of the individual spores (Rogerson & Stephenson, 1993). Ultimately, most if not all of the spores present in the fructification are adversely affected (i.e., they are rendered nonviable and/or never liberated). As such, the ecological impact that fungi have upon myxomycetes is, at least on some occasions in certain habitats, likely to be considerable. Any feature of the myxomycete that could potentially reduce the likelihood of a fructification becoming colonized would be important and it certainly seems possible that a longer stipe would have just this effect.

In the light of these conclusions, myxomycetes appear as organisms that are adapted to highly fluctuating conditions of environmental moisture levels. This is also suggested by the presence of three dormant stages (microcysts, sclerotia and spores) in the myxomycete life cycle. A continuously high moisture seems not to favour the development of myxomycetes. This factor, perhaps together with a higher level of colonization by fungi, seems to explain many of the special features of the myxomycete assemblage found at Maquipucuna. As indicated by this study, it seems probable that not the tropics but southern temperate zones with a climate characterized by warm summers with highly fluctuating rainfall patterns have the highest myxomycete biodiversity on earth. As such, eastern North America and the temperate regions of eastern Asia may be possible ‘hot spots’ for myxomycetes. The high numbers of species recorded for these two regions (>275 for eastern North America, Martin & Alexopoulos, 1969; 418 for Japan, Yamamoto, 1998) seem to support this hypothesis. However, it seems possible that future myxomycete studies of the canopy layer of tropical forests, having a microclimate with higher fluctuations in moisture than the forest floor, reveal a higher diversity at least for bark-inhabiting myxomycetes in the tropics.

Acknowledgements

We gratefully acknowledge logistical support provided by Mike Dilgers, the resident biologist of the Maquipucuna Cloud Forest Reserve, as well as the continuous help of all other staff members at the reserve. For loans of specimens, we wish to thank Dr. Jan Rammeloo, Belgium; Yukinori Yamamoto, Japan and the curators at the U.S. National Fungus Collection (BPI). We are indebted to Dr. Uno Eliasson, Sweden; David Mitchell, United Kingdom; Wolfgang Nowotny, Austria; and Yukinori Yamamoto for valuable comments towards determinations of species as well as to Jun Matsumoto, Japan, for the determination of *Didymium floccosum*. The research reported herein was supported by a grant (DEB-9705464) from the National Science Foundation.

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Mycologia, 92 (4), 2000, pp. 626-637.

Myxomycete biodiversity in four different forest types of Costa Rica

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Abstract: The moist chamber culture technique was used to examine patterns of biodiversity and distribution of myxomycetes in four different forest types in Costa Rica, focusing on the substrates represented by the bark surface of living trees and leaf litter. Rarefaction as well as bootstrap analyses were carried out to estimate the completeness of the survey in terms of the numbers of species of myxomycetes present. Both species diversity and myxomycete abundance decreased with increasing elevation and resulting higher moisture levels of the investigated forest types. The two seasonal dry forest types accounted for 90% of the total myxomycete diversity. For bark-inhabiting myxomycetes, species richness was found to be negatively correlated with epiphyte (i.e. mosses, liverworts, and lichens) coverage. For both litter and bark, a higher substrate pH tended to be positively correlated with higher species diversity. Among litter-inhabiting myxomycetes, the proportion of species with rather robust phaneroplasmodia increased with increasing elevation. All of these results indicate that the excess of moisture in continuously moist tropical forests does not favor myxomycete growth and development. Species richness and frequency patterns for both substrate types were found to be comparable with those calculated from a data set reported for a study area in the temperate zone, indicating that myxomycete biodiversity does not reach its highest levels in tropical forests.

Key Words: distribution, ecology, Neotropics, slime molds, tropical forests

INTRODUCTION

Myxomycetes (plasmodial slime molds) are phagotrophic eukaryotes that occur in association with decaying plant material in almost all types of terrestrial ecosystems. The myxomycete life cycle involves two very different trophic stages. The first of these is a true microorganism and consists of uninucleate amoebae with or without flagella, whereas the other – a distinctive multinucleate structure, the plasmodium – can achieve macroscopic dimensions (Alexopoulos 1960, Martin et al 1983). Under favorable conditions, the plasmodium gives rise to one or more fruiting bodies (sporocarps) containing spores. The spores complete the life cycle by germinating to produce the uninucleate amoeboflagellate cells. Due to both their cryptic life style and the almost complete absence of meaningful taxonomic characters in plasmodia, field studies of myxomycetes have invariably focused on the reproductive, or spore-producing, stage in the life cycle (Stephenson et al 1993). Since plasmodia are often hidden in their substrates, the fruiting bodies usually are the only readily observable indication of myxomycetes. Such features of the life cycle cause myxomycetes to approach the conditions of true eukaryotic microorganisms and thus make biodiversity assessments difficult. Consequently, this group is neglected in virtually all recently published biodiversity studies.

Beyond pure collection lists, only a few papers relating to the ecology and distribution of myxomycetes in Neotropical ecosystems have been published. Examples are the studies of Maimoni-Rodella and Gottsberger (1980) in lowland forests in Brazil, Ogata et al (1996) in a lowland rain forest on the Yucatan Peninsula, Mexico (both dealing with field collections only), and Stephenson et al (1998) in Puerto Rico (which used the moist chamber technique). The primary objectives of the study reported herein were (i) to assess biodiversity patterns of litter- and bark-inhabiting myxomycetes within examples of the major forest types of Costa Rica and (ii) to compare the resulting patterns in species diversity with those reported from studies carried out in temperate regions.

Myxomycetes form fructifications on four major substrate types: wood in all stages of decay, the bark surface of living trees, litter of decaying plants (both woody and herbaceous), and dung of herbivorous animals. Due to its rapid degradation by arthropods, dung is virtually absent in the humid tropics. Since many species associated with decaying wood cannot be obtained in moist chamber cultures, the present study focused on the two substrate types of bark and

Accepted for publication February 25, 2000.
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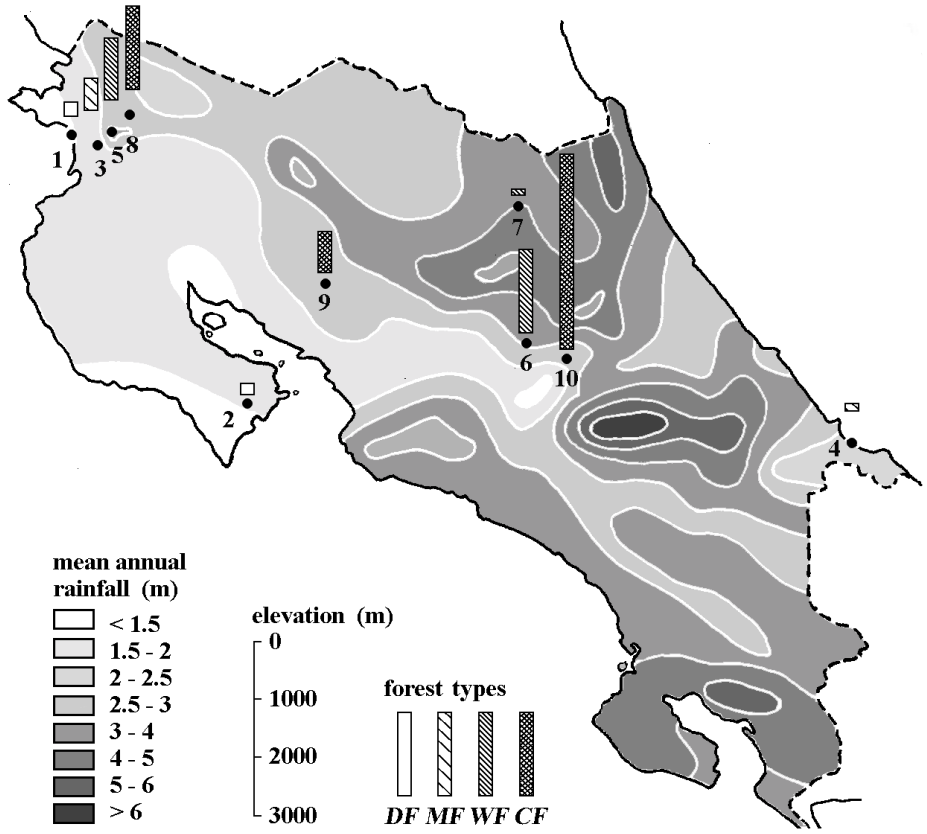

FIG. 1. Map of Costa Rica, showing zones of mean annual rainfall according to Coen (1983) and the location, elevation and classification of the sampling localities according to the four forest types of Tropical Dry Forest (*DF*), Tropical Moist Forest (*MF*), Tropical Wet Forest (*WF*), and Cloud Forest (*CF*).

litter, leaving wood-inhabiting myxomycetes for a later investigation, to be based on field collections.

MATERIALS AND METHODS

Characterization of the forest types investigated.—Substrate samples for this study were obtained from ten principal collecting sites situated within an west-east belt stretching from the Pacific to the Atlantic coast of Costa Rica (FIG. 1). All sites investigated were assigned to one of four forest types, which encompassed the Holdridge Life Zones of Tropical Dry Forest to Tropical Montane Rain Forest (Holdridge et al 1971). The numbers mentioned for the localities refer to FIG. 1; nomenclature used for tree species follows Hartshorn and Poveda (1983).

The driest forest type in Costa Rica is the Tropical Dry Forest (*DF*). It is found in coastal regions, especially in the northwest, that receive an annual precipitation of less than 2000 mm and are characterized by a long and well-pronounced dry season extending from November to May. A considerable proportion of the trees shed their leaves during the dry season entirely or partially, thus allowing the litter layer to dry out completely. Trees are often completely free of epiphytes, or their bark is covered with scattered liverworts and/or lichens when exposed to sunlight (average epiphyte coverage of 0–25%). Bark textures are diverse, ranging from smooth to deeply furrowed or flaky, both represented by tree species with soft or hard bark. Common trees are species of *Manilcara* and *Poulteria*, *Enterolobium cyclocarpum* (Jacq.) Griseb., and *Hymenaea coubaril* L. In secondary forests, the yellow flowers of the at this time leafless *Cochlospermum vitifolium* (Willd.) Spreng. are very conspicuous. Sampling localities were (1) a plot of nearly pristine forest in the Area de Conservación Guanacaste (ACG, former Hacienda Santa Rosa, 10°51'N 85°36'W, 300 m elev) and (2) a similar forest on the Peninsula de Nicoya (Refugio National de Vida Silvestre Curu, 9°50'N 85°00'W, ca 250 m elev).

Tropical Moist Forest (abbreviation *MF*) occurs at middle elevations on the Pacific side, but reaches sea level on the Atlantic side of Costa Rica. It has a less severe dry season and

TABLE I. Occurrence of all species of myxomycetes recorded from the four forest types.

Species [b]	Forest type [a]			
	DF	*MF*	*WF*	*CF*
Arcyria cf. *afroalpina* Rammeloo, Bull. Jard. Bot. Nat. Belg. 51: 229. 1981	—/2 [c]	—/16	—/1	—/—
Arcyria cinerea (Bull.) Pers.	—/6	2/10	—/1	2/7
Arcyria cinerea, yellow form	—/—	—/12	—/—	—/2
Ceratiomyxa fruticulosa (Müll.) T. Macbr.	—/—	—/—	2/—	—/—
Clastoderma debaryanum A. Blytt	2/—	—/—	—/—	—/—
Comatricha rubens Lister	—/—	—/3	—/—	—/—
Comatricha sp. A	—/—	—/1	—/—	—/—
Comatricha tenerrima (M.A. Curtis) G. Lister	—/—	—/2	—/—	—/—
Craterium concinnum Rex	—/—	—/—	—/—	—/2
Craterium leucocephalum (Pers.) Ditmar	—/—	—/1	—/—	—/—
Cribraria microcarpa (Schrad.) Pers.	1/—	—/—	1/—	—/—
Cribraria violacea Rex	19/3	6/4	2/—	2/—
Cribraria vulgaris var. *oregana* (H.C. Gilbert) Nann.-Bremek. & Lado, Proc. K. Ned. Akad. Wet. C88: 224. 1985	—/1	—/—	1/—	—/—
Didymium clavus (Alb. & Schwein.) Rab.	—/—	—/—	—/—	—/1
Didymium difforme (Pers.) S.F. Gray	—/3	—/—	—/—	—/2
Didymium iridis (Ditmar) Fr.	—/6	—/34	—/11	1/6
Didymium ochroideum G. Lister	—/—	—/14	—/2	—/3
Didymium ovoideum Nann.—Bremek.	—/2	—/—	—/—	—/1
Didymium squamulosum (Alb. & Schwein.) Fr.	—/3	—/11	—/1	—/10
Diachea leucopodia (Bull.) Rostaf.	—/—	—/—	—/—	—/1
Diderma corrugatum T.E. Brooks & H.W. Keller, Mycologia 69: 180. 1977	1/—	1/—	—/—	—/—
Diderma deplanatum Fr.	4/—	—/—	—/—	—/—
Diderma effusum (Schwein.) Morgan	—/—	—/4	—/1	—/1
Diderma hemisphaericum (Bull.) Hornem.	1/7	—/19	—/6	—/13
Diderma testaceum (Schrad.) Pers.	—/—	—/—	—/—	—/1
Diderma sp. A	—/6	—/1	—/—	—/—
Echinostelium minutum de Bary	2/—	—/—	—/—	2/—
Fuligo cinerea (Schwein.) Morgan	—/1	—/—	—/—	—/—
Lamproderma arcyrionema Rostaf.	—/—	—/15	—/—	—/—
Lamproderma scintillans (Berk. & Broome) Morgan	—/11	—/27	—/4	—/4
Licea biforis Morgan	—/—	—/1	—/—	—/—
Licea operculata (Wingate) G.W. Martin	2/—	1/2	—/—	—/—
Licea perexigua T.E. Brooks & H.W. Keller Mycologia 69: 674. 1977	2/—	—/—	—/—	—/—
Lycogala epidendrum (L.) Fr.	1/—	—/—	—/—	—/—
Macbrideola cornea (G. Lister & Cran) Alexop.	1/—	—/—	—/—	—/—
Macbrideola martinii (Alexop. & Beneke) Alexop.	7/—	4/1	—/—	1/1
Macbrideola scintillans H.C. Gilbert	9/—	—/—	—/—	—/—
Metatrichia vesparium (Batsch) Nann.-Bremek.	1/—	—/—	—/—	—/—
Paradiacheopsis cf. *acanthodes* (Alexop.) Nann.-Bremek., Proc. K. Ned. Akad. Wet. C89: 236. 1986	1/—	—/—	—/—	—/—
Paradiacheopsis longipes Hoof & Nann.-Bremek., Proc. K. Ned. Akad. Wet. C99: 48. 1996	—/—	—/1	—/—	—/—

a higher annual precipitation (2000–3000 mm) than Tropical Dry Forest. Since the proportion of deciduous trees is very low, less light penetrates through the canopy to the forest floor. Therefore, the litter layer does not dry out completely. Bark of trees remains in at least partial shade the year around. The epiphyte cover on bark (average of 10–65%) is higher than in the Tropical Dry Forest. Bark textures are more uniform, but trees with flaky or furrowed bark are still not uncommon. The tree diversity is high; only locally does a single tree species become dominant. Areas surveyed were (3) a second ACG plot (ca 500 m southeast of the Mariza Biological Station, 10°57'N 85°35'W, ca 600 m elev) and (4)

TABLE I. continued

Perichaena chrysosperma (Curr.) Lister	—/1	—/9	—/—	—/—
Perichaena corticalis (Batsch) Rostaf.	—/—	—/2	—/—	—/—
Perichaena depressa Libert	—/—	—/1	—/—	—/—
Perichaena minor var. *minor*	1/—	—/—	1/—	—/—
Perichaena minor var. *pardina* Minakata	2/—	—/4	—/—	—/—
Perichaena pedata (A. & G. Lister) G. Lister	—/—	—/7	—/—	—/—
Perichaena vermicularis (Schwein.) Rostaf.	8/2	3/24	—/—	—/1
Perichaena sp. A	—/—	—/—	—/2	—/—
Physarum cinereum (Batsch) Pers.	—/3	—/—	—/3	—/—
Physarum compressum Alb. & Schwein.	—/1	—/14	—/1	—/9
Physarum crateriforme Petch	2/—	—/—	—/—	—/—
Physarum didermoides (Pers.) Rostaf.	—/—	—/2	—/—	—/—
Physarum globuliferum (Bull.) Pers.	2/—	1/—	—/—	—/—
Physarum melleum (Berk. & Broome) Massee	—/—	—/1	—/—	—/1
Physarum cf. *notabile* T. Macbr.	—/—	—/2	—/—	—/—
Physarum pusillum (Berk. & M.A. Curtis) G. Lister	—/—	—/11	—/—	—/—
Physarum cf. *roseum* Berk. & Broome	—/—	1/—	—/—	—/—
Physarum stellatum (Massee) G.W. Martin	3/—	—/—	—/—	—/—
Physarum cf. *straminipes* Lister	—/—	—/1	—/—	—/—
Stemonitis fusca Roth	—/—	—/1	—/—	—/—
Indeterminable records	4/6	—/12	—/7	—/6
Non-fruiting plasmodia	6/—	13/5	3/5	4/5

[a] Forest types as arranged along a gradient of increasing elevation are *DF*, *MF*, *WF*, and *CF*.
[b] For names not included in Martin and Alexopoulos (1969), a reference to the protolog is given.
[c] For species records, the first value indicates records of specimens obtained from moist chambers prepared with bark, whereas the second value indicates records from moist chambers prepared with litter.

one secondary and one primary lowland forest on the Atlantic side, north of the town of Cahuita (9°45'N 82°58'W, 10–30 m elev).

The Holdridge Life Zones ranging from Tropical Wet Forest to Tropical Premontane Wet Forest were combined to form the third forest type [hereafter called Tropical Wet Forest, (*WF*)]. All of these Holdridge Life Zones are characterized by a very brief (Pacific site) or absent (Atlantic side) dry season, lowland (Atlantic side) to medium elevation (up to 1400 m, Pacific side and Central Cordillera) sites, and high precipitation (ranging from 3000–4000 mm per year). Canopy trees are evergreen, up to 55 m tall, with mostly closed but still thin covers of epiphytes, predominantly liverworts (average of 75–100%). The bark texture of trees is smooth or flaky, but thicker bark is always soft and very hydrophobic. Members of the Lauraceae, such as species of *Ocotea*, are among the more common canopy trees. The litter layer stays moist the year around. In addition to a third (5) ACG plot (lower slopes of Volcano Cacao, ca 500 m east–northeast of the Cacao Biological Station, 10°56'N 85°28'W, ca 1200 m elev) we studied (6) several small forest remnants in the highlands around San Jose (9°56'N 84°07'W, 1400–1600 m elev), and (7) a lowland evergreen rain forest at La Selva (biological station of the Organization of Tropical Studies, 10°25'N 84°00'W, ca 80 m elev).

The last forest type combines under the name Cloud Forest (*CF*) the Holdridge Life Zones of Tropical Premontane to Montane Rain Forest. This forest type occurs at high to very high elevations (1400–3400 m), has a very high annual precipitation (> 4000 mm) and is characterized by almost daily cloud exposure. Trees are almost completely covered with a thick (> 2 cm) layer of mosses and liverworts interwoven with the rhizomes of Hymenophyllaceous ferns. The bark texture of trees is mostly smooth, seldom flaky and then often shedding in thick and large platelets. Species of *Weinmannia* and *Dendropanax* are conspicuous trees at least in high elevation expressions of this forest type. The litter layer is permanently wet and often covered by a water film from excess rain water. Sampling localities were (8) a fourth ACG plot (montane *CF*) on the upper slopes of Volcano Cacao, ca. 1.2 km east-northeast of the Cacao Biological Station, 10°56'N 85°28'W, ca 1400 m elev), (9) the Monteverde region (Cloud Forest Reserve ca 3.5 km south-southeast of Santa Elena, 10°16'N 84°48'W, 1250–1350 m elev), and (10) the upper slopes of the Irazu Volcano (Parque National Volcano Irazu, San Isidro, 9°59'N 83°52'W, ca 3300 m elev).

Sampling and data analysis.—Between 1992 and 1998, from all principal study sites, a total of 476 substrate samples (bark from 1.5–2 m, litter from 0–2 m height) from all principal study sites were collected and gently air-dried. Moist chamber cultures were prepared within three weeks after collecting, as described in Stephenson et al (1998). Voucher specimens of myxomycetes obtained from these cultures were deposited in the herbarium of Fairmont State College (FWVA) and in the

personal collection of the first author, which is stored at the Herbarium Haussknecht, Jena (JE). Nomenclature used for myxomycetes follows Martin and Alexopoulos (1969) with a few exceptions, where a reference to a protolog is given (see TABLE I). The percentage of positive moist chambers where at least myxomycete plasmodia were observed was used as an indicator for the proportion of substrates suitable for myxomycete growth. Since sometimes a plasmodium fails to form a fructification in culture, the number of positive moist chambers in a series can be higher than the number of determinable specimens from the same series. In a similar way, the ratio of records per moist chamber can be seen as an estimator for the population density of myxomycetes.

To estimate whether or not the survey was exhaustive in terms of the species recorded, a bootstrap analysis (modified from Efron 1982, compare Krebs 1989) was carried out. The sequence of samples (moist chambers) was permutated randomly and the number of recorded species was plotted against the number of moist chambers (samples). The mean of 100 plots of species versus samples was subjected to a regression analysis, using a saturation formula $y = ax / (b + x)$, where x is the record number, *y* the number of species recorded, and the parameter *a* refers to the maximum number of species to expect. In addition, Preston's Octave Scale Method (Preston 1948) was employed as an independent approach. For comparison of myxomycete biodiversity within forest types, Shannon's formula $H' = \sum (p_i \ln p_i)$, which is based on the proportion p_i of the records belonging to one species to the total number of records made for the respective survey, was used (Shannon and Weaver 1963).

For comparisons among different myxomycete assemblages, the coefficient of community index $CC = 2c/(a + b)$, where *a* is the total number of species in the first data set being considered, *b* is the total number of species in the second data set, and *c* is the number of species common to both data sets, was applied to pairwise combinations of the various data sets (Mueller-Dombois and Ellenberg 1974). The value of CC ranges from 0 (when the data sets being compared share no species in common) to 1.0 (all species are present in both data sets). As an indicator for overall taxonomic diversity, we used the mean number of species per genus (S/G), as described by Stephenson et al (1993). Species diversity within the data sets was compared using two different methods – rarefaction analysis (Hulbert 1971) and the bootstrap analysis explained above.

RESULTS

Species diversity.—For this study, 171 moist chamber cultures were prepared with bark samples from living trees, with almost all of these samples originating from trees in primary forests. For litter, 305 cultures were prepared, with 68 of the 305 samples collected in secondary forests belonging to the two seasonal dry forest types. From the 583 records obtained from all 476 cultures prepared, 508 could be identified. Another 35 records consisted of fructifications that did not mature properly and thus remained indeterminable, together with 40 additional records of plasmodia that could not be induced to develop fructifications. As shown in TABLE I, a total of 60 taxa was recorded, four of which are apparently undescribed. These are a yellow form of *Arcyria* from aerial litter, similar to *A. cinerea*; a slender, long-stalked and minute *Comatricha* similar to *C. penicillata* Nann.-Brem. & Y. Yamam. (Proc. K. Ned. Akad. Wet. C86: 223. 1983), represented by a single, but excellent mature sporocarp from a bark culture; a minute *Diderma* from leaf litter, and a *Perichaena* of *Licea*-like appearance also recorded from leaf litter. Our study adds 32 taxa to the first comprehensive survey of Costa Rican myxomycetes, published by Alexopoulos and Saenz (1975), which was based mainly on field collections and therefore depicts a somewhat different species assemblage.

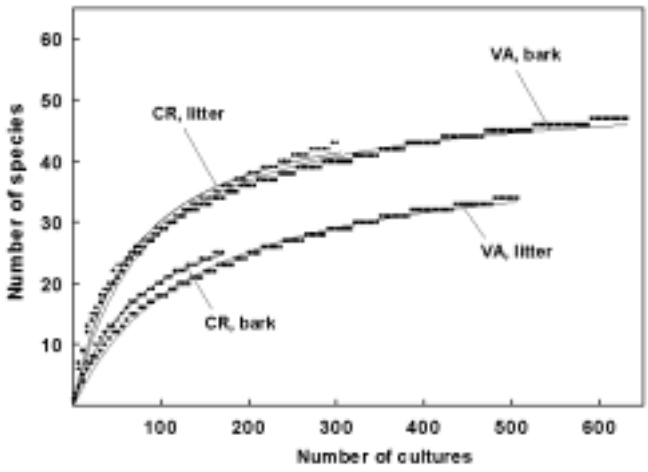

FIG. 2. Bootstrap analysis of the randomly permutated sequence of samples (moist chambers) versus mean cumulative species numbers for bark- and litter-inhabiting myxomycetes from tropical forests of Costa Rica (CR) and temperate upland forests from Virginia (VA). Small dots indicate the increase in species number with the number of cultures considered (means of 100 runs, each with a randomly permutated sequence of cultures). The solid line shows the results of the regression analysis. Parameter values for the best fit were found to be $A = 35.6$, $B = 74.1$, mean square error 0.16 for bark-inhabiting and $A = 50.7$, $B = 67.3$, mean square error 1.45 for litter-inhabiting myxomycetes from Costa Rica and $A = 51.9$, $B = 81.8$, mean square error 0.99 for bark-inhabiting and $A = 42.5$, $B = 137.4$, mean square error 0.43 for litter-inhabiting myxomycetes from Virginia.

FIGURE 2 shows the results of the bootstrap analysis. The mean number of records (not shown) increased in a nearly linear fashion with the sample number, indica-

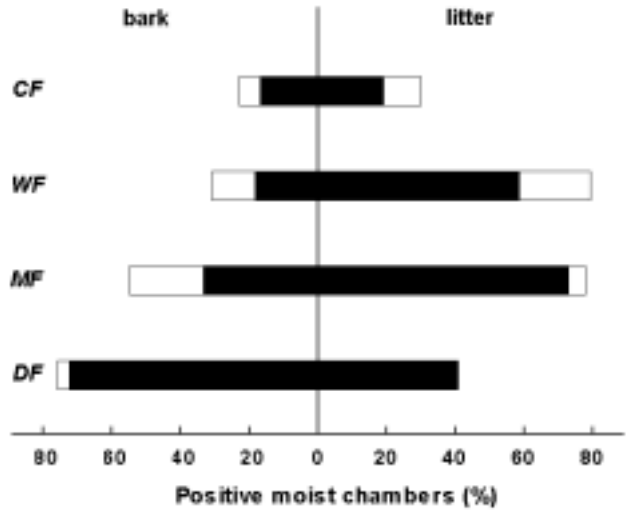

FIG. 3. Percentage of positive moist chambers for samples of bark from living trees (left side of the diagram) and samples of litter (right side) in the four forest types, which are arranged along a gradient of increasing elevation (abbreviations as in FIG. 1). Closed bars indicate the proportion of moist chambers yielding myxomycete fructifications, and the open portions add those with plasmodia that could not be induced to fruit.

ting that the chosen number of 100 repetitions should be sufficient for the analysis. A fit of the mean of 100 plots of species versus samples with a saturation function results in 36 species to be expected for bark and 51 for litter, respectively, equaling a recovery rate of 70 and 84 % for the two substrate types. With 33 species to be expected for bark as a substrate and 72 for litter, Preston's Octave Scale Method gave comparable results (TABLE IV).

Myxomycete distribution.—For both of the substrate types investigated, the proportion of positive moist chambers decreased dramatically with increasing elevation (FIG. 3). The ratio of records per moist chamber shows the same pattern, also indicating decreasing myxomycete abundance (TABLE II, III). Not surprisingly, the total species diversity within a given forest type also decreases, with 34 species recovered from the *DF*, 36 from the *MF*, 16 from the *WF*, and 20 from the *CF* as total numbers for both substrate types. When comparing the two seasonal dry forest types *DF* and *MF* with the two continuously moist forest types at higher elevations (*WF* and *CF*), myxomycete species diversity was noticeably lower in the latter (*DF* + *MF*: 22 species of bark- and 38 species of litter-inhabiting myxomycetes; *WF* + *CF*: 7 and 21 species, respectively). With 54 species, the two seasonal dry forest types accounted for 90% of the total number of species encountered. Additional species present in the higher elevation forest types were five litter-inhabiting myxomycetes (TABLE I), and the usually wood-inhabiting *Ceratiomyxa fruticulosa*, recorded twice from mossy bark in the *WF*.

Species diversity patterns along the elevational gradient differ for myxomycetes from bark (25 species recorded) and litter (43 species). With 21 taxa, species diversity for bark-inhabiting myxomycetes has a clear maximum in the *DF* (compare TABLE II). All species that were recorded from bark in the higher elevation forest types (*MF*, *WF*, *CF*) are not strictly bark-inhabiting and were found on lush epiphytic moss and liverwort mats covering the bark. These were *Arcyria cinerea* and *Physarum* cf. *roseum* from the forest type *MF*, *Ceratiomyxa fruticulosa* and *Cribraria vulgaris* var. *oregana* (*WF*), and *Didymium iridis* (*CF*). Thus, all preferentially bark-inhabiting species are present in the Tropical Dry Forest (*DF*), but only three of them (*Cribraria violacea*, *Macbrideola martinii*, and *Echinostelium minutum*) also occur (albeit rarely) at higher elevations. When comparing the total coverage of epiphytic lichens, mosses and liverworts in the cultures prepared with bark with the number of recorded species (FIG. 4), it becomes obvious that a closed epiphyte cover hampers myxomycete growth. On the other hand, many cultures prepared with from bark with low epiphyte cover also produced no myxomycetes.

Litter-inhabiting myxomycetes reached their maximum diversity in the Tropical Moist Forest (*MF*, 33 species, TABLE III). The low number of species as well as records in the *WF* is probably due to the lower number of cultures prepared, since in the *CF* the species number rises again but does not reach the maximum recorded for the forest type *MF*. As in the case of bark-inhabiting myxomycetes, cultures from the higher elevation forest types *WF* and *CF* added only a few species. These were *Perichaena* sp. A. (*WF*), and *Craterium concinnum*, *Diachea leucopodia* and *Diderma testaceum* (all *CF*). Except for the *Perichaena*, all species are also known from field collections made at lower elevations.

To determine whether or not differences in substrate pH among the four forest types are a possible explanation for the different levels of biodiversity, the substrate pH was recorded for all cultures and plotted against the number of myxomy-

TABLE II. Comparison of the assemblages of bark-inhabiting myxomycetes in the four forest types.

	Forest type			
	DF	*MF*	*WF*	*CF*
Substrate pH, range	5.2–7.5	5.3–7.4	5.8–7.6	4.3–7.4
Substrate pH, mean ± SE	6.59 ± 0.07	6.69 ± 0.07	6.65 ± 0.09	6.35 ± 0.13
Number of cultures prepared	59	43	24	54
Number of species	21	8	5	5
Total records	82	32	10	12
Mean records per culture	1.39	0.74	0.42	0.22
Shannon diversity index H'	1.11	0.80	0.67	0.68

TABLE III. Comparison of the assemblages of litter-inhabiting myxomycetes in the four forest types.

	Forest type			
	DF	*MF*	*WF*	*CF*
Substrate pH, range	4.7–8.2	5.4–7.9	5.9–6.9	4.5–7.6
Substrate pH, mean ± SE	6.35 ± 0.07	6.46 ± 0.07	6.27 ± 0.09	5.88 ± 0.08 [a]
Number of cultures	48	111	39	119
Number of species	16	33	11	18
Total records	64	275	45	77
Mean records per culture	1.33	2.48	1.15	0.65
Shannon diversity index H'	2.52	2.97	2.02	2.47
Proportion of orders [b]				
Ceratiomyxales	—	—	—	—
Echinosteliales	—	—	—	—
Liceales	6.9	2.7	—	—
Trichales	19.0	32.9	12.1	15.2
Stemonitales	19.0	19.8	12.1	7.6
Physarales	55.2	44.6	75.8	77.3

[a] Statistically significant difference when compared with the mean pH values for forest type *DF* (delogarithmated pH values, Mann-Whitney Rank Sum Test, $p < 0.001$).
[b] Proportion of each of the six orders of myxomycetes, based on the total number of records (%).

cete species recorded in a culture (FIG. 5). As a general tendency, the more acidic substrates yielded no or only one species, and most of the cultures with more than one species had a circumneutral pH. However, the range of pH values for the substrates in a given forest type was much larger than the differences in the mean pH values among all the forest types, although a weak tendency for more acidic substrates to be associated with higher elevations was found to exist (TABLE II, III).

Among the six orders of myxomycetes, almost no species with protoplasmodia (characteristic of the Ceratiomyxales, Echinosteliales and the genus *Licea* of the Liceales) were recorded from litter (TABLE III). The proportion of myxomycetes with aphanoplasmodia (members of the Stemonitales) decreased with increasing elevation of the forest types, whereas the proportion of species with phaneroplasmodia (Physarales and probably almost all members of the Trichales) increased. Since bark-inhabiting myxomycetes almost disappeared in the high-elevation forest types (only five species recorded from two forest types *WF* and *CF*), a similar comparison is impossible for this group. In contrast to litter-inhabiting myxomycetes, species with protoplasmodia were regularly found on bark.

Comparison with a data set from temperate zones.— The assemblage of myxomycetes associated with bark and litter in the upland forests of a region in southwestern Virginia were studied by Stephenson (1988, 1989) with 632 (bark) and 507 (litter) moist chamber cultures, respectively. The total species numbers recovered from Costa Rica (60 taxa from 476 cultures) and Virginia (63 taxa from 1139 cultures) are similar. Also, the ratio of species per

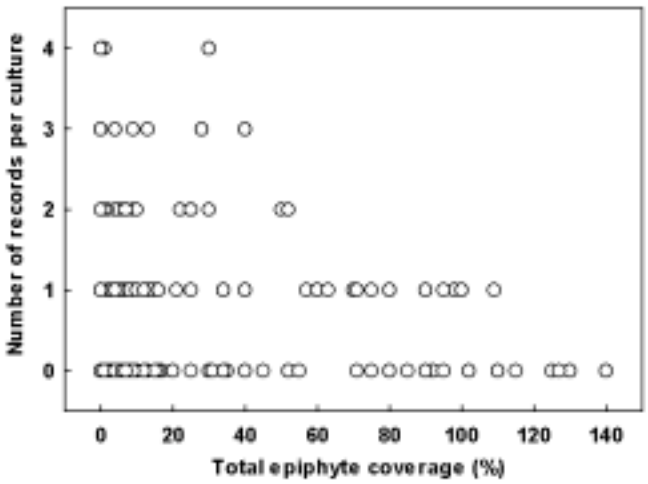

FIG. 4. Total coverage of epiphytes (mosses, liverworts, and lichens) vs number of species obtained from a moist chamber for the 171 bark substrate samples. Since the three components of epiphyte cover frequently overlap, coverage values can exceed 100 %.

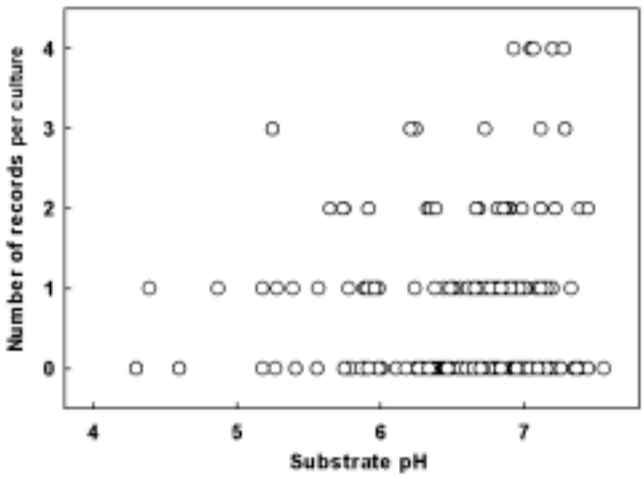

FIG. 5. Range of pH values for all substrate samples processed versus the number of species obtained from a given sample.

genus differs only slightly (3.0 for Costa Rica vs 2.4 for Virginia). The Costa Rican data set has more litter taxa (43 vs 34) but fewer bark taxa (25 vs 47, TABLE IV). Coefficient of community values are low for the assemblages of myxomycetes associated with the two substrate types: 0.22 for bark-inhabiting and 0.26 for litter-inhabiting myxomycetes, with an overall degree of similarity of 0.29 for both floras. The three most common bark-inhabiting myxomycetes in Costa Rica (*Cribraria violacea*, *Macbrideola scintillans* and *M. martinii*) were very rare or, in the case of the latter species, absent in Virginia. In contrast, the two most common species in the Virginia data set (*Echinostelium minutum* and *Licea parasitica*) are very rare or absent in Costa Rica, leaving the cosmopolitan but very variable species *Arcyria cinerea* as the only bark-inhabiting myxomycete that is fairly common in both study areas. Litter-inhabiting myxomycetes also show a low degree of similarity between the two regions. *Didymium iridis* and *D. squamulosum*, *Lamproderma scintillans* and *L. arcyrionema* as well as *Perichaena vermicularis* are examples of common litter-inhabiting species in Costa Rica. However, except for two records of *L. scintillans*, these taxa were not recorded in Virginia, whereas *Diderma effusum* and *Cribraria microcarpa* were common litter-inhabiting myxomycetes in West Virginia but rare in Costa Rica. Once again, *Arcyria cinerea* was the only common element in the two myxomycete assemblages.

Values of species richness for the data sets from bark and litter for each of the two study areas were first compared using rarefaction analysis (FIG. 6), based on the number of myxomycete records from the smallest data set (bark from Costa Rica with 103 records). The numbers of species to be expected were in the same order of magnitude for each of the four data sets (between 20 and 27, TABLE IV). Using the bootstrap method, a comparison analogous to the rarefaction method but based on the number of moist chamber cultures from the smallest data set (171) can be carried out, resulting in numbers between 23 and 36 species to be expected. With both the bootstrap method as well as Preston's Octave Scale Method, maximum numbers of species to be expected can be calculated for each data set, leading to fairly similar values for both methods (TABLE IV). All three methods, but with the least pronounced results from the rarefaction analysis, reveal a higher diversity for litter- versus bark-inhabiting myxomycetes in Costa Rica, but the opposite relationship for Virginia.

DISCUSSION

Species diversity.—It seems to be a general feature of many Neotropical myxomycetes that they are rare in terms of records as well as in terms of the number of sporocarps per colony. Only 25 of the 60 taxa identified in the present study were represented by more than three records, and 14 others were recorded

TABLE IV. Results of statistical analyses for bark- and litter-inhabiting myxomycetes from tropical forests of Costa Rica (CR) and temperate upland forests of Virginia (Vi).

	Costa Rica		Virginia	
	Bark	Litter	Bark	Litter
Number of species	25	43	47	34
Number of records	103	405	1107	398
Number of cultures	171	305	632	507
Mean records per culture	0.60	1.33	1.75	0.78
Mean frequency	0.040	0.023	0.021	0.029
Frequency distribution[a]	0.837	0.943	0.957	0.821
Comparison of diversity				
Bootstrap method	25	36	34	23
Rarefaction analysis	25.0	26.7	23.0	20.5
Number of species to expect				
Bootstrap method	35.6	50.7	51.9	42.5
Preston's Octave Scale Method	32.5	72.2	78.9	46.2

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

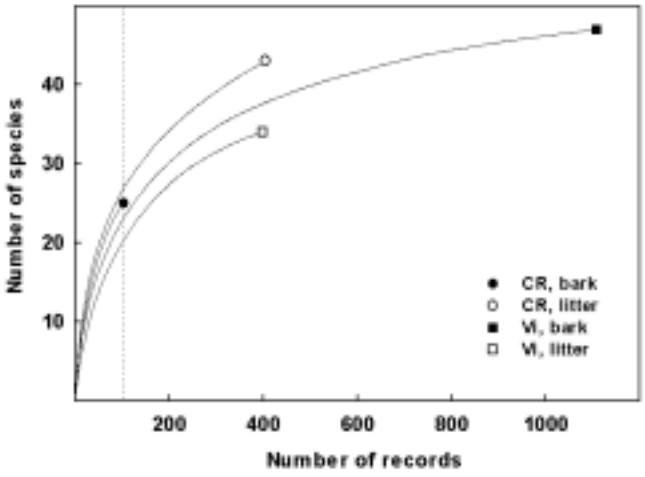

FIG. 6. Rarefaction analysis for bark- and litter-inhabiting myxomycetes from tropical forests in Costa Rica (CR), and temperate upland forests of Virginia (VA). Shown are the rarefaction curves constructed for each data set; the dotted line indicates the record number (103) of the smallest data set.

only once, an abundance pattern very similar to that found by Bills and Polishook (1994) for the microfungi occurring in the leaf litter of a lowland rain forest in Costa Rica. Myxomycete specimens appearing in moist chamber cultures from Neotropical regions, especially those occurring on bark, are difficult to identify, since usually only a few sporocarps per culture are formed. For example, *Macbrideola martinii* was recorded 14 times on bark but only once with more than 10 sporocarps and five times with a single sporocarp (mean = 4 sporocarps per culture). *Echinostelium minutum*, a species that usually forms large colonies, occurred four times, but with only 5, 7, 40, and 55 sporocarps, respectively.

Both analyses, the bootstrap method as well as Preston's Octave Scale Method, provided comparable figures for the total number of species to expect (36 vs 33 for bark-, and 51 vs 72 for litter-inhabiting myxomycetes, respectively). Comparing the actual numbers of species recorded with these estimations, the survey is complete to 69% vs 76% for bark-, and 84% vs 60% for litter- inhabiting myxomycetes, respectively. However, both estimations are valid only under the assumption that each substrate type was investigated with equal intensity (i.e., with comparable numbers of moist chamber cultures prepared) for all forest types, a condition fulfilled only roughly (TABLE II, III). In addition, Preston's Octave Scale Method assumes a lognormal distribution of the frequencies of the species (Ludwig and Reynolds 1988). As tested by constructing the respective graphs log (records) versus the rank of the species (not shown), the frequency distribution of the litter sample comes much closer to a geometric one (coefficient of a linear regression r = 0.94) than it does the frequency distribution of the bark sample (r = 0.84, TABLE IV). Hence, the precondition for applying Preston's Octave Scale Method is not really fulfilled for the litter sample. This results in an overestimation of the number of species to be expected and accounts for the higher figure in comparison to the bootstrap analysis,

resulting in an apparently lower degree of completeness of the survey. In contrast, the lower goodness of fit obtained with the bootstrap analysis for the litter sample (FIG. 2) indicates an underestimation of the number of species to be expected when using the bootstrap method. Thus, it can be assumed that our investigation was about 70–75% complete for bark-inhabiting and about 70–80% complete for litter-inhabiting myxomycetes, which should be sufficient for recovering all of the more common species.

Myxomycete distribution.—Both the percentage of positive cultures as well as the mean number of records per culture decreased with increasing elevation of the investigated forest type. This indicates a lower proportion of substrates suitable for myxomycete growth as well as a lower abundance of myxomycetes in high elevation forests (FIG. 3). These results are in sharp contrast with the diversity pattern reported for epiphytic mosses, lichens and liverworts along an elevational gradient in the Colombian Andes (Gradstein et al 1989, Wolf 1993), where diversity in all three groups steadily increased with increasing elevation until the Paramo region was reached. Our personal observations in Costa Rica indicate that bark epiphytes undoubtedly exhibit a similar pattern. Thus, abundance, but also diversity of myxomycetes, seems to decrease with the increasing abundance and diversity of bryophytes and lichens.

This pattern is especially pronounced for bark-inhabiting myxomycetes (FIG. 4). A high epiphyte cover seems to be one, although not the only, reason for their low abundance and diversity. In contrast to similar habitats in temperate zones (the "cool rain forests" of Western Great Britain and Ireland), which have a rich flora of bark-inhabiting myxomycetes (e.g., McHugh 1998), seasons are absent in tropical rain forests, allowing continuous growth of mosses, lichens and fungi. By using nutrients from the bark that then become unavailable for bacterial growth, these groups of organisms may be potential competitors of myxomycetes. On the other hand, it is well known that mossy logs and boulders can harbor a rich myxomycete flora (e.g., Ing 1983). Moreover, FIG. 4 shows that bark cultures from the low elevation forest types, which are almost free of epiphytes, also frequently lack myxomycetes. In the cultures prepared from the *DF*, total epiphyte cover was always less than 100%, ranging from 0–80% (mean 12 ± 19%, 59 bark samples). Consequently, an additional reason for the low diversity and abundance of bark-inhabiting myxomycetes noted in our study must exist. An outwashing effect by heavy rains is one possible further explanation. For many parts of Costa Rica, a high percentage of the total annual precipitation is concentrated in less than 15 d (Coen 1983, Portig 1965). These heavy tropical rains are likely to clear almost all myxomycete plasmodia and spores from the bark surface. In addition to this mechanical effect, a leaching effect caused by the sheer amount of rainfall cannot be ruled out, with soluble nutrients as well as microorganisms being removed from the bark.

In contrast to bark-inhabiting myxomycetes having their highest abundance and species richness in the *DF*, species inhabiting litter seem to be better adapted to a moderate dry season not desiccating the litter layer completely, the conditions that exist in the *MF*. This pattern is similar to that reported for litter-inhabiting myxomycetes in Puerto Rico (Stephenson et al 1998), with 24 species obtained from 500 substrate samples collected in five forest types along an elevation gradient ranging from 350–1000 m. The elfin forest, comparable to the *CF* in this study, had the lowest number of species. Maimoni-Rodella and Gottsberger (1980), comparing two 10 x 10 m sampling plots in a seasonal dry (Cerrado) and an evergreen forest in Brazil on the basis of field collecting of myxomycetes over one year, also found a much higher abundance of litter-inhabiting myxomycetes in the seasonal dry forest (75.6% vs 2.2% of all fructifications recorded from litter). In general, litter- and bark-inhabiting myxomycetes seemingly prefer seasonal dry tropical forests in comparison to continuously moist rain forests. One possible explanation for this pattern is the fact that myxomycetes are usually induced to fruit when the substrate dries out. Presumably, in the continuously moist higher elevation forests where substrates rarely dry out, myxomycetes may often fail to complete their life cycle and thus do not produce spores. Myxomycetes may survive as non-fruiting phaneroplasmodia for a long time, as known from laboratory cultures and also suggested by the higher proportion of non-fruiting phaneroplasmodia found in the high elevation forest types. However, in this case, efficiency of dispersal and thus the ability to colonize new substrates is dramatically reduced, as is also the case for fructifications developed under very moist conditions, where the spores cannot dry out to become airborne. Two lines of evidence indicate that

continuously moist substrates are unfavorable for myxomycete reproduction. First, for litter-inhabiting myxomycetes, samples from secondary forests yielded more records than those from primary forests. Second, aerial litter (collected 1.5–2.5 m above ground) was richer than forest floor litter (primary forest, forest floor litter: 137 cultures, mean 0.66 records per culture; primary forest, aerial litter 100, 1.25; secondary forest, forest floor litter 46, 2.98; and secondary forest, aerial litter 22, 4.45). Presumably, aerial litter in open secondary forests that are richer in gaps tends to dry out faster than forest floor litter in a closed canopy primary forest.

Low substrate pH appears to be a limiting factor for growth and development of most species of myxomycetes (Härkönen 1977), which may simply result from the fact that most bacteria do not grow well under these conditions. The data presented in FIG. 5, which indicate that moist chambers with a higher pH tend to be richer in species, support this observation. Although a weak tendency for decreasing pH values with increasing elevation exists, litter as well as bark shows a fairly wide range of pH values for each of the four forest types (TABLE II, III). Consequently, pH differences do not appear to represent a major explanation for the biodiversity pattern observed in this study.

Myxomycetes with protoplasmodia have microscopically small plasmodia that give rise to only one fruiting body per plasmodium, whereas these with aphanoplasmodia, but especially with phaneroplasmodia, achieve macroscopic dimensions and usually form a whole colony of fruiting bodies from a single plasmodium (Alexopoulos 1960). In this study, except for two records of *Licea operculata* on litter, species with protoplasmodia were confined to bark. Among litter-inhabiting myxomycetes, the general pattern was that of an increasing number of species with more robust plasmodia with increasing elevation (and moisture) of the forest types. In the *CF*, over 90% of all litter-inhabiting species recorded have phaneroplasmodia, which may be the only plasmodium type able to survive for long periods of time in continuously moist substrates.

In summary, the data presented herein suggest that myxomycete diversity is highest in tropical forests with fluctuating environmental conditions and a not too severe dry season. An excess of moisture as found in rain forests and cloud forests at high elevations does not appear to favor myxomycetes. However, it must be noted that the present study was limited to myxomycetes from only two of the major substrate types upon which these organisms occur.

When comparing the Costa Rican data set of bark- and litter-inhabiting myxomycetes to a similar data set from the temperate forests of Virginia (Stephenson 1989), the numbers of species recorded are fairly similar to one another, in spite of the higher number of moist chamber cultures composing the Virginia data set (TABLE IV). The absolute species numbers for both areas are even more comparable (60 species for Costa Rica vs 63 for Virginia). Remarkable is the low coefficient of community value (0.29) calculated for the two data sets, which does not support the assumption that most species of myxomycetes are cosmopolitan.

To compare diversity in the four data sets (litter- and bark-inhabiting myxomycetes from both areas), the bootstrap method as well as rarefaction analysis was used. As a computer simulation revealed, the two methods produced identical results when the calculation was based on numbers of records. Both the algorithm of Hulbert (1971), as well as the averaging of the species contributions obtained by randomly permutating the sample sequence in the bootstrap analysis, consider the probability of a species being represented in a subsample of a certain size. However, instead of record numbers, the bootstrap analysis in FIG. 2 was based on the number of cultures prepared; hence, the records of myxomycetes were assigned to discrete and comparable sample units. In contrast to the rarefaction method, the latter methods allows the question of the number of species to be expected when the substrate sampling is continued towards an indefinitely large number of samples to be assessed. As shown in TABLE IV and in FIG. 6, the comparison of the four data sets via rarefaction analysis at the level of the smallest data set (Costa Rican bark with 103 records) results in fairly similar species numbers (between 20–27). This is in accordance with the results of Peet (1974) who showed that for small sizes of subsamples rarefaction may predict the same number of species if the underlying communities differ markedly in the species' relative abundances. This is the case, as indicated by the mean frequencies for the four data sets, which range from 0.02–0.04 (TABLE IV). This problem can be avoided when abundance is based not on absolute record numbers but on units of comparable substrate samples, as is the case for the

bootstrap analysis (FIG. 2). Here, the total numbers of species to be expected differ between the four data sets, as numbers of species estimated at the level of the smallest data set (bark from Costa Rica with 171 cultures) do. Except for the shortcomings caused by the necessity of assuming a lognormal distribution of species frequency, Preston's Octave Scale Method confirms the figures for the total numbers of species to be expected. Therefore, it can be safely concluded that (i) the diversity of myxomycetes as revealed with the moist chamber method is very similar in Neotropical and temperate forests and (ii) litter-inhabiting myxomycetes have higher diversity and higher abundances in Neotropical forests than in temperate forests, whereas bark-inhabiting myxomycetes exhibit higher values for both parameters in temperate forests. Although the empirical experience of the authors from field collecting of myxomycetes in both areas seems to confirm these results, detailed comparative studies, especially for wood-inhabiting myxomycetes, are necessary to determine if this diversity pattern holds true for all ecological groups of myxomycetes.

ACKNOWLEDGEMENTS

We wish to thank all Costa Rican authorities, and especially Maria M. Chavarria Diaz from the Area Concervación de Guanacaste, for helping us organize the field work. This research was supported by a grant from the National Science Foundation (DEB-9705464).

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Nova Hedwigia 72 1—2 259—270 Stuttgart, Februar 2001

Foliicolous liverworts as a microhabitat for Neotropical Myxomycetes

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With 2 figures and 2 tables

Schnittler, M. (2001): Foliicolous liverworts as a microhabitat for Neotropical Myxomycetes. – Nova Hedwigia 72: 259-270.

Abstract: Leaves covered with epiphyllous liverworts and lichens were sampled at six localities in Ecuador, Costa Rica and Puerto Rico and screened with the moist chamber method for the presence of myxomycetes. Eleven species of myxomycetes were recovered, with *Arcyria afroalpina* as a new record for the Neotropics. Three species (*Arcyria cinerea*, *Didymium iridis* and *D. squamulosum*) were recorded with a high frequency (between 59 and 66%) in the moist chamber cultures. Evidence is presented that these three species may occur regularly on epiphyll-covered leaf surfaces as populations of myxoamoebae. Unusual small numbers of sporocarps found in the cultures, along with the occurrence of atypically small sporocarps suggest a microhabitat poor in nutrients. Lowland rain forests with a high annual rainfall seem to provide the best conditions for the growth of epiphyllous myxomycetes. With the plasmodial slime moulds, the study presented herein adds a new group of organisms to the community of epiphyllous cryptogams.

Keywords: Myxomycetes, foliicolous liverworts, microhabitat, moist chamber culture

Introduction

One distinctive feature of tropical evergreen forests is the occurrence of a specialized group of liverworts and lichens on the living, often leathery leaves of understory plants. Recent studies of these assemblages of foliicolous liverworts and lichens indicate a surprisingly high species diversity in this habitat. For example, Lücking (1999) reported more than 250 species of lichenized fungi from a single locality in an Amazonian rain forest, with more than 80 species occurring on a single, medium-sized palm leaf.

Myxomycetes (plasmodial slime moulds) are well-known inhabitants of decaying plant material such as wood and litter, where the majority of the ca. 900 species known world-wide can be found

(Mitchell 1999). Both of the two trophic stages - the unicellular myxamoebae and a distinctive multinucleate structure, the plasmodium - feed upon bacteria, yeasts and other microorganisms.

During a study of myxomycete ecology carried out in Costa Rica, an effort was made to screen all available microhabitats for the occurrence of myxomycetes. Among others, ten moist chamber cultures were prepared with small pieces of living leaves covered by liverworts from the cloud forest at Monteverde. All ten cultures yielded myxomycetes, although often with only 1 to 5 tiny sporocarps present. The present study was undertaken to investigate epiphyllous liverwort covers as a possible new microhabitat for Neotropical myxomycetes.

Materials and methods

Study sites

Four different types of evergreen rain forests, ranging from lowland to high Andean cloud forests, were investigated. For each locality, forest type and structure of the vegetation are described, emphasising in particular features that might influence myxomycete diversity. All study sites represent primary forests, with no or only a very limited degree of human disturbance.

In Ecuador, three sites were sampled in November 1998, the first month of the rainy season. All are situated within an elevational gradient in the western Andean cloud forests of the Macquipucuna Reserve near the small town of Calacalí, ca. 40 km W of Quito (Pichincha Province).

Site 1 (abbreviation *Ec1*) is a SW-exposed valley slope of a side creek of Rio Tulambi, along the Palmitos Trail ca. 2.5 km SE Marianitas (ca. 1.15 km SW of the Macquipucuna Foundation Lodge), elev. 1300 ± 75 m (00°07'15" N, 78°38'05" W ± 250 m). The annual rainfall is about 2500 mm (2453 mm registered at the village of Nanegalito, ca. 5 km SW and situated at roughly the same elevation). In spite of this rather high value, the influence of a dry season is still remarkable, with less than 100 mm average monthly rainfall from May to November. Leaves of understory shrubs as well as the litter layer can dry out almost completely during a week with no rains. Nevertheless, the continuously humid atmosphere in the river valley supports leaves with dense but not totally closed covers of epiphyllous liverworts, more rarely lichens. The forest canopy was closed except for a few treefall gaps, formed by evergreen trees with medium to large leaves. The forest at this site can be assigned to the Tropical Moist Forest in the classification of Holdridge et al. (1971).

Site 2 (*Ec 2*) is located near the NNW-exposed first summit of the Cerro de Sosa massive, ca. 6 km SE Marianitas (ca. 3.5 km S Macquipucuna Foundation Lodge), elev. 1900 ± 150 m (00°05'40" N, 78°37'00" W ± 1 km). Annual rainfall can be estimated at between 3300 and 3700 mm, and daily cloud exposure is also common during the dry season. Leaves of understory plants were usually covered with almost closed mats of epiphyllous liverworts, with lichens occurring only rarely on younger leaves. The forest canopy was formed by tall evergreen trees; members of the Clusiaceae, Cunoniaceae and Lauraceae were most abundant. The canopy was almost completely closed. In the Holdridge classification, this would be a Tropical Premontane Wet Forest.

Site 3 (*Ec3*) is located near the highest summit of the reserve, Cerro Montechristi, ca. 20 m below the top of a ridge running SW to NE, ca. 5.7 km NW of the village of Yunguillas (ca. 2 km NW of 'Rolandos Finca'), elev. 2720 ± 75 m, (00°03'15" N 78°35'55" W ± 500 m). Annual rainfall is very probably between 3500 and 4000 mm, with daily, long periods of cloud exposure also occurring during the dry season. Relatively strong winds allow epiphyllous liverworts to grow only in sheltered sites, but then with almost closed mats. Long curtains of epiphytic mosses, together with a lush epiphyte cover of bromeliads, ferns and members of the Cyclanthaceae are characteristic of this cloud forest. Forest floor litter stays continuously wet, and leaf surfaces of understory plants dry out only for a short period during the day (or stay continuously wet). The trees are small, 10–20 m tall, and the canopy is only about 70% closed. In the Holdridge system, this would be a Tropical Lower Montane Rain Forest.

In Costa Rica, two sites were sampled in March 1999 (end of the dry season). The first of these was a lowland forest and the second a montane cloud forest. Site 1 (*CR1*) is situated at the La Selva Biological Station of the rain forest reserve of the Organisation of Tropical Studies (Province Heredia, near Puerto Viejo), between 500–800 m of the Camino Experimental Sur, elev. 50 ± 25 m (10°25'53" N 84°00'26" W ± 150 m). This is a tall evergreen forest rich in subcanopy and understory palms, thus providing excellent conditions for foliicolous liverworts. Annual rainfall is 3991 ± 748 mm (measured over 22 years); with no effective dry season. Almost all understory plants have liverwort-covered leaves, with especially pronounced and closed layers present on older palm leaves. The forest is a very diverse Tropical Wet Forest in the Holdridge classification (Tosi 1969).

Site 2 (*CR2*) is a part of the Monteverde Reserve of the Tropical Science Center (Puntarenas Province) at the Sendero Bosque Nuboso ca. 3.5 km SSE of the Santa Elena settlement, near the Continental Divide, elev. 1530 ± 200 m (10°17'55" N 84°47'00" W ± 500 m). Due to the trade winds, clouds prevail most of the year; the annual rainfall is probably higher than 3000 mm. Similar to the situation at the highest sampling site in Ecuador, plants in sheltered sites have a rich epiphyll cover, mostly consisting of liverworts. Trees are stout, often not exceeding 15 m in height, but the canopy is nearly closed. The respective Holdridge Life Zone is the Tropical Lower Montane Rain Forest (Tosi 1969).

The Puerto Rican site (*PR*) is the Elfin Forest at El Yunque Trail in the Luquillo Mountains (elev. 900 ± 200 m, 18°18'20" N 65°47'40" W ± 250 m), situated ca. 300–500 m NNW Mt. Britton. The site is described in detail in Stephenson et al. (1999). Annual rainfall measured at the nearest weather stations is between 3848 (Rio Blanco, elev. 546 m) and 4209 mm (Pico del Este, elev. 1051 m); the area is classified as Tropical Lower Montane Rain Forest (Brown et al. 1983). In comparison with the other five sites, the forest is much more open due to hurricane influence. Most trees have small, thick and coriaceous leaves, especially the most common trees at the sampling site (*Tabebuja rigida* Urban, Bignoniaceae, and *Calyptranthes krugii* Kiaersk, Myrtaceae). The site was visited in February 2000, during an unusual dry spell including almost two weeks with no cloud coverage.

Sampling

For each studied locality, three in Ecuador, two in Costa Rica and one in Puerto Rico, about 20 moist chamber cultures were prepared. The material for each culture was collected over a distance of approximately 10 m along a transect 200–250 m in length and 6 m in width (3 m to the left and right of a small trail or a baseline marked with a rope). Scissors were used to cut pieces of ca. 1.5 by 1.5 cm from living leaves of understory shrubs and treelets, more rarely tall herbs. The main criterion for this study was that leaves were alive, found at a height of at least 1 m, and have at least a 60% coverage of epiphyllous liverworts and/or lichens. Occasionally occurring leaves with small pillows of apparently non-foliicolous mosses (e.g. *Orthotrichum*) that can accumulate larger amounts of detritus particles were excluded. Within one 10 m sector of a transect, 15–25 leaf pieces were sampled, each originating from a randomly selected and different individual plant. The most commonly sampled plants were small understory palms (Arecaceae, in particular members of the genera *Chamaedorea* and *Geonema*), leathery leaves of small understory shrubs (often members of Rubiaceae), epiphytic Cyclanthaceae (mostly *Asplundia* spp.), and fronds of various terrestrial ferns. All sampled leaves grew within 1 and 2.5 m height above ground under a mostly closed canopy. Leaf pieces were immediately placed in paper bags and allowed to dry out gradually without applying heat or using a dehydrator.

Moist chamber cultures

All moist chamber cultures were set up within a week after returning from the respective study site. About 15 leaf pieces from a 10 m section of a transect were placed on three layers of filter paper in one Petri dish, with the epiphyll-covered leaf surface up. Cultures were moistened with distilled water adjusted to pH 7.0. After 24 h, all leaf pieces were saturated with water and lay flat on the filter paper. Excess water was then poured off, and the pH of the wet liverwort cover was measured with a solid state electrode, using an Orion model 610 pH meter. For each culture, pH was determinated for three randomly chosen leaf pieces. Cultures were maintained in a greenhouse up to three months under diffuse light at a temperature of 22–25 °C and checked five times (days 6, 14, 28, 47 and 81 after excess water was poured off). All myxomycete species and their abundances (as numbers of sporocarps developed) were recorded.

Species identification and data evaluation

Mature sporocarps were air-dried and mounted in small boxes. In addition, permanent slides were prepared using polyvinyl lactophenol as a mounting medium. Due to the lack of pigments, sporocarps of *Arcyria* were mounted in polyvinyl lactophenol mixed with methylene blue, to stain capillitium and spores. Specimens are deposited in the private collection of the author at the Herbarium Haussknecht, Jena (JE). In addition, duplicates were placed in the herbarium of Fairmont State College (FWVA). Descriptions of specimens use the terminology of Lado & Pando (1997), with colours described according to Kornerup & Wanscher (1981).

To estimate to what extent the survey was exhaustive in terms of recorded species, a bootstrap analysis, as explained in detail in Schnittler & Stephenson (2000), was carried out. The sequence of samples (moist chambers) was permutated randomly, and the number of recorded species was plotted against the number of moist chambers (samples). When plotting record numbers versus samples for the mean of 100 runs, the number of records increased in a nearly linear fashion with the numbers of samples, indicating that 100 runs are sufficient for the analysis. The mean of 100 plots of species versus samples was then 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.

Results

A high proportion (127 out of 131 or 97%) of the prepared moist chamber cultures was positive for myxomycetes (Table I). Excluding the doubtful records of *Comatricha pulchella* and *Physarum pusillum*, only eleven species of myxomycetes were recorded. Three of these (*Arcyria cinerea*, *Didymium iridis* and *D. squamulosum*) were very common. Occasionally found throughout the study were *Lamproderma scintillans*, *Diderma effusum*, *D. hemisphaericum* and *Physarum compressum*, whereas all other recorded myxomycetes were rare. Most species appeared with very small sporocarp numbers (Table II). This phenomenon was correlated with the frequent occurrence of solitary dwarf sporocarps. Fructifications consisting of a single sporocarp were not unusual. Correlating with this, microscopically small plasmodia were frequently observed in the cultures; sometimes several separate plasmodia appeared on different leaf pieces within a moist chamber. Among the seven fairly common species, differences in development time were found, with the three very common species developing faster than the four less common ones (Table II). After day 81, no new sporocarps developed. This coincided with the decay process of the leaf pieces in the moist chambers. The green chlorophyll colour was still clearly visible until day 28 and, except for small and very local outgrowths of apparently endophytic fungi, no fungal contamination was observed. Later, the leaf pieces turned black and started to decay. At day 47, all leaf pieces were black and very soft, but mostly not overgrown with fungi. At day 81, dense lawns of hyphomycetes were not uncommon on the decaying leaf pieces.

Table I. Summary data for the six series of moist chamber cultures prepared with leaf pieces overgrown with epiphyllous liverworts, with abbreviations for the study sites as mentioned under Material and methods.

Study site	*Ec1*	*Ec2*	*Ec3*	*CR1*	*CR2*	*PR*
Elevation (m)	1300	1900	2720	50	1530	750-900
Annual rainfall (mm)	2500	3300-3700	3500-4000	4000	>3000	3800-4200
Number of cultures	21	20	20	28	23	19
pH (mean ± SE)	7.44± 0.05	7.86 ± 0.08	7.27 ± 0.09	7.08 ± 0.08	7.46 ± 0.12	5.91 ± 0.60
% positive cultures	100	100	85	100	96	100
Number of records	52	51	33	82	59	40
Average number of records per culture	2.48	2.55	1.65	2.93	2.57	2.11
Number of species	5	6	5	7	7	9

Table II. Number of records, mean sporocarp numbers with standard error, and average developmental time for the seven more common myxomycete species. Given is the number of records where the highest number of sporocarps was counted on the respective day. Data from the six study sites are pooled. Numbers referring to the peak day for the occurrence of the respective species are printed in bold.

Myxomycete species	Number of records	Mean number of sporocarps	Development time, days 6	14	28	47	81
Arcyria cinerea	78	7.0 ± 1.4	-	**41**	20	16	1
Diderma effusum	12	11.5 ± 3.9	-	3	-	4	**5**
Diderma hemisphaericum	11	3.8 ± 0.8	-	2	-	4	**5**
Didymium iridis	87	10.2 ± 1.4	1	**72**	13	2	-
Didymium squamulosum	88	7.9 ± 0.9	-	**54**	24	9	-
Lamproderma scintillans	10	29.5 ± 8.7	-	-	1	**8**	1
Physarum compressum	16	6.4 ± 1.8	-	2	**8**	6	-

In the following annotated species list, the symbol '?' indicates species represented by scanty or immature records only that did not allow a definitive determination. For a few taxonomically interesting records a collection number is given. In parentheses, the number of records for each study site is indicated (bold face), with the mean number of sporocarps and the respective standard error following after a slash.

Arcyria afroalpina Rammeloo – **1** record (13722, *Ec3*, **1**/11).

Sporocarps scattered over several pieces of leaves in one moist chamber culture, always solitary and displaying a remarkable variation in size. Stalk long and slender, often twisted, (0.3-)0.7-1.4 mm long, at the base 70-100, on top 50-70 µm wide; arising from a very small, disk-like hypothallus, in colour like the ochraceous-yellow (4B4) sporotheca; the whole lumen densely filled with spore-like cells, these often deformed by mutual pressure, globose to ellipsoid and (13-)15-20(-23) µm diam. Sporothecae globose to subglobose, (0.15-)0.25-0.55 mm diam., with a small calyculus (130-)150-250 µm diam., which is present in small sporocarps only as a

collar-like extension of the stalk, smooth. Capillitium firmly attached to the calyculus, not expanding in mature sporocarps, consisting of a branched network of thin threads, (1.3-)1.6-2.2(-2.6) µm wide, colourless under transmitted light, wrinkled and ornamented with scattered to dense warts in an irregular pattern. Spore mass the same colour as the sporotheca, spores colourless under transmitted light, globose, and almost regularly covered with warts, (10.2-)10.4-11.5(-12.0) µm diam.

Comparisons with the excellent description given by Rammeloo (1981a, b) as well as his specimen 4997 (isotypus) leave no doubt that the Ecuadorian specimen represents *A. afroalpina*, the first record of this species outside the East African Mountains. For the specimens of *Arcyria* found in the present study, this was the only one with ochraceous sporocarps. All characters match the original description, except for the slightly thinner capillitium (described as 1.8-3.0-4.5 µm wide).

Arcyria afroalpina was recorded several more times in samples of aerial and forest floor litter from the Ecuadorian as well as from the Costa Rican sites. Whereas the epiphyllous specimen mentioned above is undoubtedly *A. afroalpina*, several specimens morphologically intermediate between *A. afroalpina* and *A. cinerea* were found on litter. Such forms also were mentioned by Rammeloo (1981b) for the East African mountains.

Arcyria cinerea (Bull.) Pers. – **78** records(*Ec1*, **20**/5.4 ± 1.9; *Ec2*, **17**/4.6 ± 1.1; *Ec3*, **4**/2.2 ± 0.3; *CR1*, **20**/9.9 ± 4.8; *CR2*, **15**/8.0 ± 2.2; *PR*, **2**/25.0 ± 18).

Appearing regularly as solitary, widely scattered sporocarps varying considerably in size, always on slender stalks filled with spore-like cells (9-)12-15(-18) µm diam. Stalks very different in length: (0.4-)0.7-1.0(-1.25) mm, (18-)23-55(-60) µm wide at the base and roughly the same diameter on top, with inconspicuous, disk-like hypothalli. Sporothecae light grey (4B1) to creamy white (4B1-4A1), seldom pure white, globose in small sporocarps but elongated and almost cylindrical in larger ones, (0.1-)0.2-0.27(-0.4) mm wide, (0.12-)0.25-0.45(-0.75) mm high. Calyculus small and disk-like to shallowly cup-shaped, (80-)120-550(-700) µm wide, plicately folded and minutely rough, colourless under transmitted light. Capillitium in larger sporocarps almost smooth at the base and clearly warted at the apex of the sporotheca, but more irregularly ornamented and not differentiated in dwarf sporocarps, (1.3-)1.5-2.0(-2.5) µm diam. Spore mass the same colour as the sporotheca, colourless under transmitted light, almost smooth or with single, widely scattered warts, typically 6.5-8.5 µm diam., but some specimens deviated by larger spores 8-10.5(-11) µm diam.

Although the specimens with larger spores may represent intermediate forms between *Arcyria afroalpina* and *A. cinerea*, three characters allow all specimens to be assigned to *A. cinerea*. These are the always grey to cream, never ochraceous colour, the occurrence of larger sporocarps with the elongated and cylindrical sporothecae, and finally the dimorphous capillitium described by Härkönen (1977) as typically for *A. cinerea*. Further investigations, including also specimens from aerial and forest floor litter, are necessary to draw a clear demarcation between *A. afroalpina* and *A. cinerea*.

Comatricha* ? *tenerrima (M.A. Curtis) G. Lister – **2** records (13910, *Ec2*, **1**/2; 17544, *PR*, **1**/1).

Both specimens did not mature well and do not allow a definite determination.

Diachea leucopodia (Bull.) Rostaf. – **1** record (17095, *PR*, **1**/52).

A species commonly seen on ground litter in Puerto Rico, here appearing on day 28 on the partly decayed leaf pieces.

Diderma effusum (Schwein.) Morgan – **12** records (*Ec2*, **1**/6; *CR1*, **3**/1.3 ± 0.5; *PR*, **8**/29.1 ± 17.5). Occurring with very short sporocarps. The specimens from Costa Rica have spores (7.8-)9-12(-12.5) µm diam., larger and darker than usually reported for *D. effusum*.

Diderma hemisphaericum (Bull.) Hornem. – **11** records (*Ec1*, **1**/3; *CR1*, **1**/5; *CR2*, **3**/3.0 ± 1.1; *PR*, **6**/4.2 ± 1.5).

Found as small groups of gregarious sporocarps, often accompanied by sessile ones.

Didymium difforme (Pers.) S.F. Gray – **3** records (*Ec2*, **1**/2; *CR2*, **2**/4.0 ± 1.0).

Although usually reported as occurring with plasmodiocarps, this species was seen only with very small sporocarps.

Didymium iridis (Ditmar) Fr. – **88** records (*Ec1*, **14**/8.4 ± 3.1; *Ec2*, **15**/12.4 ± 3.7; *Ec3*, **13**/5.1 ± 1.2; *CR1*, **26**/17.7 ± 3.6; *CR2*, **12**/2.8 ± 0.5; *PR*, **8**/5.2 ± 1.6).

Almost all fructifications consisted of widely scattered and solitary sporocarps that varied remarkably in size. Often dwarf sporocarps appeared, with stalks shorter than 0.3 mm and sporothecae less than 0.15 mm diam. The spores are slightly darker than typical for this species, and the columella is often poorly developed. Evenly spaced lime crystals give the surface of the sporotheca a powdered appearance, which makes the species clearly distinguishable from *D. squamulosum* in general habit.

Didymium squamulosum (Alb. & Schwein.) Fr. – **87** records (*Ec1*, **14**/4.9 ± 1.1; *Ec2*, **16**/7.5 ± 2.4; *Ec3*, **9**/8.6 ± 2.7; *CR1*, **21**/10.9 ± 2.4; *CR2*, **19**/5.1 ± 1.0; *PR*, **8**/18.8 ± 8.6).

As it was the case for the previous species, widely scattered, often minute sporocarps were regularly found, perhaps arising from separate small plasmodia. All specimens had lime crystals forming a flaky crust.

Lamproderma arcyrionema Rostaf. – **1** record (17435, *PR*, **1**/22).

A species very common on dead, aerial litter especially of *Heliconia* and *Musa* in all regions studied. The single specimen appeared after 49 days of culture on the already decayed leaf pieces.

Lamproderma scintillans (Berk. & Broome) Morgan – **10** records (*Ec1*, **1**/4; *CR1*, **6**/36.2 ± 13.0; *CR2*, **2**/27.0 ± 20.0; *PR*, **1**/20).

Occurring in groups of gregarious, never scattered, sporocarps with the typical characters of this species, commonly found in ground and aerial dead litter.

Physarum compressum Alb. & Schwein. – **16** records (*Ec2*, **1**/1; *Ec3*, **5**/11.2 ± 4.8; *CR1*, **6**/3.8 ± 1.9; *CR2*, **3**/6.0 ± 2.1; *PR*, **1**/5).

Small groups with gregarious, stalked and laterally flattened sporocarps were most common; minute and/or sessile sporocarps were mostly accompanied by typical ones.

Physarum* ? *pusillum (Berk. & M.A. Curtis) G. Lister – **1** record (*CR1*, **1**/2).

The single specimen did not mature well, thus leaving the determination doubtful.

Discussion

Until now, living leaves of rain forest plants were not known as a microhabitat for myxomycetes. However, independent of the present study, Eliasson (1999) detected myxomycete fructifications on herbarium specimens of vascular plants from Ecuador, collected without regard to the occurrence of epiphyllous organisms. He was the first to indicate a possible importance of living leaves as myxomycete microhabitats. Interestingly, none of the five species he reported was found in this study. Unfortunately, the poor data accompanying the herbarium collections do not allow one to determine whether these are truly epiphyllous species or simply fructifications from plasmodia migrating to the leaves from another microhabitat.

Compared with other microhabitats as leafy litter on the forest floor or bark of living trees, epiphyllous liverwort communities seem to be generally much poorer in numbers of myxomycete species (Schnittler & Stephenson 2000). The bootstrap analysis for the completeness of the survey predicts 11.3 species, with 11 found among the 317 myxomycete records from 131 cultures prepared (six records are from unidentified plasmodia which failed to develop into fructifications). As such, the data fitted well with a saturation model (Fig. 1). Therefore, the number of moist chamber cultures (including almost 2000 leaf pieces) can be regarded as sufficient to detect all of the more common

species. However, due to the heterogeneity of the study sites, reaching from Wet to Lower Montane Rain Forest and spanning an elevational gradient from 50 to 2700 m, the species inventory of the study sites varies somewhat. The site with the most disturbed forest, Puerto Rico, harboured the highest number of species (9). The bootstrap analysis, performed with the pooled records from all six sites, does not consider this heterogeneity.

On the other hand, all six sites clearly share an assemblage of common species (Fig. 2). The average frequency of the three most common species on epiphyllous liverwort covers was surprisingly high, with 0.59 for *Arcyria cinerea* and 0.66 for both *Didymium iridis* and *D. squamulosum* (Fig. 2). At least the three most common species of myxomycetes (*Arcyria cinerea*, *Didymium iridis* and *D. squamulosum*) are very probably regular inhabitants of liverwort-covered leaves. Several lines of evidence seem to support this. First, all three species were found with very scattered and often solitary sporocarps considerably smaller than typical for fructifications of these species in other microhabitats. In addition, tiny phaneroplasmodia 1–3 mm in extent were frequently observed in the first two weeks of culture. Plasmodia migrating from the litter layer to fruit on living plants are much larger, and their

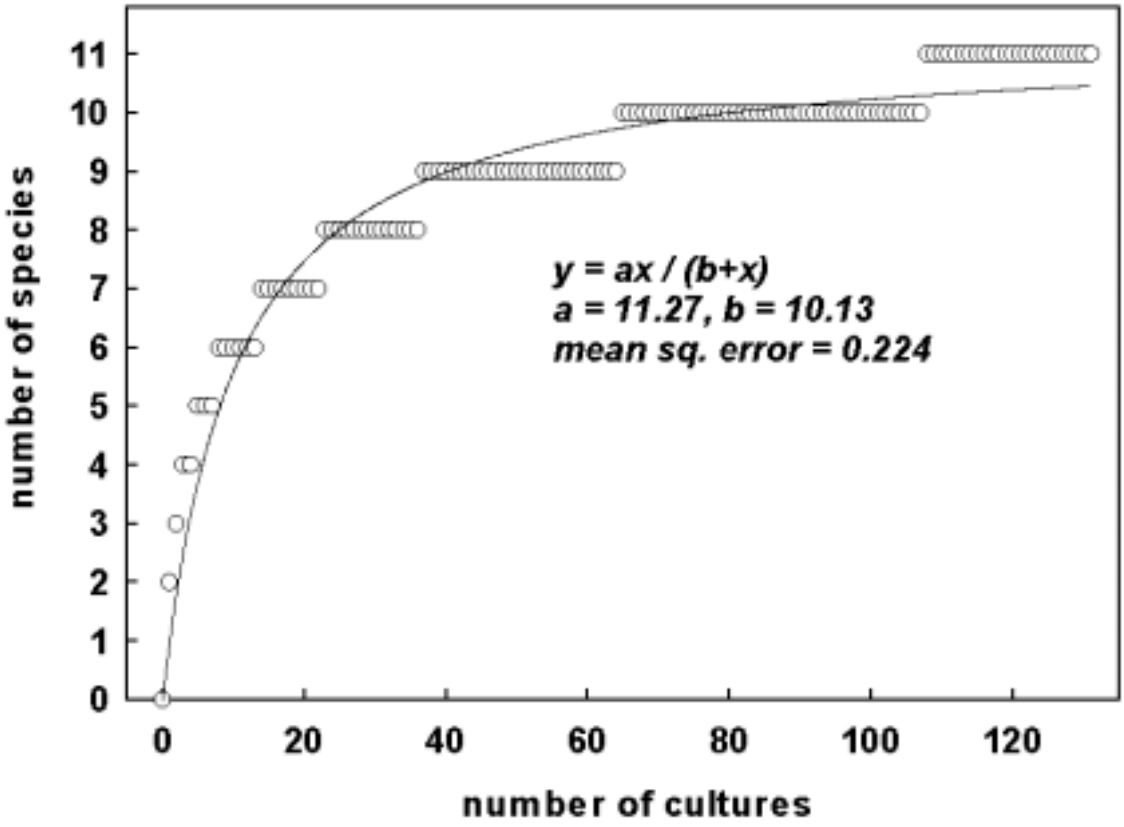

Fig. 1. Bootstrap analysis of the randomly permutated sequence of samples (moist chamber cultures) versus accumulated species numbers (open circles). The presented values are the mean of 100 runs. The solid line shows the result of a regression analysis using a saturation function. In this model, *a* is the maximum number of species to be expected.

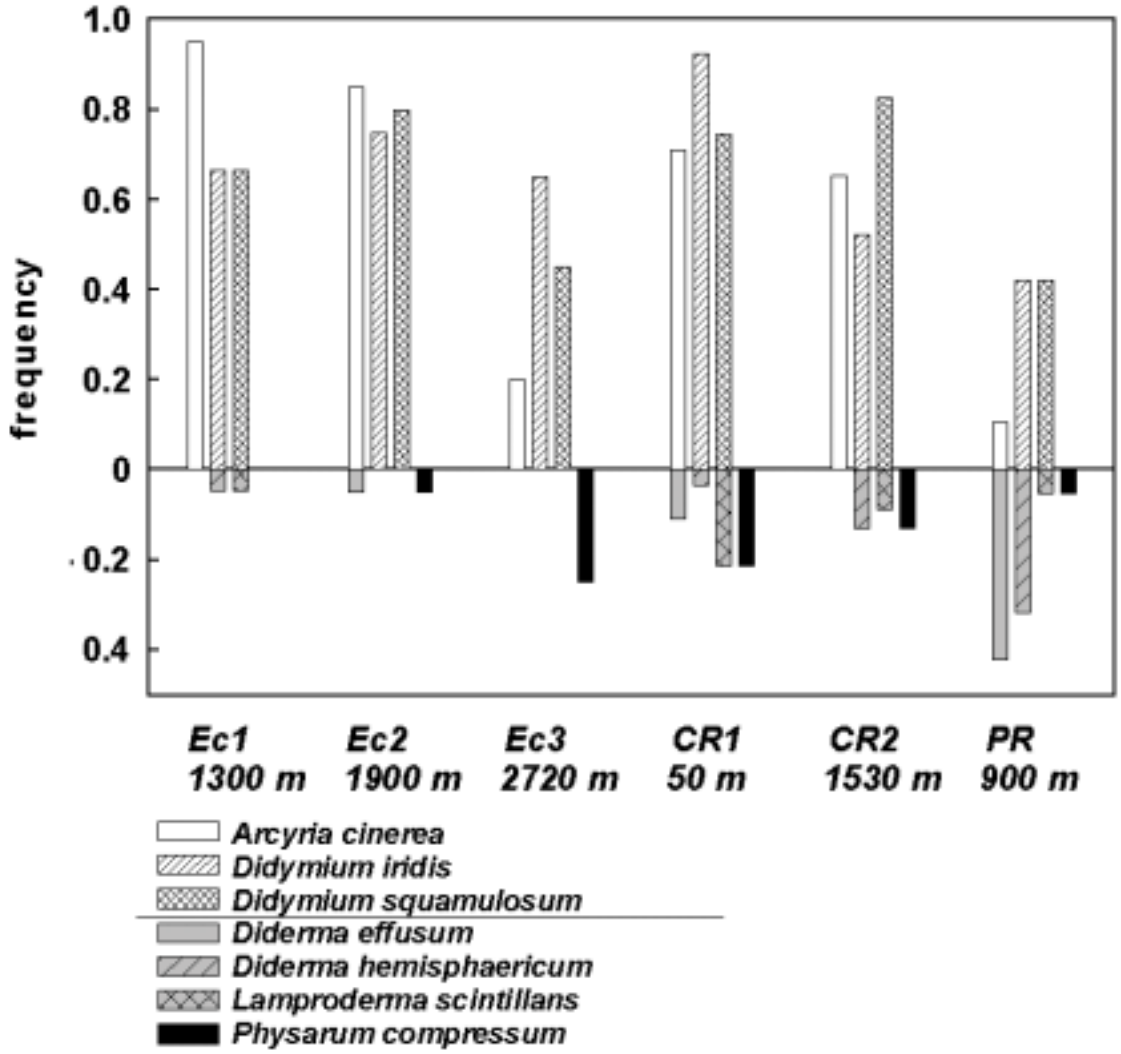

Fig. 2. Frequencies of the three most common myxomycete species (upper part) and the four less commoner species (lower part) in the moist chamber series from each of the six study sites (abbreviations as explained in Materials and methods).

presence on the leaf surfaces would have been easy to detect during the first days of culture. Second, the high frequencies of the three species in the cultures almost exclude the possibility that migrating plasmodia of litter myxomycetes were collected with the leaf pieces. Third, the sporocarps of *Arcyria cinerea* deviate considerably from the typical form of this species. Such differences include the very small size, the very pale, almost white colour and spores that were often found to be larger than usual for *A. cinerea*. Although modifications caused by the extreme conditions of the microhabitat cannot be ruled out, these forms may represent a separate biospecies. Fourth, in the majority of the cultures, fructifications were seen after 14 days (Table II). Although sporocarps may develop from spores in pure culture in a week (J. Clark, pers. comm.), this short development time points towards the presence of myxamoebae and microcysts on the leaves and makes it less likely that the leaves

function as a pure spore trap. Lastly, all three of the most common myxomycetes developed often sporocarps before the decay process of the leaves began, as indicated by the still green colour of the leaf pieces at day 14. Therefore, small populations of myxamoebae can assumed to be present among the epiphyllous liverworts and lichens on the leaf surfaces; perhaps the amoebae prey upon bacteria or unicellular algae in this microhabitat. The occurrence of mostly dwarf sporocarps, often correlated with the presence of tiny plasmodia, points towards a low nutrient supply. On the other hand, myxobacteria, especially members of the genus *Myxococcus*, developed on the leaf pieces with high frequencies (0.86, 0.95, 0.90, 0.54, 0.83 and 0.37 in the culture series from sites *Ec1*, *Ec2*, *Ec3*, *CR1*, *CR2* and *PR* respectively). This indicates a rather rich microbial flora on the leaf surfaces that should supply enough bacteria to sustain small populations of myxamoebae. The presence of myxamoebae does not necessarily mean that fructifications will occur under field conditions, since such myxamoebal populations may survive indefinitely by cell division (Clark 1992). A direct leaf-to-leaf dispersal of myxamoebae as well as their dormant stages (microcysts) by rainwater or leaf-dwelling insects is conceivable.

Whereas the three most common species of myxomycetes are probably present as populations of myxamoebae, the occurrence of the four less commoner species (*Lamproderma scintillans*, *Diderma effusum*, *D. hemisphaericum* and *Physarum compressum*) may result from spores trapped by the epiphyll-covered leaf surfaces. Evidence for such an assumption can be derived from several facts. First, these four species appeared almost an order of magnitude more rare then the three most common species. Second, they had often a much longer developmental time (Table II), which makes the development from spores possible. Third, at least the colonies of *Lamproderma scintillans* were significantly larger, and consisted of gregarious colonies of sporocarps, which points towards the utilisation of decaying leaf material. The sporocarps of the epiphyllous frutifications were mostly of the size typical for the species and showed no significant deviations in morphological characters.

Among the six localities investigated, the Tropical Wet Forest of La Selva (*CR1*) seemed to provide the best habitat conditions for epiphyllous myxomycetes, followed by the two Ecuadorian sites having Tropical Moist Forest (*Ec1*) and Tropical Premontane Wet Forest (*Ec2*). The three sites located at a high elevation in relation to the latitude (*Ec3*, *CR2* and *PR*, all Tropical Lower Montane Rain Forest) showed lower frequencies of epiphyllous myxomycetes. Although still supplying almost closed epiphyllous covers on some leaves, especially of liverworts, the wind-exposed and hurricane-battered ridges of the Luquillo Experimental Forest in Puerto Rico showed the lowest myxomycete frequencies. However, it had with nine species the highest diversity, undoubtedly resulting from litter species which where able to develop on the thick, decaying leaves of the Elfin Forest trees. Except for this site, the average pH values of all cultures were fairly similar (Table I). In all cases, pH values were higher than those measured for forest floor litter from the same study sites.

When considering the species involved, none of the myxomycetes found in this study seems to be specialized for living leaves as a microhabitat. *Arcyria cinerea* was found in the typical form (with much larger, longer and dark grey sporocarps) as well as in the var. *digitata* Schwein. to be common on wood from the same study sites. All seven myxomycete species more common in this study were found to occur in forest floor litter from the same localities (unpubl. data) and were observed regularly in a moist chamber study of forest floor litter from Puerto Rico (Stephenson et al. 1999). *Arcyria afroalpina* is a new record for the Neotropics, but more collections of this species were made from aerial litter than from living leaves (unpubl. data). However, the epiphyllous specimens of *A. cinerea*

differed in a number of characters from the typical, wood-inhabiting forms; also the sporocarps of *Didymium iridis* were smaller and had darker spores than typical for this species. For *D. iridis*, the only one of the three most common myxomycete species grown extensively in pure culture, a mixture of mostly geographically-based sibling species and nonheterothallic (presumably apomictic) lines was detected in comprehensive mating experiments (Clark & Mires 1999). Consequently, the existence of specialized epiphyllous biotypes of myxomycetes may be conceivable. The observed deviations in morphological characters from the typical form of a particular species (especially in *Arcyria cinerea*) provide some evidence to support such an assumption. More studies, such as axenic culture of epiphyllous *Didymium* specimens and moist chamber cultures of twigs with leaves kept alive by watering are necessary to understand more completely the ecology of epiphyllous myxomycetes.

Acknowledgements

I thank all Costa Rican and Ecuadorian authorities for helping us to organise the field work. Special thanks go to the resident biologists of the Macquipucuna and Monteverde Reserves, Mike Dilgers and Bob Carlson, as well as Dr J. Lodge (Center for Forest Mycology Research, USDA Forest Service, Puerto Rico) for logistical help and useful recommendations for choosing study sites. I am indebted to Dr J. Rammeloo (National Botanic Garden of Belgium, Meise) for providing a loan of the isotype of *Arcyria afroalpina*. I owe thanks to Dr U. Eliasson (University of Göteborg, Sweden) for valuable comments, and to Dr O. Petrini for his interesting review of this paper. I am most grateful to Dr S.L. Stephenson (Fairmont State College, WV, USA) for continuous encouragement and proof-reading of the manuscript. This research was supported by a grant from the National Science Foundation (DEB-9705464).

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Received 4 February 2000, accepted in revised form 25 July 2000.

Chapter 12. Inflorescences of Neotropical herbs as a new microhabitat for Myxomycetes

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Mycologia (in review)

Abstract: An assemblage of myxomycetes associated with the inflorescences of large Neotropical herbs, a microhabitat not previously known to support these organisms, is described and characterized ecologically from a number of study sites in Costa Rica, Ecuador, and Puerto Rico. Thirty-one different taxa were represented among the 652 specimens of myxomycetes recorded in the field or obtained from 358 moist chamber cultures prepared with decaying floral parts. When these data were compared with comparable data obtained from 696 moist chamber cultures prepared with other kinds of litter from the same study sites, thirteen species of myxomycetes were found to be relatively more common in the inflorescence microhabitat and six of these exhibit a strong preference for this microhabitat. Three of the six species are new records for the Neotropics. Correspondence analysis of the data set compiled for inflorescences indicated that the assemblage of species present is relatively consistent across all of the various study sites. At least two of the species (*Physarum compressum* and *Ph. didermoides*) most commonly encountered prefer a substratum with a very basic pH. The actual myxomycete substrata in inflorescences are the rapidly decaying floral parts enclosed by the massive, still living bracts. Very probably, leftovers of floral nectar or secrete from extrafloral nectaries, which occur in *Heliconia* and the species of *Costus* investigated in this study, provide the basic resource for a rapidly developing community of yeasts and bacteria. A high density of these organisms is suggested by the frequent occurrence of myxobacteria in the moist chamber cultures prepared with floral parts. Results from canonical correspondence analysis indicate that a substratum pH between 8 and 9 and the presence of massive, compact inflorescences on plants occurring at lower elevations in localities with moderate annual rainfall provide optimal conditions for the assemblages of inflorescence-inhabiting myxomycetes. An incidental method for the dispersal of myxomycete spores by birds that pollinate the flowers or feed upon the fruits seems possible and may account for the high degree of preference exhibited by some of the inflorescence-inhabiting myxomycetes, for which the term "epiflorous" is proposed.

Key Words: ecology, inflorescence, Neotropics, slime molds

Introduction

Myxomycetes (plasmodial slime molds) are common inhabitants of various kinds of decaying plant material, with about 970 species known worldwide (Mitchell 1999). Well-known substrata for myxomycetes are decaying wood, forest floor litter, or the dung of herbivorous animals. However, these substratum types, which have been the focus of almost all published studies of myxomycete diversity, were found to be relatively poor in terms of both species abundance and diversity in tropical forests (Schnittler and Stephenson 2000). On the other hand, several types of aerial litter, such as fallen leaves trapped in tree branches or dead but still attached leaves of *Heliconia*, proved to be productive for myxomycetes in moist chamber cultures. Moreover, during field surveys in Costa Rica and Ecuador, myxomycete fructifications were observed rather frequently on the living inflorescences of large tropical herbs. The primary objective of the study reported herein was to investigate the assemblage of species of myxomycetes occurring in this new microhabitat, including field observations as well as results obtained from moist chamber cultures.

Materials and Methods

Plants investigated.—One species of *Costus* (Costaceae), *Hedychium coronarium* (Zingiberaceae), three species of *Calathea* (Marantaceae), and eight species of *Heliconia* (Heliconiaceae) were included in the present study. Myxomycete fructifications were observed on inflorescences of most of these plants in the field. All 13 species are large herbaceous monocots with inflorescences ranging in height from approximately 1.0 to 3.5 m. In addition, one species of *Psychotria* (Rubiaceae) was found to support myxomycete fructifications in the field. The latter is a shrub about 1 to 3 m tall with densely clustered inflorescences on terminal branches, with each inflorescence framed by scarlet red bracts. The names of all of the species of plants investigated in this study along with brief descriptions of the general features of their inflorescences are provided in TABLE I.

Study sites.— Plants at nine different study sites in Costa Rica, Ecuador and Puerto Rico were investigated for the presence of inflorescence-inhabiting myxomycetes. The species of plants surveyed in the various study sites are listed in TABLE II.

The three study sites in Costa Rica are described in detail by Schnittler and Stephenson (2000). At La Selva (abbreviation *CR1*, biological station of the Organization of Tropical Studies, 10°25'N 84°00'W, elevation 40–80 m, mean annual rainfall 2700 mm) populations of several species of *Heliconia* occurring in the general vicinity of the station as well as in stream valleys and tree fall gaps were investigated. In the classification of Holdridge et al. (1971), La Selva belongs to the zone of Tropical Wet Forest. The second study site at Monteverde (*CR2*, Cloud Forest Reserve ca 3.5 km SSE of Santa Elena, 10°16'N 84°48'W, elev 1250–1350 m, annual rainfall ca 3800 mm) is classified as Tropical Premontane Rain Forest. One species each of *Calathea* and *Heliconia* were

studied, the latter in two subsequent years. The third study site is situated on the Atlantic coast near Cahuita (*CR3*, Cahuita National Park, 09°43'N, 82°49'W, elev 10–30 m, annual rainfall ca 2200 mm) and belongs to the Tropical Moist Forest zone. In an open swamp forest, two species of *Heliconia* and one species of *Calathea* was investigated.

In Ecuador, cloud forests on the western Andes and a lowland forest in the eastern portion of the country were visited. Three study sites are situated on the western slope of the Andes within the Maquipucuna Cloud Forest Reserve, located ca 40 km W of Quito (Pichincha Province, see Schnittler et al [2001] for a detailed description). The first study site (*Ec1*, 00°07'N, 78°38'W, elev 1250–1300 m, annual rainfall 2500 mm) is a Tropical Moist Forest, supporting one large species of *Heliconia*, several species of *Calathea*, and a tall species of *Costus* in tree fall gaps and clearings. The second study site (*Ec2*, 00°06'N 78°37'W, elev 1900 ± 150 m, annual rainfall ca 3500 mm) is a middle elevation cloud forest located near the NNW-exposed first summit of the Cerro de Sosa massive. In the understory of the forest, which can be classified as a Tropical Premontane Wet Forest, one small species of *Calathea* that is endemic to the Andes formed locally dense populations. A third study site (*Ec3*, 00°03'N 78°36'W, elev 2700 ± 175 m, annual rainfall ca 4500 mm), belonging to the zone of Tropical Lower Montane Rain Forest and located at Cerro Montechristi, the highest summit of the reserve, had no plants producing inflorescences suitable as microhabitats for myxomycetes. The Yasuni field station of the Pontifical Catholic University of Ecuador, located on the Rio Tiputini, a tributary of the Rio Napo, was chosen as a fourth Ecuadorian study site (*Ec4*, Prov. Napo, 00°38'S 76°36'W, elev ca 50 m, annual rainfall ca 2700 mm). This Amazonian lowland forest supports several species of *Heliconia* and the species of *Psychotria* investigated in this study. The forest at Yasuni is classified as Tropical Moist Forest.

In Puerto Rico, plants occurring in two study sites on the Luquillo Experimental Forest were investigated. The first was the general vicinity of the El Verde field station of the University of Puerto Rico (*PR1*, 18°20'N 65°49'W, elev 125–200 m, annual rainfall ca 2300 mm) with a tabonuco forest, classified as Tropical Premontane Wet Forest. At this study site, the only species of *Heliconia* indigenous to the island is fairly common in tree fall gaps and stream gullies. At a second study site, the Icacos valley in the Mt. Britton area (*PR2*, 18°16'N 65°47'W, elev 650–700 m, annual rainfall ca 3500 mm), margins of forest roads were often characterized by dense populations of the introduced herb *Hedychium coronarium*. The surrounding palo colorado forest belongs to the Tropical Premontane Rain Forest. Detailed descriptions of these sites can be found in Brown et al (1983).

Sampling.—Samples from a total of 358 inflorescences, each providing material for one moist chamber culture, were collected from 14 different plant species in all of the various study sites, with all field work carried out between 1998 and 2000. In addition, the same inflorescences, or sometimes more if the population of the respective plant species was large enough, were surveyed in the field for fructifications of myxomycetes. Soft, decaying floral parts, not the mostly massive and still living bracts or developing fruits, provided the material used for preparing moist chamber cultures. All cultures were prepared within a week after returning from the field, using disposable plastic Petri dishes lined with filter paper. Cultures were moistened with distilled water adjusted to pH 7.0. After 24 h, excess water was poured off and the pH of the wet substratum was measured with

a flat surface electrode, using an Orion model 610 pH meter. For each culture, pH was determined for three randomly chosen substratum pieces. Cultures were maintained in a greenhouse up to four months under diffuse light and at a temperature of 22–25 C and checked on five occasions (days 6, 17, 47, 81 and 109 after excess water was poured off). The number of sporocarps was counted or estimated for each colony of myxobacteria and myxomycetes observed in the field or in culture. Voucher specimens of myxobacteria and myxomycetes obtained from these cultures and from the field surveys are deposited in the herbarium of Fairmont State College (FWVA) and in the personal collection of the first author, which is stored at the Herbarium Haussknecht, Jena (JE). Nomenclature used for myxomycetes follows Martin and Alexopoulos (1969) with a few exceptions, where a reference to a protolog is given, whereas nomenclature for myxobacteria follows Reichenbach (1993). Names of vascular plants are given according to Berry and Kress (1991) for *Heliconia* and Jørgensen and León-Yánez (1999) for the other plant species mentioned.

For each myxomycete record, a number of biotic and abiotic parameters were measured directly, estimated or determined from published data and various other sources of information available at a particular study site. Site parameters were average annual rainfall and elevation, whereas microhabitat parameters included the sampling height above the ground, light intensity, wind exposure, and pH of the substratum. Summary data on these parameters, including the variation that existed among the plants studied, are given in TABLE I and II.

Element analysis.—Subsamples of dried leafy litter from 11 series of samples collected for moist chambers to be prepared with this substratum type and subsamples of dried flower parts from 9 series of samples collected for moist chambers to be prepared from material from inflorescences were sent to Brookside Laboratories (New Knoxville, Ohio) for analysis of element concentrations. Each subsample was obtained by pooling a small fraction (about one gram dry weight) of the material later used for each of the ca 20 moist chamber cultures making up one series. Samples were treated by standard nitric acid-perchloric acid digestion methods, modified slightly from the standard method in that a smaller sample weight and reduced acid amounts were utilized. Trace elements were analyzed on a thermo jarell ash inductively coupled plasma spectrometer (ICP).

Data analysis.—To estimate the completeness of the survey in terms of the species recorded, a bootstrap analysis, as described in detail by Schnittler and Stephenson (2000), was applied to the data set obtained from the moist chamber component of the survey. In brief, the sequence of samples (moist chambers) was permutated randomly and the number of recorded species was plotted against the number of moist chambers (samples). The mean of 100 plots of species vs samples was then subjected to a regression analysis, using a saturation formula $y = ax/(b+x)$, with the parameter a giving an estimate for the total number of species to be expected. Alternatively, a first-order jackknife estimation of species richness according to Heltsche and Forrester (1983) was carried out. The respective formula for the number of species S to be expected is $S = S_{obs} + ((n-1)/n) * S_{un}$, with S_{un} as the number of species observed in only one sample, S_{obs} the total number of species observed, and n as the number of samples.

For the correspondence analysis (CA) of the same data set, values of myxomycete frequency in a series of moist chambers prepared from the same plant species were used. An initial detrended correspondence analysis showed a length of gradient larger than 2, indicating an unimodal distribution of species scores. Accordingly, CA was

applied for the final analysis. Since a downweighting of rare species resulted in a similar ordination diagram, the basic diagram was used in the analysis. For the canonical correspondence analysis (CCA), each moist chamber culture was regarded as one sample, and weighted abundance values were calculated for each species of myxomycete by dividing the absolute number of sporocarps recorded in a particular culture by the mean value for all cultures yielding the same species. Consequently, the sum of all weighted abundances for all cultures with the species in question is equal to the number of records for this species. This equalizes the often very different fructification numbers of the species (compare TABLE III). Ordinations were carried out with the program Canoco (Ter Braak 1988). Each myxomycete record was coded for nine environmental parameters, using numerical values for elevation, annual rainfall, sampling height, pH, and length and diameter of the inflorescences. The arrangement of the bracts was quantified with a four-part scale (compare TABLE I). Light intensity over the course of a day was estimated using five categories ranging from complete darkness over various degrees of shade to full sunshine. Wind exposure was described using a scale consisting of four categories ranging from fully sheltered to strongly exposed. For CA, the resulting eigenvalues, ranging between 0 and 1, are a measure of the extent to which species distribution can be explained by the respective ordination axis (Ter Braak 1987). CCA was used to assess the relative importance of the recorded abiotic and biotic parameters. For the biplot presented as FIG. 3a, species scores and these of the environmental variables on the canonical axes were symmetrically scaled to mean 1 and sd 1. The centroids of the environmental variables were associated with species by the use of an Euclidian distance matrix.

Results

For the entire study, 732 records of myxomycetes from inflorescences were considered; 652 of these could be assigned with some certainty to a particular taxon. The remainder consisted of 10 indeterminable records, mostly remnants of old and weathered fructifications, and 70 plasmodia that could not induced to fruit in culture. About one-third (209) of the records are represented by field collections, whereas the other 453 were obtained from 358 moist chamber cultures prepared with decaying floral parts of the 14 species of plants investigated. Thirty-one different taxa of myxomycetes were recorded from the inflorescence microhabitat. The annotated species list that follows includes the 13 most common taxa (i.e., those represented by >5 records). For the record numbers given, the abbreviation "fc" indicates specimens observed in the field, whereas "mc" indicates records obtained from moist chamber cultures. Values for pH are given for both range and mean (± SE) for all records.

Arcyria cinerea (Bull.) Pers. (ARCcin, 13 records, fc 0, mc 13, pH 7.1 ± 0.5, range 6.5–7.9)

Our specimens represent the typical form of the species, having cream-white to gray, short to long-cylindrical sporothecae on stalks 1 to 1.5 times longer than the sporotheca. In almost all cases, the spores have a diameter of less than 8 µm and are ornamented with scattered, blunt warts.

This species was recorded from all countries and in four different study sites; it was found most often on *Heliconia latifolia* (*CR3*, 7 records). *Arcyria cinerea* is common on aerial and ground litter in most Neotropical forests.

Arcyria cf. *cinerea* (Bull.) Pers., dwarf form (ARCcin, dwarf, 30 records, fc 1, mc 29, pH 7.9 ± 0.7, range 6.5–9.2)

A detailed description of this taxon, which constitutes at least a distinct biotype, is provided by Schnittler (2001). It can be distinguished from typical specimens of *Arcyria cinerea* on the basis of the much smaller size, a pure white color, and a tiny, globose to elongated sporotheca on a stalk (3–)4–10 times longer than the sporotheca. The spores are often larger than 8 µm and more densely covered with warts. Since this taxon may intergrade with *A. afroalpina* Rammeloo, a thorough statistical analysis of characters is necessary before it can be described formally (Schnittler and Stephenson, in prep).

The taxon was observed on inflorescences of various species of plants from all of the sites investigated, but it was more common on other types of aerial litter (e.g. decaying leaves and palm fronds) as well as on covers of epiphyllous liverworts on living leaves.

Didymium iridis (Ditmar) Fries (DDYiri, 60 records, fc 7, mc 53, pH 8.2 ± 0.7, range 6.5–9.8)

Our specimens represent the typical form of the species. In contrast to the concept proposed by Clark and Mires (1999), specimens possessing a discoid pseudocolumella are separated under the name *D. bahiense* Gottsb., to maintain comparability with previous studies by other workers.

The species was found on various species of plants in all study sites except *Ec2* and *Pr2*. It is very common on all types of aerial litter.

Didymium squamulosum (Alb. & Schwein.) Fr. (DDYsqu, 28 records, fc 8, mc 20, pH 8.2 ± 0.6, range 6.7–9.2)

This species was found on various species of plants from all study sites except *Ec2* and *Pr2*. It is common on leafy litter, both aerial and ground.

Lamproderma arcyrionema Rostaf. (LAManm, 28 records, fc 0, mc 28, pH 7.7 ± 0.4, range 6.9–8.5)

Our specimens represent a form with very long, slender stalks.

With a few exceptions, this species was common only on the inflorescences of *Hedychium coronarium* (*PR2*, 25 of the 28 records). It is fairly common on aerial litter.

Perichaena cf. *dictyonema* Rammeloo (PERdic, 38 records, fc 0, mc 38, pH 8.5 ± 0.4, range 7.2–9.3)

The assignment of our specimens to this species is tentative. SEM micrographs and a more detailed taxonomic discussion are provided by Schnittler et al (2001). Specimens of *Perichaena* cf. *dictyonema* are very uniform in habit and clearly distinct from all other species of *Perichaena* encountered by us in the Neotropics. It seems to form fructifications on very moist substrata covered with a film of water. The small, globose sporothecae blend in well with the color of decaying inflorescence parts. Both factors may explain why this species is known exclusively from moist chamber cultures.

Perichaena cf. *dictyonema* was recorded from all study sites except those in cloud forests (*Ec2*, *PR2*, and *CR2*) and occurred on all plants with larger, more compact inflorescences that can accumulate an appreciable amount of water. Our records are the first for the species from the western hemisphere. Other than inflorescences, it was recorded on only two other occasions. The first was on the decaying, fleshy sheaths of the understory palm *Chamaedorea tepijiote* Liebm. and the second on decaying banana leaves, in both cases above the ground.

Perichaena vermicularis (Schwein.) Rostaf. (PERver, 17 records, fc 4, mc 13, pH 7.8 ± 0.6, range 6.9–9.1)
As recorded in this study, *Perichaena vermicularis* is characterized by very small, plasmodiocarpous fructifications, with a thin, membranous peridium.
The species was recorded from all countries except Puerto Rico and was most common on inflorescences of *Calathea ischnosiphonoides* (*Ec2*, 9 records). It is fairly common on various kinds of (mostly aerial) litter.

Physarum compressum Alb. & Schwein. (PHYcom, 174 records, fc 48, mc 126, pH 8.5 ± 0.6, range 6.4–9.7)
In accordance with the concept proposed by Irawan et al (2000), forms resembling *P. nicaraguense* T. Macbr. are included here. In our material, forms characterized by a cluster of sporothecae on a common stalk appeared only rarely and seemed to intergrade with typical forms.
This species was recorded from all countries and plants except *Hedychium coronarium*. It is common on aerial litter with a basic pH.

Physarum didermoides (Pers.) Rostaf. (PHYdio, 117 records, fc 66, mc 51, pH 8.6 ± 0.6, range 6.8–9.8)
This species was recorded from all lowland sites included in our study. It was most common on *Costus guanaiensis* (19 records) and *Heliconia mariae* (63 records). Both plants have very compact, rather large inflorescences and their decaying floral parts are characterized by a very basic pH. Although represented by a few collections in herbaria, the species was not encountered by us on any substrata other than inflorescences.

Physarum cf. *limonium* Nann.-Brem. K. Ned. Akad. Wet. Proc. C 69: 357. 1966 (PHYlim, 6 records, fc 2, mc 4, pH 8.2 ± 0.5, range 7.7–8.9)
The specimens assigned to this species in the present study have yellow sporocarps with long, limeless stalks. Except for the color, they are very similar to the typical form of *Physarum pusillum*. The form we recorded is described in detail (as *P.* cf. *oblatum*) in Schnittler et al (2001). All six of our specimens are fairly uniform in habit.
Physarum cf. *limonium* was recorded from all countries and four study sites. In addition to inflorescences, it was recorded once from aerial litter (decaying banana leaves).

Physarum melleum (Berk & Broome) Massee (PHYmel, 24 records, fc 23, mc 1, pH 7.3 ± 0.8, 6.0–8.8)
Except one record from *Calathea plurispicata*, this species was common on only two host plants: *Hedychium coronarium* (*PR2*, 2 records, but at least 10 plasmodia in moist chambers that did not form fructifications but could be assigned with some certainty to *Physarum melleum*, based upon the experience of the authors) and *Psychotria poeppigiana* (21 records, along with 6 plasmodia that could be assigned to *Ph. melleum*). Based upon

the pH values recorded, this species appears to be unable to inhabit inflorescences of *Costus* and *Heliconia*, which are characterized by a very basic pH. This species is fairly common on leafy litter, both aerial and ground.

Physarum pusillum (Berk. & M.A. Curtis) G. Lister, badhamioid form (PHYpus, 57 records, fc 23, mc 34, pH 8.1 ± 0.7, range 6.2–9.8)
Our specimens possess a short, rather stout stalk and a capillitium composed of a solid network of lime tubes. In accordance with the comments of Martin and Alexopoulos (1969: 326), we include this form, although it is clearly separable from the typical form that was found more rarely, in *P. pusillum*.
This species is known from most of the study sites, including those in cloud forests, and was recorded from most of the plants sampled. In addition to inflorescences, *Physarum pusillum* was recorded several times from decaying but still attached banana leaves.

Physarum superbum Hagelst. (PHYsup, 26 records, fc 13, mc 13, pH 8.1 ± 0.7, range 7.1–9.2)
This species, not previously known from the Neotropics, was recorded from all countries and all study sites except *CR2* and *Ec2*. It was represented by four additional records from aerial litter, with two of these from decaying banana leaves.

Another 18 species were encountered on decaying floral parts of living inflorescences, none of them represented by more than five records. These additional species are an apparently undescribed taxon belonging to the genus *Arcyria*, *Comatricha* ? *lurida* Lister, *C.* ? *tenerrima* (M.A. Curtis) G. Lister (both represented by very scanty specimens leaving the determination doubtful), *Didymium difforme* (Pers.) S.F. Gray, *D. bahiense* Gottsb., *D. nigripes* Fr., *D. ochroideum* G. Lister, *Diderma effusum* (Schwein.) Morgan, *D. hemisphaericum* (Bull.) Hornem., *Lamproderma scintillans* (Berk. & Broome) Morgan, *Perichaena chrysosperma* (Currey) Lister, *P. depressa* Libert, *P. pedata* (Lister & G. Lister) G. Lister, *Physarum cinereum* (Batsch) Pers., *Ph. javanicum* Racib., *Ph. pusillum*, typical form, *Ph. serpula* Morgan, and *Stemonitis fusca* Roth. All of these species were recorded more often on other substratum types, especially aerial litter, from the same study sites.

FIG. 1 shows the rank-abundance plot developed for all myxomycete records from inflorescences. The two most common species (*Physarum compressum* and *Ph. didermoides*) account for 291 (44%) of all (652) determinable records. Collectively, the 13 more common species listed above (represented by more than five records) constitute 613 records (94% of the total number for all records).

The moist chamber component of this survey (28 species from 453 records in 358 moist chambers) was analyzed by a bootstrap procedure to estimate the total number of species to expect for these cultures. A fit using a simple saturation function $y = ax / (b+x)$ gives an estimate of 31 species to expect (a = 31.02, b = 57.77, mean square error = 1.21). However, a model extended by a linear term cx (assuming a steadily increasing number of rare species to appear in the cultures with one record

each) shows a much better fit (a = 18.86, b = 18.74, c = 0.03, mean square error = 0.15). According to this model, 19 species can be expected regularly in the cultures, with one additional rare species appearing once every 33 cultures. A jackknife estimate of 35.98 was found for the total number of species to be expected.

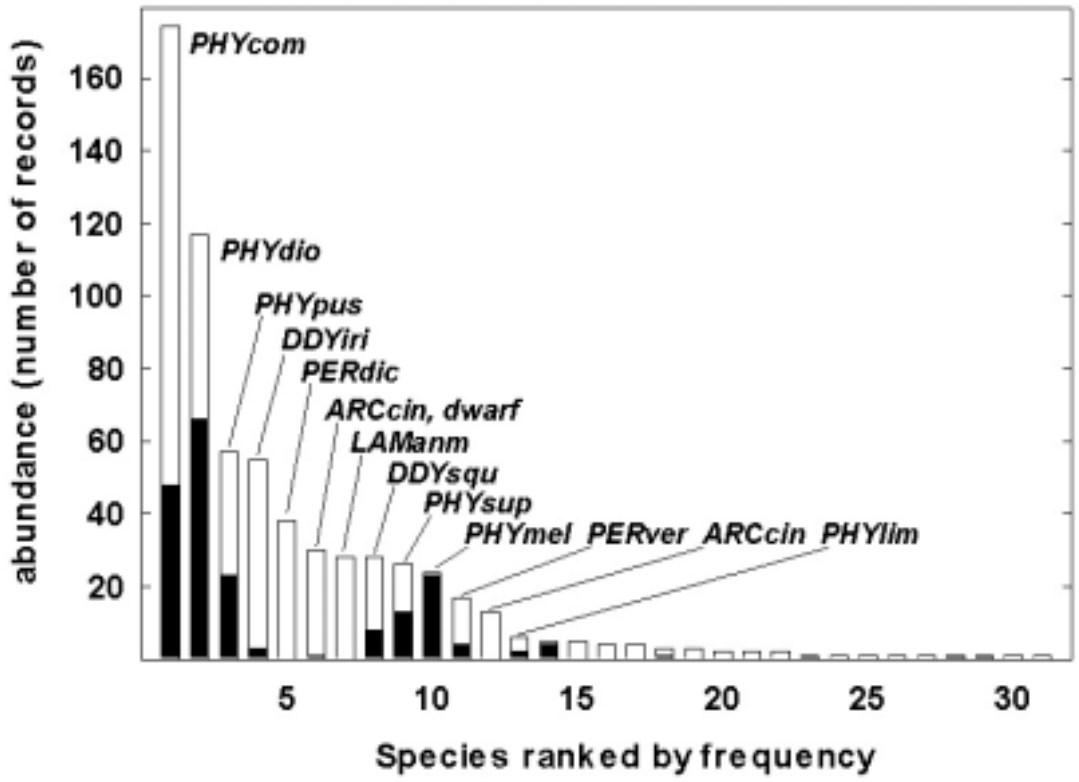

FIG. 1. Frequency distribution of all 652 determinable specimens of myxomycetes recorded from inflorescences (both field surveys and moist chamber cultures). Dark sectors of the bars represent records of field collections, whereas white sectors indicate records obtained from moist chamber cultures. The 13 most common species, represented by more than 5 records, are labeled. Abbreviations are the same as those mentioned in the annotated species list.

All of the more common species observed in the field also were recorded from moist chamber cultures. Three species (*Lamproderma arcyrionema*, *Perichaena* cf. *dictyonema* and the typical form of *Arcyria cinerea*) were recorded only from moist chamber cultures. Of the 13 more common species, one (the dwarf form of *Arcyria cinerea*) is apparently new to science, and three others (*Perichaena dictyonema*, *Physarum* cf. *limonium* and *Ph. superbum*) are new records for the Neotropics. Eleven of the 13 more common species were recorded from all three of the countries investigated. Accordingly, CA of the data from moist chamber cultures shows no clustering of series of samples sites from a particular country (FIG. 2).

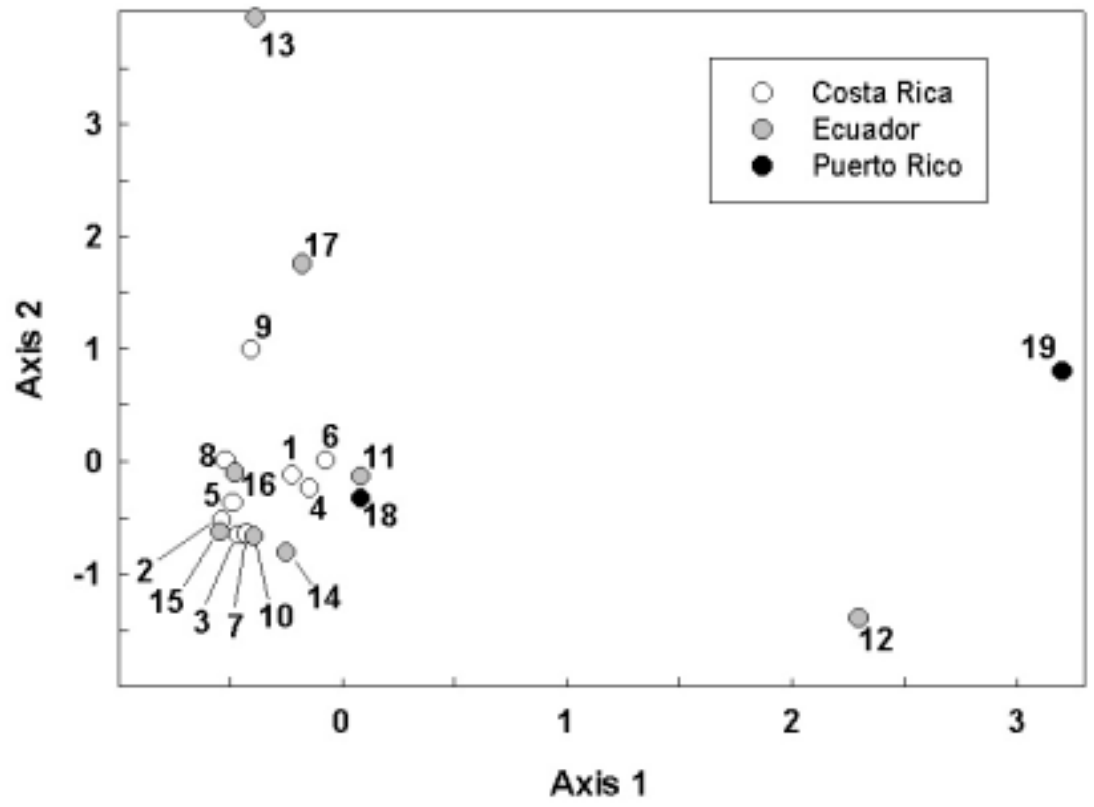

FIG. 2. Results of a correspondence analysis of the frequency of myxomycete records for the 19 series of moist chamber cultures prepared from samples collected in the various study sites. Numbers for the series of moist chamber cultures prepared with different plants are the same as those used in TABLE II.

A comparison of the inflorescence data with the data obtained from 696 moist chamber cultures prepared with other kinds of (mostly aerial) litter substrata collected in the same study sites was used to assess the degree to which the assemblage of myxomycetes inhabiting inflorescences is specific for this microhabitat. As shown in TABLE III, six taxa appear much more frequently (more than five times as often) in moist chambers prepared with inflorescence material than in those prepared with other types of litter substrata. These taxa are *Perichaena* cf. *dictyonema*, *Physarum compressum*, *Ph. didermoides*, *Ph.* cf. *limonium*, *Ph. pusillum* (badhamioid form), and *Ph. superbum*. An analysis of the productivity of the moist chambers (based upon the number of sporocarps per moist chamber) confirms this pattern.

Members of the Physarales (represented by 8 of the 13 more common species and 5 of the 6 species displaying a strong preference for inflorescences) constitute the majority of the myxomycetes associated with the inflorescence microhabitat, followed by members of the genera *Arcyria* and *Perichaena*, both belonging to the Trichiales (4 of the 13 more common species). *Lamproderma arcyrionema* is the only member of the Stemonitales represented among the 13 more common species.

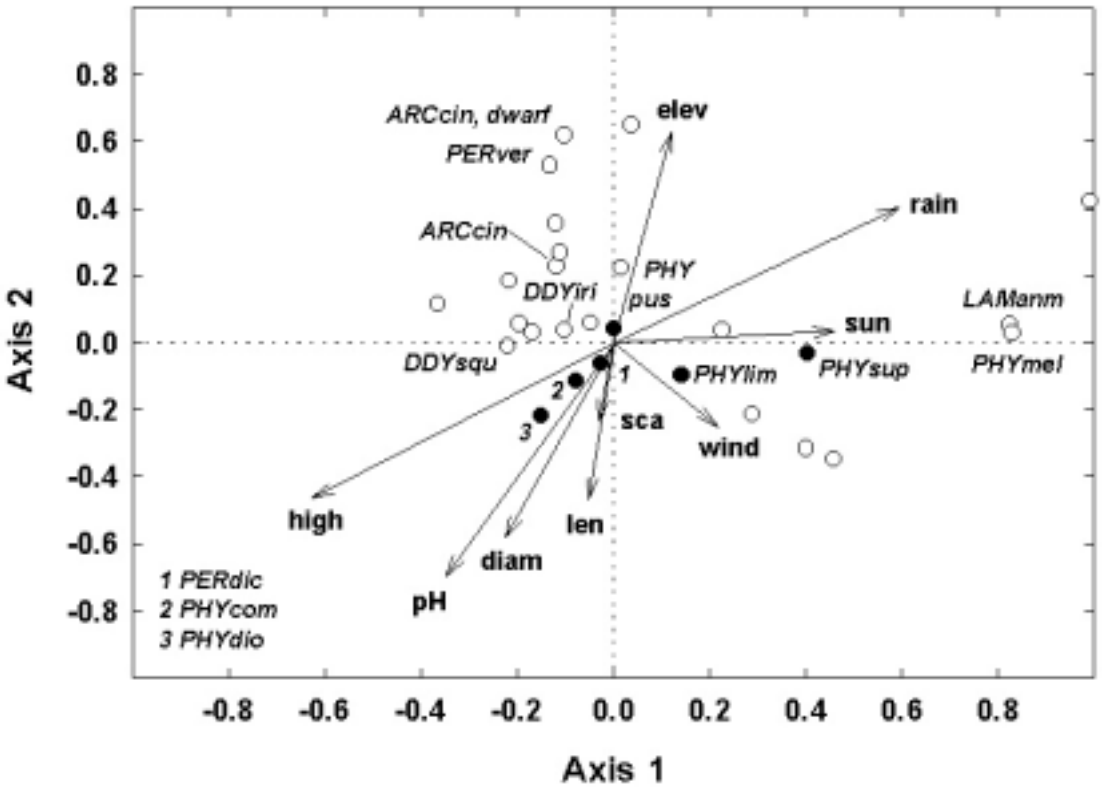

FIG. 3a. Biplot of a canonical correspondence analysis of all 250 moist chamber cultures yielding at least one determinable myxomycete record. Abbreviations of the environmental parameters are: diam = diameter, len = length of the inflorescence; pH = pH value of the decaying floral parts; sca = tightness of the scales or bracts; high = sampling height; sun = light intensity; wind = wind exposure; elev = elevation and rain = annual rainfall at the study site. Abbreviations for the 13 more common myxomycetes are as indicated in the annotated species list. Filled circles indicate the species scores for the six species of myxomycetes with a strong preference for inflorescences, whereas open circles indicate scores for all other species.

Compared with other litter substrata, decaying floral parts from inflorescences have about the same levels of nitrogen but are richer in phosphorus, potassium, and several trace elements, such as magnesium, manganese, zinc, and copper (TABLE IV). In contrast, inflorescences have lower levels of iron and aluminum. In addition, decaying floral parts of inflorescences exhibit very basic pH values (TABLE II). The mean pH for the substrata of the 358 moist chamber cultures prepared with inflorescences was 8.08 ± 0.04 as opposed to 7.00 ± 0.02 for the 696 cultures prepared with samples of leafy litter from the same study sites. The very frequent occurrence of myxobacteria, which are known to be predatory on other bacteria, suggests the presence of a rich bacterial flora. From the 358 moist chambers prepared with inflorescences, there were 401 records of myxobacteria (75% of all cultures were positive for myxobacteria), whereas the 696 moist chambers prepared with other kinds of litter yielded 456 records of myxobacteria (51% of all cultures were positive). The three largest species of myxobacteria were especially more productive in moist chambers prepared with

inflorescences. *Chondromyces crocatus* produced an average of 128 ± 13 fructifications (from 153 records) on inflorescences, compared with 93 ± 20 fructifications (44 records) on other kinds of litter. The differences for *C. lanuginosus* were 80 ± 23 fructifications (10 records) on inflorescences as compared to 29 ± 8 fructifications (32 records) on other litter, whereas *Stigmatella aurantiaca* produced a mean of 161 ± 50 fructifications (41 records) on inflorescence as compared to 99 ± 12 fructifications (122 records) on other litter.

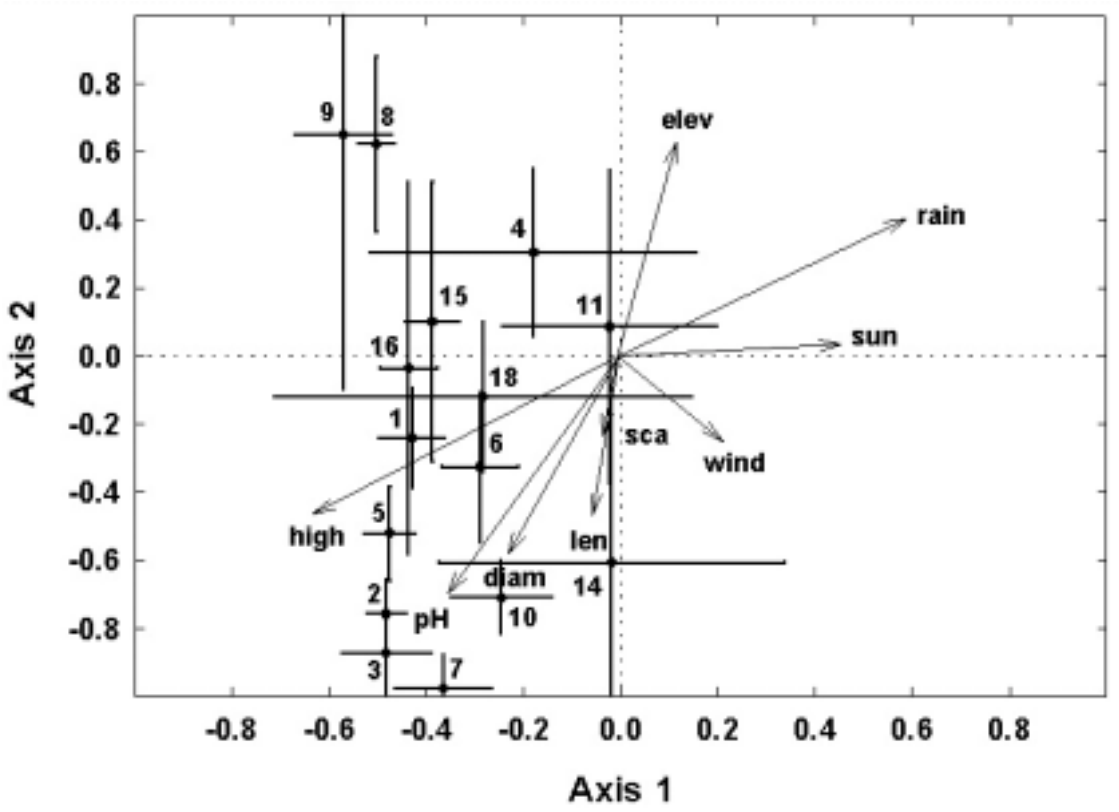

FIG. 3b. Means of the sample scores for all moist chamber cultures belonging to one series in relation to the biplot scores of the environmental parameters. Vertical and horizontal lines indicate the standard error for the first two axes, respectively. Numbers for the series of moist chamber cultures prepared with different plants are as listed in TABLE II. The means for four series of cultures (12, x = 2.45, y = −1.15; 13, x = −0.30, y = 2.58; 17, x = −0.45, y = 2.52 and 19, x = 3.51, y = 0.38 exceed the range indicated and are not shown.

The values recorded for pH are the most important of all the environmental parameters included in the CCA (FIG. 3a). Sampling height as well as the three parameters (length, diameter and bract arrangement) describing the inflorescences sampled act in the same direction. As such, the largest and most compact inflorescences (e.g., those produced by *Heliconia mariae*, *Costus guanaiensis*, and *Calathea plurispicata*) are characterized by the most basic pH for their decaying floral parts (TABLE II). In contrast, the two environmental parameters of annual rainfall and elevation act in the opposite

direction; light intensity and wind exposure are less important. From the six species of myxomycetes showing a high preference for inflorescences, *Physarum didermoides*, *Ph. compressum*, and *Perichaena* cf. *dictyonema* cluster in the direction of the environmental parameter pH.

A second biplot combining the means of all sample scores belonging to one series of moist chamber cultures (i.e., prepared with material from the same plant species at the same locality) with the environmental parameters is provided in FIG. 3b. Most of the plant species investigated cluster together, with *Heliconia velligera* (*Ec4*, series 12), *Psychotria poeppigiana* (*Ec4*, series 13), *Calathea ischnosiphonoides* (*Ec2*, series 17) and *Hedychium coronarium* (*PR2*, series 19) as the exceptions. Comparing the standard errors obtained by calculating the means of the sample scores of all cultures belonging to one series, some species of *Heliconia* with large inflorescences (e.g., *H. mariae*, series 2 and 7; *H. pogonantha*, series 3) tend to have the most uniform myxomycete assemblages.

Physarum compressum, as the most common species encountered in the entire survey, has a clear preference for very basic substrata, as indicated by the comparison of moist chamber cultures positive for this species with the total for cultures prepared with all kinds of litter substrata (FIG. 4a). In cultures of material from inflorescences, this species is significantly more productive than in cultures prepared with other litter substrata (FIG. 4b, TABLE III). *Psychotria poeppigiana*, the only dicot investigated in this study, had a clearly lower pH (mean 6.6) than all of the monocots. *Physarum melleum* was the most common species on this plant, and except for *Ph. compressum* (one record) and *Ph. pusillum* (two records), none of the other inflorescence-preferring myxomycetes was found on this substratum.

Discussion

Prior to the present study, the inflorescences of living plants were not known as a microhabitat for myxomycetes. However, temporary accumulations of water (phytotelms) in bromelids, but also in erect-flowering species of *Heliconia*, form a special habitat for other organisms, including arthropods (Richardson 1999). The information reported herein adds yet another aspect to these "microcosms" – the existence of a stable and specific assemblage of "epiflorous" myxomycetes on decaying floral parts of inflorescences, especially those of giant herbaceous plants belonging to the order Zingiberales. Several lines of evidence support this, since (i) this assemblage was found on numerous plant species and in several localities throughout the Neotropics, with 11 of the 13 more common species occurring in all three of the countries investigated, (ii) no evidence of clustering of series of moist chamber cultures from a certain locality was found in the CA shown in FIG. 2, (iii) a few myxomycete species,

especially *Physarum compressum* and *Ph. didermoides*, are exceedingly common in the inflorescence microhabitat, and (iv) six of the myxomycete taxa showed a clear preference for this microhabitat.

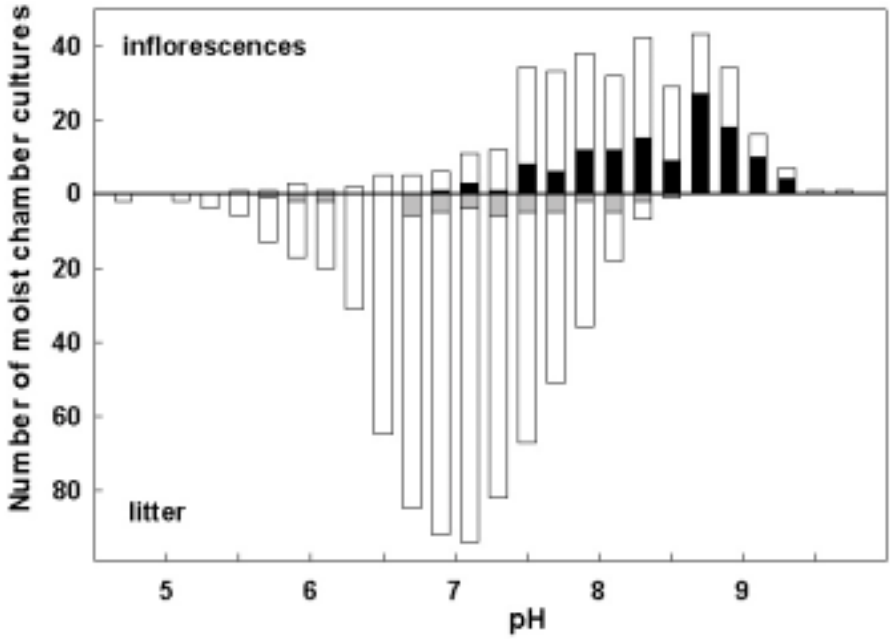

FIG. 4a. Comparison of the pH values (in units of 0.2) for the 696 moist chamber cultures prepared from litter (white bars, lower half of the graphics) with the 358 cultures prepared from material from inflorescences (grey bars). The upper half of the graphics shows the number of moist chambers positive for *Physarum compressum* from litter (white bars) and inflorescences (black bars).

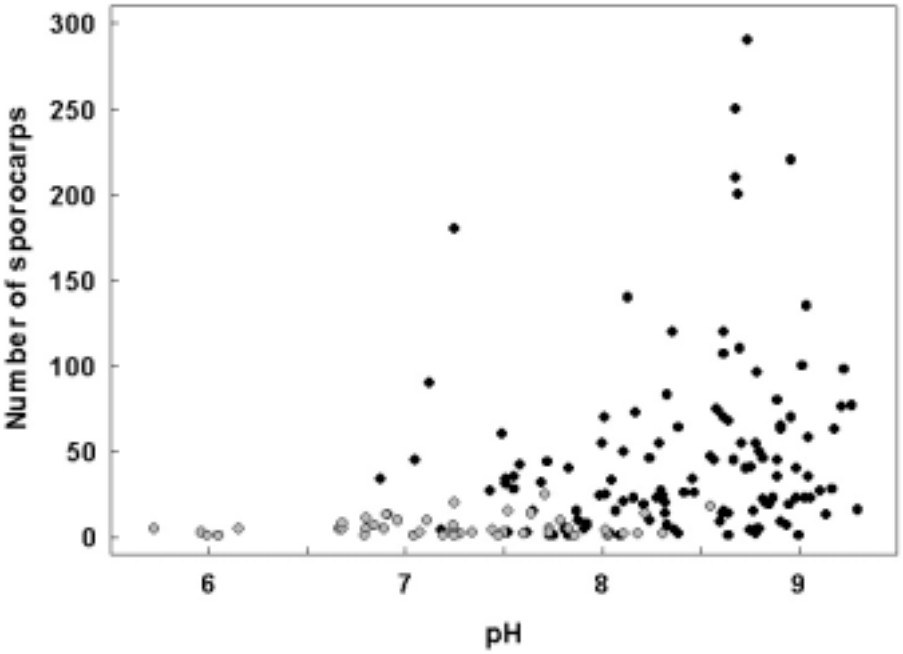

FIG. 4b. Relationship between colony size (numbers of sporocarps counted or estimated) and substratum pH for *Physarum compressum* from moist chamber cultures prepared with litter (open circles) and inflorescences (filled circles).

As indicated by the data presented in the rank-abundance plot (FIG. 1), the results from the field survey and moist chamber culture components of this study complement each other, and the high number of rare "tail" species in comparison to the few very common species suggests a rather exhaustive survey for the plant species investigated. Moreover, for the moist chamber component of the study, the bootstrap method estimates the survey to be complete to 90% with a simple saturation model (31 species to be expected, 28 found in reality). The jackknife estimate as a nonparametric model results in a degree of completeness of 78% (36 species to be expected). However, as to expect for organisms capable of long-distance dispersal via airborne spores, a rather high number of species should be very rare, since they may develop occasionally from spores carried into the "microcosm" but do not occur regularly as members of the assemblage. A saturation model extended by a linear term for these species provided a significantly better fit to the data and gave an estimate of 19 species to expect regularly, with 22 species recorded more than once in reality. This would equal a survey complete to 86% for the species found more than once. Therefore, it can be assumed that the present study revealed about four fifths of all myxomycete species to be expected for the surveyed plant species. However, as shown by the examples of *Hedychium coronarium* and *Psychotria poeppigiana*, which do not cluster with the other plant species in the CA, new plant species, especially those not belonging to the order Zingiberales, may add more species to this ecological assemblage.

The assemblage of myxomycetes associated with inflorescences is rather poor in species. A comparison with the myxomycetes recorded from other litter substrata shows that more than half of the 13 more common species are ubiquists, occurring with about the same frequency or even more often on other litter substrata (TABLE III). Prominent examples are *Didymium squamulosum* and *D. iridis*, both very common on all kinds of aerial litter. Both species are several times more common on other litter substrata than on inflorescences. On the other hand, six species of myxomycetes, including the two taxa (*Physarum compressum* and *Ph. didermoides*) most common in this microhabitat, show a clear preference for inflorescences. The preference values derived from both frequency and productivity in moist chamber cultures (TABLE III) reveal two clear-cut groups of species. These are ubiquists, with preference values well below 5, and specialists, with values of 10 and more. This pattern is confirmed by the experience of the authors from several years of rather intense field surveys in the Neotropics (see comments in the annotated species list).

One obvious feature of the assemblage of myxomycetes associated with inflorescences is the prevalence of a few genera, especially *Perichaena* and *Physarum*, among the 13 more common species, but especially among the six species that seem to display the strongest preference for this microhabitat. These genera seem to have a rather high proportion of species specialized for surviving on basic substrata. A study from a desert in Kazakhstan (Schnittler and Novozhilov 2000), a totally

different habitat but also with a high proportion of basic substrata, revealed a similar high proportion of these two genera among the assemblage of species recorded (among the 27 species recorded where 4 members of the genus *Perichaena* and 5 species of *Physarum*).

The results from CCA (limited to the moist chamber component of this study), when considered along with the data obtained from the field survey, may help provide an answer to the question of why inflorescences constitute a special microhabitat for myxomycetes in the Neotropics. The most obvious factor is the very basic pH of the decaying floral parts of almost all of the inflorescences investigated (TABLE II). Except for *Psychotria poeppigiana* (mean pH 6.6), the only plant not belonging to the Zingiberales, all other plants had mean pH values above 7.5. In the compact inflorescences of *Heliconia mariae*, values between 8 and 9 were recorded. As such, inflorescences appear to represent some of the most basic substrata available for myxomycetes in Neotropical forests. Only the fleshy, herbaceous stems of species of *Heliconia* or *Musa*, essentially other portions of the plants producing the inflorescences that were investigated, display similar pH values (e.g., a series of moist chambers prepared from aerial banana leaf litter collected in study site *Ec4* had pH values between 7.4–8.0). Not unexpectedly, the few records of the six taxa of inflorescence-preferring myxomycetes came from other substrata exhibiting similar rather high pH values. These included the fleshy sheaths of the understory palm *Chamaedorea tepijiote* and, even more often, aerial litter of *Heliconia* or *Musa*. In accordance with this, pH is the environmental parameter explaining most of the variance in species distribution in the CCA (FIG. 3a), and the two most common myxomycetes clearly exhibit a preference for high pH and cluster with the environmental parameter pH. *Physarum compressum* seems to be a good indicator species for these very basic microhabitats. Perhaps due to the higher contents of some nutrients in the inflorescences, the colonies of this species are larger on this substratum and indicate a pH optimum between 8.5 and 9.0 for this myxomycete (Figs. 4 a, b).

The largest and most compact inflorescences have the highest pH values and the most consistent assemblages of myxomycetes, as indicated by the smaller standard errors of their sample scores in the second CCA biplot (FIG. 3b). Accordingly, *Costus guanaiensis* and *Heliconia mariae* have the highest values of inflorescences positive for myxomycetes in the field (TABLE II). *Physarum didermoides*, the inflorescence-preferring species with the highest productivity, was found most often on these two plants (16 and 43 of the 66 field records, respectively). At La Selva, large populations of *H. mariae* occurring on the grounds of the biological station supported large colonies of this species in two subsequent years, and the number of records could have been increased several fold by checking more inflorescences.

A description of flower features, pollination ecology, and seed dispersal of *Costus guanaiensis*, as observed at the Maquipucuna reserve in Ecuador (site *Ec1*), may illustrate the function of such

inflorescences as a special microhabitat for myxomycetes. This plant is a very large herb, up to 4 m tall, and produces a single flower head on the end of a shoot. The inflorescence is a cylindrical, cone-like spike with 50–120 densely imbricate, persistent, sturdy, green bracts with a scarlet-red margin. Each bract is 3–4 cm long and supports one flower. The corolla is pale orange, up to 6 cm long, and each flower blooms only one day. A hummingbird (*Phaethornis yaruqui*, white-whiskered hermit) was regularly seen patrolling the plants, each morning visiting the 1–3 flowers of each inflorescence in bloom. By the following day, the decay of the corolla had begun, with its remnants more or less enclosed by the densely appressed bract, thus creating a "natural moist chamber." A nectarial "callus" (extrafloral nectary) at the base of the bract provides a sugar-containing solution (to support ants that protect the inflorescence), perhaps ensuring optimal conditions for a community of yeasts and bacteria degrading the corolla remnants. Not surprisingly, myxobacteria, indicating also a community rich in other bacteria, developed quickly in moist chamber cultures prepared with corolla remnants (*Chondromyces crocatus* as the most common species, followed by *C. lanuginosus*, *Stigmatella aurantiaca* and *Myxococcus* sp.). The flowering sequence in the inflorescences is ascending, with the terminal flowers the last to bloom. With often more than 75 flowers in one inflorescence, a flowering period of 2–3 months can be assumed. Judged from the flowering sequence, 3–5 weeks after bloom the myxomycetes begin to form fructifications on the outer surface of the still living bracts. Here, the fructifications can easily dry out, which allows the spores to become airborne. At this time, the uppermost bracts still produce flowers, whereas the lowermost bracts are already open, exposing the white seed capsules with black seeds for bird dispersal. The yellow-rumped tanager (*Ramphocelus icteronotus*) was seen regularly plundering these capsules. With a dry weight of 105 ± 9 mg (n=7) per corolla and 50–120 flowers per inflorescence, 5–12 g of substratum are available for myxomycete growth. On the 16 inflorescences with colonies of *Physarum didermoides* observed in the field, numbers ranging from 15 to 1100 sporocarps were recorded (mean 219 ± 87). With an estimated number of 10^5 spores per sporocarp, on average more than two millions of spores per inflorescence were available for dispersal.

Based upon our field observations as well as results from CCA, inflorescences with the following features provide the best conditions for myxomycetes: (i) rather massive and compact, (ii) possessing rather large, slightly fleshy corollas, as is often the case for flowers pollinated by birds or bats, (iii) with sturdy, tightly appressed bracts that appear to create "natural moist chambers" for the corolla parts, (iv) having an extended flowering period that provides enough decaying material to support large colonies of myxomycetes, and (v) with submersed flowers in water-filled or saturated bracts that leak remaining nectar, or the presence of extrafloral nectaries that secret a sugar solution to provide

initial support for a community of yeasts and bacteria associated with the decomposition of the floral parts. Extrafloral nectaries can be found in many species of *Costus* and in all species of *Heliconia* (Kubitzki 1998). For some species of *Heliconia* pollinated by birds, one flower has accumulated already by the time of anthesis (usually the early morning) more than 100 µl of nectar with a concentration of 15–20% sucrose-equivalents (Pedersen and Kress 1998). Especially in species with erect, massive bracts collecting rainwater, the nectar leftovers not used by the pollinator leak out and provide a medium rich in nutrients for yeasts, which are likely to grow in the watery solution enriched with nectar and the decaying floral parts.

Among the species of *Heliconia*, three groups can be recognized on the basis of inflorescence structure: (1) erect inflorescences 10–25 cm long and with very sturdy bracts developing phytotelms (*H. orthotricha*, *H. stricta* and *H. caribaea*), mostly plants of wet stream gullies and tree fall gaps; (2) pendant and massive inflorescences 30–120 cm long and with short bracts (*H. griggsiana*, *H. mariae*, *H. pogonantha* and *H. velligera*), mostly plants of open habitats and characteristically forming rather large, monoclonal populations; and (3) erect inflorescences 20–40 cm long and relatively narrow but with very long and distant bracts that rarely collect enough water to form a phyotelm (*H. latispatha*), mostly woodland species. Judged from the average percentage of positive moist chambers, there are no significant differences among the three groups (70, 85, and 83% positive cultures, respectively). However, in the field, myxomycetes were observed only on flowers of the first two groups (37, 43, and 0% positive inflorescences, respectively).

The general pattern of decreasing species richness of myxomycetes with increasing elevation in the Neotropics, reported by Stephenson et al (1999) and Schnittler and Stephenson (2000), also seems to apply to the assemblages of myxomycetes associated with inflorescences. Most of the plant species producing inflorescences suitable as potential substrata can be found only at lower elevations. In Ecuador, the highest site (*Ec3*) had no species of *Heliconia* or *Calathea*, and the mid-elevation site (*Ec2*) had only a single species (*Calathea ischnosiphonoides*, with a very small inflorescence). Only the low elevation site (*Ec1*) had a variety of large species of *Heliconia*. The three species of myxomycetes (*Physarum didermoides*, *Ph. superbum*, and *Perichaena* cf. *dictyonema*) with the highest preference values for inflorescences were not observed at the high elevation sites (*CR2* and *Ec2*), and the highest elevation site in Puerto Rico (*PR2*) produced only *P. superbum*, which was recorded from a population of the introduced *Hedychium coronarium* growing in an open habitat (the margin of a road). In the CCA (FIG. 3), these myxomycete species cluster in the opposite direction of the environmental parameters elevation and mean annual rainfall.

The high preference values for the six species of inflorescence-inhabiting myxomycetes (*Physarum didermoides* was never recorded by us from any other microhabitat) raise the question of whether they

are dispersed by the pollinating or seed-consuming animals that visit these same inflorescences. More evidence, especially direct evidence of viable spores on feathers or bills of pollinating birds, would be necessary to answer this question. *Ph. didermoides* seems to be restricted largely to the species of *Costus* and *Heliconia* that are bird-pollinated (Kubitzki 1998). In the present study, the only exceptions were a few records from moist chamber cultures prepared with material collected from a population of *Calathea plurispicata* almost immediately adjacent to a population of *Costus guanaiensis* in Ecuador (site *Ec1*). New world species of *Calathea* are usually pollinated by euglossine bees (Kennedy 1978). However, the species of hummingbird mentioned above was also observed to make occasional visits to the flowers of *Calathea*. Although hummingbirds were observed repeatedly on the flower heads of *Psychotria poeppigiana* with its conspicuous, scarlet-red bracts, *Ph. didermoides* was not recorded on this plant, for which the inflorescence had the lowest pH of any plant species investigated. It seems quite possible that more detailed studies of this microecosystem, being a well-circumscribed "island" with its own distinctive community of microorganisms, including myxomycetes, bacteria and perhaps yeasts, will add a new story of interspecies relationships to the ecological web of Neotropical forests.

Acknowledgements

We are indebted to Mike Dilger, the resident biologist of the Maquipucuna Cloud Forest Reserve, for identifying the bird species visiting *Costus guanaiensis*, and the staff of the herbarium of the Pontifical Catholic University of Ecuador in Quito (QCA) for providing comparison material for identification of some of the species of *Heliconia* investigated. For help in organizing field work in Puerto Rico, we wish to thank Dr. D. Jean Lodge (USDA Forest Service, Sabana work station). This research was supported by a grant from the National Science Foundation (DEB-9705464), with additional funding from the National Geographic Society.

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TABLE I. Plant species surveyed for the occurrence of inflorescence-inhabiting myxomycetes.

Plant species [a]	Inflorescence Length x diam (cm)	Height (m)	Bracts [b]	Description
Calathea plurispicata H.A. Kenn.	3–5 x 12–17	1–1.7	3	erect, 15–30 overlapping scaly bracts, cream-white, asymmetric flowers, corolla ca. 1.5 cm long
C. ischnosiphonoides H.A. Kenn.	1.5–2 x 8–12	0.8–1	3	erect, 10–20 rarely overlapping bracts, corolla white, ca. 1 cm long
C. crotalifera D. Watson (= *C. insignis*)	2.5–3 x 9–12	0.8–1.3	3–4	erect, 20–40 densely arranged, overlapping yellow bracts with small, cream-white flowers
Costus guanaiensis Rusby	4–7 x 15–20	2.5–3.5	4	erect, very compact cone, 50–120 appressed bracts, corolla pale yellow, up to 5 cm long
Hedychium coronarium J. König	5–7 x 7–10	0.8–1.2	2–3	erect to pendant, 10–20 loosely arranged bracts, each with a white, showy flower
Heliconia caribaea Lam.	7–8 x 12–17	1.2–1.8	2	erect, 7–15 very tough yellow bracts collecting rain water, flowers 3–7 per bract, green
H. griggsiana L.B. Sm.	10–20 x 80–120	2.2–3.2	2–3	pendant, 10–20 long red bracts, flowers reddish
H. lathispatha Bentham	20–25 x 20–40	1.0–1.8	1	distant, erect, 9–15 cm long scarlet-red bracts, narrow and rarely collecting rain water, corolla yellow
H. mariae J.D. Hooker	8–10 x 20–55	1.8–2.5	4	pendant, very compact, 50–200 distichously arranged scales each with 5–9 red flowers
H. orthotricha L. Anderss.	8–9 x 30–45	1.0–1.5	2	erect, similar to *H. caribaea* but bracts deep pink
H. pogonantha Cufodontis	8–10 x 80–120	0.8–1.8	2–3	pendant, 15–30 short red bracts distant from each other
H. stricta Huber	7–8 x 15–20	0.8–1.4	2	erect, similar to *H. caribaea* but bracts orange
H. vellerigera Poepp.	10–15 x 110–180	0.7–1.8	2	pendant, similar to *H. pogonantha* but bracts orange, bronze villous, corolla yellow
Psychotria poeppigiana Müll. Arg.	2–3 x 1.5–2	1.0–3.0	4	erect, compact clusters of 30–50 tiny tubular flowers and calyx scales enclosed by two scarlet-red bracts

[a] Species names after Jørgensen & León-Yánez (1999) for Ecuador, Berry & Kress (1991) for Costa Rica and Puerto Rico.
[b] Arrangement of bracts: 1 = distant, clearly separated from each other, 2 = bracts adjacent but not overlapping, 3 = bracts overlapping but loose, 4 = bracts tightly appressed and overlapping each other.

TABLE II. Statistical data for field surveys and series of moist chamber cultures prepared with 14 different plant species from nine study sites in Ecuador, Costa Rica and Puerto Rico.

Sample number [a]	Study site [b]	plant species	field survey	moist chamber cultures		
			myxomycete records [c]	myxomycete records [c]	pH [d] (mean ± SD)	pH (range)
1	*CR1*	*Heliconia latispatha*	0/18 (0%)	18/18 (100 %)	8.44 ± 0.43	7.62–9.17
2	*CR1*	*Heliconia mariae*	12/19 (63%)	19/19 (100%)	8.70 ± 0.27	8.00–9.02
3	*CR1*	*Heliconia pogonantha*	1/21 (5%)	8/21 (38%)	8.77 ± 0.26	8.14–9.12
4	*CR2*	*Calathea crotalifera*	1/19 (5%)	13/19 (68%)	8.09 ± 0.38	7.50–8.83
5	*CR2*	*Heliconia latispatha*	0/20 (0%)	11/20 (55%)	7.91 ± 0.35	7.38–8.41
6	*CR3*	*Calathea plurispicata*	5/10 (50%)	6/10 (60%)	8.46 ± 0.22	8.13–8.85
7	*CR3*	*Heliconia mariae*	19/24 (79%)	23/24 (96%)	8.95 ± 0.33	8.05–9.52
8	*CR2*	*Heliconia latispatha*	0/16 (0%)	16/16 (100%)	8.59 ± 0.29	7.83–9.03
9	*CR3*	*Heliconia latispatha*	0/20 (0%)	19/20 (95%)	7.45 ± 0.33	6.72–8.04
10	*Ec4*	*Heliconia orthotricha*	12/23 (52%)	17/20 (85%)	8.41 ± 0.38	8.99–7.55
11	*Ec4*	*Heliconia stricta*	5/23 (22%)	16/20 (80%)	7.77 ± 0.27	8.24–7.12
12	*Ec4*	*Heliconia vellerigera*	2/10 (20%)	8/8 (100%)	8.30 ± 0.10	8.39–8.07
13	*Ec4*	*Psychotria poeppigiana*	30/96 (31%)	15/24 (63%)	6.60 ± 0.50	7.33–5.43
14	*Ec1*	*Calathea plurispicata*	7/17 (41%)	10/16 (63%)	8.53 ± 0.28	8.11–9.04
15	*Ec1*	*Costus guanaiensis*	25/44 (57%)	13/13 (100%)	8.32 ± 0.12	8.16–8.53
16	*Ec1*	*Heliconia griggsiana*	7/14 (50%)	10/11 (91%)	8.09 ± 0.28	7.63–8.61
17	*Ec2*	*Calathea ischnosiphonoides*	8/21 (30%)	19/21 (91%)	7.60 ± 0.34	6.92–8.23
18	*PR1*	*Heliconia caribaea*	0/28 (0%)	13/28 (46%)	8.09 ± 0.38	8.69–7.46
19	*PR2*	*Hedychium coronarium*	1/35 (0.3 %)	30/30 (100%)	7.51 ± 0.45	8.03–6.06

[a] One series of moist chamber cultures constitutes one sample.
[b] For abbreviations of study sites see "Material and Methods".
[c] Number of inflorescences positive for myxomycetes / number of inflorescences cultured and surveyed (% positive).
[d] Mean of pH values from all inflorescences used for preparation of moist chamber cultures.

TABLE III. Occurrence data for the 13 most common myxomycetes (more than 5 records) from 358 moist chamber cultures prepared with decaying floral parts of living inflorescences, compared with their occurrence in 696 moist chamber cultures from the same sites prepared with various types of litter.

Species	% positive moist chamber cultures		specificity quotient [a]	mean number of sporocarps (number of records)		specificity quotient [b]	Preference [c]
	inflorescence	litter		inflorescence	litter		
Arcyria cinerea (dwarf form)	8.1	19.3	0.4	4.7 (29)	15.8 (134)	0.3	0.1
Arcyria cinerea (typical form)	3.6	5.3	0.7	28.4 (13)	13.7 (37)	2.1	1.4
Didymium iridis	14.5	24.0	0.6	21.5 (53)	10.3 (167)	2.1	1.3
Didymium squamulosum	5.6	17.4	0.3	8.9 (20)	8.9 (121)	1.0	0.3
Lamproderma arcyrionema	7.8	3.0	2.3	34.5 (28)	37.8 (21)	0.9	2.4
Perichaena cf. *dictyonema*	10.6	0.3	36.9	28.2 (38)	14.0 (2)	2.0	74.4
Perichaena vermicularis	3.6	1.1	3.2	3.3 (13)	17.1 (8)	0.2	0.6
Physarum cf. *limonium*	1.1	0.1	7.8	11.8 (4)	7.0 (1)	1.7	13.1
Physarum compressum	35.2	6.6	5.3	52.2 (126)	6.2 (46)	8.4	44.8
Physarum didermoides	14.3	—	∞	138.5 (51)	—	∞	∞
Physarum melleum	0.3	1.3	0.2	165.0 (1)	109.3 (9)	1.5	0.3
Physarum pusillum (badhamioid form)	9.5	1.6	6.0	12.0 (34)	5.6 (11)	2.1	12.9
Physarum superbum	3.6	0.6	6.3	83.5 (13)	6.5 (4)	12.8	81.2

[a] Calculated as quotient of positive moist chamber cultures from inflorescences vs litter.
[b] Calculated as quotient of the mean number of records in moist chamber cultures from inflorescences vs litter.
[c] Calculated as quotient of the mean number of sporocarps multiplied by the mean number of records for moist chamber cultures from inflorescences vs litter (mean numbers of records weighted to equalize the different number of cultures carried out for both substratum types).

TABLE IV. Nutrient analysis for leaf litter (from ground and aerial sources) and decaying floral parts of living inflorescences.

element	litter [a] mean	S.E.	inflo [b] mean	S.E.
N (%)	1.72	0.10	1.75	0.21
P (%)	0.07	0.004	0.26	0.05
K (%)	0.24	0.04	1.64	0.36
Ca (%)	1.90	0.10	1.46	0.35
Mg (%)	0.25	0.02	0.60	0.13
B (ppm)	31.09	5.18	38.02	6.75
Fe (ppm)	524.43	184.25	266.53	84.62
Mn (ppm)	216.95	33.49	730.58	146.91
Cu (ppm)	9.52	0.91	16.14	3.79
Zn (ppm)	55.82	11.56	84.52	6.63
Al (ppm)	1543.66	311.83	244.40	84.28

[a] Mean values calculated from 11 samples with leaf litter (Costa Rica, 1 aerial, 4 forest floor litter, and Ecuador, western Andes, 3 aerial, 3 forest floor litter); each sample composed from aliquot material of substratum of ca 20 moist chamber cultures.

[b] Mean values calculated from 9 series of moist chambers (samples 1–5, 7, 14, 16 and 17 in TABLE II), each sample composed from aliquot material used for all moist chambers prepared for this series.

Ecology and world distribution of *Barbeyella minutissima (Myxomycetes)*

Mycol. Res. 104 (12): 1518-1523 (December 2000). ***Printed in the United Kingdom***

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received 24 September 1999, accepted 17 February 2000

On the basis of all accessible records from the literature and our own field observations and collections, the ecology of the rare myxomycete *Barbeyella minutissima* is described. Analysis of these data, derived mainly from the Northern Ammergauer Alps (Germany) and the Appalachian Mountains (USA: West Virginia, North Carolina), permit the microhabitat requirements of this myxomycete and its ecological associations with other myxomycetes and bryophytes to be elucidated in some detail. *Barbeyella minutissima* appears to have a distribution centred in montane spruce-fir forests, where it is regularly associated with three other species of myxomycetes – *Colloderma oculatum*, *Lamproderma columbinum*, and *Lepidoderma tigrinum*. Several leafy liverworts are associated with *Barbeyella*. Particularly noteworthy is *Nowellia curvifolia*, which seems to be an indicator organism for this myxomycete. A world distribution map of *Barbeyella minutissima* is provided, along with conclusions relating to the putative range of the species.

INTRODUCTION

The minute myxomycete *Barbeyella minutissima*, described by Meylan (1914) from the Swiss Jura Mountains, was long thought to be exceedingly rare. Indeed, this species has been recorded from a limited number of localities, where it is often represented by collections of only a few sporocarps. Some reports indicate that *B. minutissima* is more common but restricted to special microhabitats; these include descriptions of abundant fruitings from western North America (Kowalski & Hinchee 1972), from the Appalachians in eastern North America (Stephenson 1983), and from the German Alps (Schnittler & Novozhilov 1998).

Here, we attempt to elucidate the ecology and world distribution of *B. minutissima*. The relatively small fruiting bodies of most myxomycetes, produced only a few days in the year in often very hidden habitats, make it especially difficult to obtain distribution data. As such, with the first world distribution map produced for a myxomycete, this paper represents an effort to demonstrate the possibilities and limitations of deriving ecological characterisations for these organisms by means of a careful compilation of literature data combined with information obtained from field studies.

MATERIALS AND METHODS

To obtain distribution data for *Barbeyella minutissima*, all literature records were assembled into a data base, and geographical co-ordinates and localities were reconstructed and specified as exactly as possible. In addition, all currently active myxomycete specialists were asked for any as yet unpublished records. Furthermore, all accessible herbarium collections were checked for the presence of other myxomycetes and bryophytes, and the type of woody substratum was identified by microscopic examination of features of the pieces still present as parts of the collection. Extensive collections and field observations were made during a two-week long investigation in the Northern Ammergauer Alps, Bavaria, as well as during several days in the Applachians (Blister Run, West Virginia, see below), where developing sporocarps could be brought back to the laboratory and observed under the microscope.

The following list encompasses all localities from which *Barbeyella minutissima* has been collected, based upon all information available to the authors. Herbarium abbreviations and collection numbers are given for all specimens examined by us during the present study. Small letters preceding the collection numbers refer to private collectors (gf, G. Galindo Flores; ne, H. Neubert; sc, M. Schnittler; yy, Y. Yamamoto). For published records, a literature citation is provided in parentheses. With a few exceptions for which references are given, names of myxomycetes follow Martin & Alexopoulos (1969). Morphological terms used for descriptions of sporocarps are those found in Lado & Pando (1997).

1. **Finland**, Kittilan Lappi, Kittilä: decayed, wet *Picea*, on liverworts and bare wood, Homevuotso, Enontekiön Lappi, *ca* 500 m, 67° 30’ N 24° 90’ E ± 25 km, Nov. 1981 (Härkönen 1981); 2. **Finland**, Enontekiö, Vuontisjärvi: very decayed

Picea, on liverworts, Saivokero, *ca* 500 m, 68° 25' N 24° 10' E ± 25 km, Nov. 1981 (Härkönen 1981); 3. **Germany**, Baden-Württemberg, Upper Rhine Valley: a few sporocarps on bark of *Malus*, near Bühl, *ca* 200 m, 48° 40' N 08° 08' E ± 25 km, Nov. (Neubert *et al.* 1993: 46); 4. **Germany**, Baden-Württemberg, Black Forest: on a mossy log of *Abies alba*, Wildsee bei Ruhestein, *ca* 930 m, 48° 45' N 8° 30' E ± 50 km, Nov. 1991 *ne2156* (Neubert *et al.* 1993: 46); 5. **Germany**, Bavaria, Karwendelgebirge; Garmisch-Partenkirchen: on a decorticated logs of *Picea*, moist wood covered with a thin moss and algae layer, in a narrow, deep left side valley of the valley 'Partnachklamm', spruce-fir woodland *ca* 800 m SSO of the 'Kochelberg-Alm', 1050 ± 20 m, 47° 31' 55" N 10° 24' 20" E ± 3 km, 18-24 Oct. 1994, *M. Schnittler sc5367, 5388, 5359, 5404, 5435, 5442, 5447* (Schnittler & Novozhilov 1998); 6. **India**, Himachal Pradesh, Dalhousie: on liverworts, subalpine spruce-fir woodland >1200 m, Katalope Wildlife Sanctuary 32° 33' 00" N 76° 02' 30" E ± 10 km, 07 Sept. 1971 (Lakhanpal & Mukerji 1976); 7. **India**, Himachal Pradesh, Kulu: Jagat Sukh 19° 30' N 96° 50' N ± 25 km, 24 Sept. 1971, *S.S. Dhillon*, BPI 818217 (in a collection of *Lepidoderma tigrinum*); 8. **Japan**, Nagano: Kiso forest 36° 00' N 137° 40' E ± 25 km (Emoto 1933); 9. **Japan**, Hokkaido: on decayed, decorticated wood covered with liverworts, 43° 30' N 143° 00' E ± 50 km, 08 June 1991, *Y. Yamamoto yy11686* (Yamamoto 1995); 10. **Japan**, Kochi Prefecture: on decayed, decorticated wood covered with liverworts, Monobe-mura, Mt. Miune, *ca* 900 m, 33° 30' N 133° 30' E ± 25 km, 23 Nov. 1992, *Y. Yamamoto yy12857*; 11. **Mexico**, Tlaxcala, Mpio. Huamantla: bosque de *Pinus-Abies*, Volcan La Malintzi, *ca* 3300 m, 19° 20' N 97° 50' W ± 25 km, 30 Jan. 1986, *L. Villarreal gf1252, 1334a* (BPI 819189); 12. **Mexico**, Veracruz, Los Gallos; Mpio. de Xico: on decayed wood and mosses, coniferous forest, Cofre de Perote 19° 30' N 96° 50' W ± 25 km (Villarreal 1983); this locality: Bosque de *Pinus-Abies*, 2850 m, 30 June 1986, (BPI 818239, in a collection of *Lepidoderma tigrinum*); 13. **Poland**, Bialowieza National Park: primeval woodlands, Puszcza Bialowieska 52° 40' N 23° 52' E ± 15 km, 1926 (Jarocki 1931); 14. **Poland**, Eastern Carpathians: several localities in the Czarnohora range, 1100 - 1400 m, 49° 30' N 22° 30' E ± 75 km, Aug. – Sept. 1924-25 (Jarocki 1931); same locality: in piceto Zarosiak, *ca* 1300 m, Sept. 1932, LE 47318 [H. Krzemieniewska, Myxom. Poloniae Exsciccati #144]; 15. **Romania**, Carpathian Mts.: Neamtu, near the monastry, 48° 50' N 23° 10' E, Aug. 1926 [exsiccate series M. Brandza.] (TRTC 7880, discovered in #7, *Diderma montanum*), Oct. 1926 (TRTC 7923, in #95, *Diderma montanum*); 16. **Switzerland**, Canton Vaud, Jura Mts.: ad hepaticas: *Lophozia longiflora*, *L. longidens*, *Blepharostoma trichophyllum*, Le Chasseron, Deueriaz-Dessus, *ca* 1400 m, 47° 45' N 6° 30' E ± 40 km, Sept. 1913 (Meylan 1914, type locality, holotypus in LAU; recently refound at the same locality. B. Ing, pers. comm.); 17. **Switzerland**, Jura Mts.: found twice near St. Croix, *ca* 1200 m, 46° 50' N 6° 30' E ± 10 km, leg. Ch. Meylan (Lister 1925: 163); 18. **USA**, California, El Dorado Co.: mossy, dead wood, Luther Pass, *ca* 2310 m, 38° 35' N 120° 15' W ± 40 km (Kowalski 1973); 19. **USA**, California, Humboldt Co.: Big Lagoon School, 41° 12' N 124° 10' W ± 40 km, 30 Jan. 1972 *CHSC 12121, 13493* (Kowalski 1973); 20. **USA**, California, Mendocino Co.: leafy liverworts, MacKericher Beach State Park 39° 30' N 123° 45' W ± 50 km, 23 March 1970 (Kowalski 1973); nearby: on moss, Simpson Lane, 2 Mi east of Hwy 1, 15 April 1976, *CHSC* (not seen), 21. **USA**, California, Placer Co.: decayed wood, Serene Lake, *ca* 2010 m, 39° 10' N 120° 15' W ± 40 km, 28 June 1971 (Kowalski 1973); 22. **USA**, North Carolina, Swain Co., Great Smoky Mountains National Park: Mt. Collins; 1768m, 35° 30' N 83° 30' W ± 10 km, May 1983, 1984, Sept. 1985, *FWVA 1557, 2399, 2404, 3336, 3587, 3620, 3634, 3635, 3645, 3649, 3662, 3663, 3668, 3679, 3680, 3682, 3684, 3686-3688* (Stephenson 1983); 23. **USA**, Oregon, Crater Lake National Park: decaying wood near melting snow, Munson Ridge, *ca* 1950 m, 43° 00' N 122° 10' W ± 20 km, June 1967 (Curtis 1968); 24. **USA**, Virginia, Grayson Co.: on liverworts on a moderately decayed piece of wood, Mt. Rogers, 1720 m, 36° 40' N 81° 30' W ± 10 km, 07 Oct. 1986, *FWVA 4292* (Stephenson 1983); 25. **USA**, Washington, Mt. Rainer National Park: Cayuse Pass, *ca* 1410 m, 46° 55' N 121° 50' W ± 25 km, 25 June 1970, *CHSC 10716, 10793* (Kowalski & Hinchee 1972); this locality, Panther Creek, 790 m, *CHSC 10713*; 26. **USA**, Washington, Whatcom Co.: on liverworts *ca* 16 Mi East of Glacier, *ca* 1200 m, 48° 52' N 121° 40' W ± 15 km, 18 June 1970, *D.T. Kowalski, CHSC 10448* (=BPI 819188), *10454, 10549, 10555*; 27. **USA**, West Virginia, Pocahontas Co., Appalachian Mts, on liverworts on decorticated wood, Gaudineer Scenic Area, *ca* 1100 m, 38° 51' 00" N 79° 45' 06" W ± 10 km, 11 Sept. 1996, *S. Stephenson, FWVA 4225, 7075*; 04 Oct. 1997, *M. Schnittler sc11300*; 28. **USA**, West Virginia, Randolph Co., Appalachian Mts.: Blister Run, 1112 m, 38° 51' N 79° 45' W ± 5 km, 26 Oct. 1993, *FWVA 2299, 3936* (Stephenson 1983); 23 Aug. 1997, *Y. Novozhilov, FWVA 9042*; 04 Oct. 1997, *M. Schnittler, sc11287, 11295*.

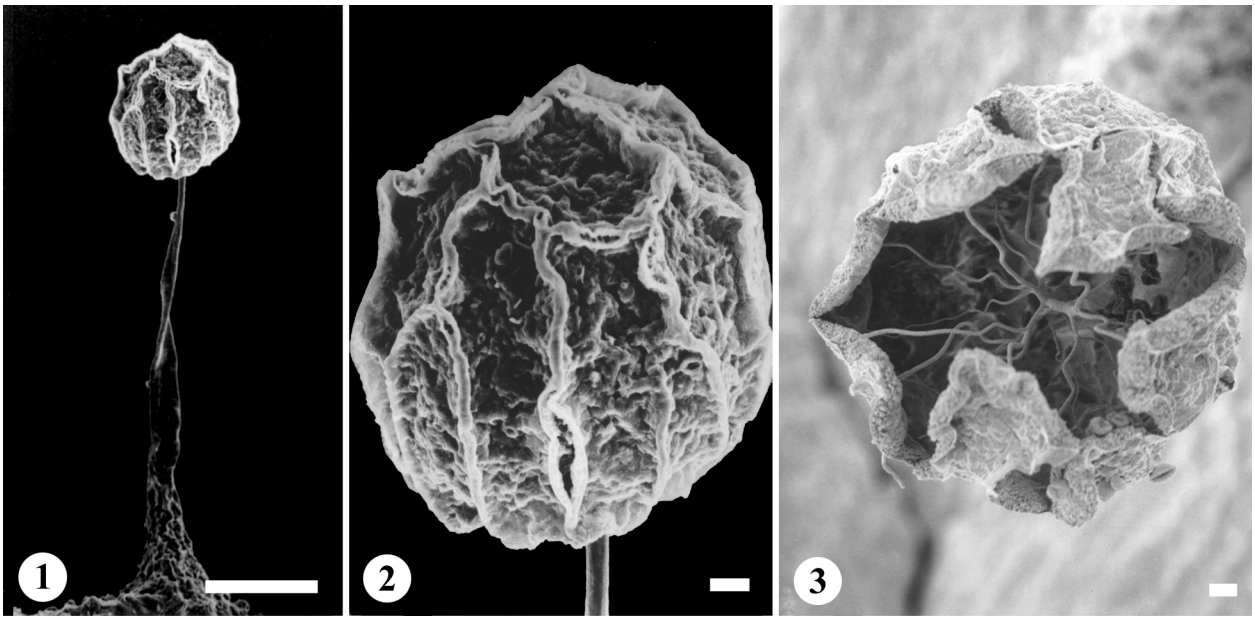
RESULTS AND DISCUSSION

Sporocarp morphology

Barbeyella minutissima is a very distinctive myxomycete; the species can be identified easily by the tiny, black and long-stalked sporocarps. Since detailed taxonomic descriptions were given by Kowalski & Hinchee (1972) as well as by Lakhanpal & Mukerji (1976), we only add our own observations from field studies. As seen in the Northern Ammergauer Alps (loc. 5), and thus confirming the report of Jarocki (1931), *Barbeyella minutissima* develops apparently from a protoplasmodium that first emerges as a transparent, colourless and hemispherical protoplasmic mass about 1.5 times the diameter of the mature sporocarp. Later, it becomes sprinkled with darker tints and turns finally dark in the centre. As in the *Stemonitales*, the translucent milky white protoplasma mass moves up the stalk, lengthening it as a result. As a next step, capillitium and peridium are formed, and finally the remaining protoplasm segregates into spores. The whole process takes about one day at room temperature. The mature sporocarps, which are usually scattered but occur often in large colonies, range from 0.2–0.4(–0.9) mm in height (Fig. 1). At maturity, the peridial plates open with a zipper-like structure, releasing the dark, spinulose warted spores (Fig. 2). An inner, tree-like branched system of capillitial threads, arising from the columella and connected to the peridial plates (Fig. 3), hinders these plates from breaking away at maturity, allowing the sporotheca to work like a capsule of a poppy plant, releasing spores continuously over a longer time.

Distribution

Unfortunately, numerous records of *Barbeyella* lack exact information about microhabitat and elevation. Perhaps all collections from the European mountains were made late in the year and at elevations between 500 and 1300 m. The specimens from western North America date from March to September and were collected mostly at higher elevations,



Figs. 1 - 3. SEM micrographs showing the habit of *Barbeyella minutissima.* Figs. 1 and 2 show specimen sc5404 from the German Alps, Bavaria, Fig. 3 shows specimen FWVA 3620 from the Great Smoky Mountains, eastern North America. **Fig. 1.** Habit of a whole sporocarp. Bar = 100 µm. **Fig. 2.** Sporotheca with the plates of the peridium breaking along pre-formed ridges. One large and several small fissures are visible along the dehiscence lines. Bar = 10 µm. **Fig. 3.** Opened mature sporocarp showing the branches of the capillitium. Bar = 10 µm.

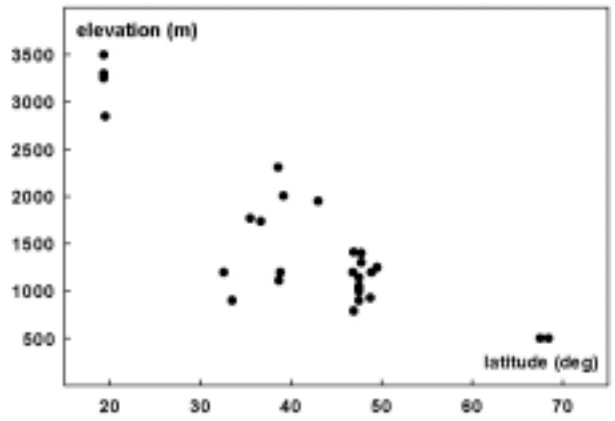


Fig. 4. Diagram of latitude and elevation data for 27 localities from which *Barbeyella minutissima* was collected.

ranging from 2000-2300 m. Two California records may originate from lower elevations, but these were collected in January. The southernmost records are from Mexico, where specimens were collected at elevations between 3000 and 3500 m. In Europe, *Barbeyella* seems to be occur in mountainous and altomontainous regions, but it is not a true alpine myxomycete like the nivicolous species. As indicated by the Finnish record, *Barbeyella* can be found exceptionally in the boreal zone at lower elevations. Collections from eastern North America were mostly from mountainous and altomontainous regions. As shown in Fig. 4, a correlation exists between elevation and latitude.

The two Finnish records originated from the boreal zone, and the Polish record from the Bialowiecza Forest came from the edge to this forest zone. In spite of intensive searching, *Barbeyella* was not found in light, larch-dominated boreal woodlands influenced by a continental climate (Novozhilov 1993). It thus seems evident that *Barbeyella* has a predominantly mountainous distribution, with an optimum in montane to altomontane spruce-fir forests. In Fig. 5, the putative range of the species is constructed by superimposing the ranges of mountainous regions (orobioms), as defined by Walter & Breckle (1986), and the world ranges of the genera *Abies* and *Picea*. This results in a fragmented range pattern dispersed throughout the mountains of the temperate part of the northern hemisphere. This putative range includes all known records except the two from Finland and the one from the Bialowiecza Forest in Poland. An unique curiosity is a record from moist chamber, reported from the Rhine valley on bark of *Malus* after three days of culture (Neubert et al. 1993: 46).

Ecology

All collections are very probably from coniferous forests. None of the 41 collections examined in this study was on deciduous wood, and in all cases the wood was decorticated. Spruce or fir dominate in most of the montane localities from which the majority of the records of *Barbeyella* are known: *Picea abies* (L.) Karst. *Abies alba* L. (Germany, Schnittler & Novozhilov 1998), *P. rubens* Sarg. / *A. balsamea* (L.) Mill. (northern) and *A. fraseri* (Pursh) Noir. (southern Appalachian Mts., Adams & Stephenson 1991), *P. smithiana* / *A. pindrow* (northwestern India, Stephenson & Adams 1995).

As indicated by the substrate citations, mostly liverworts on decorticated wood, *Barbeyella* is restricted to a continuously moist and cool environment. The specimens examined show a very uniform microhabitat: strongly to slightly decayed, always decorticated wood of coniferous trees, overgrown by liverworts (40-100% coverage). Table 1

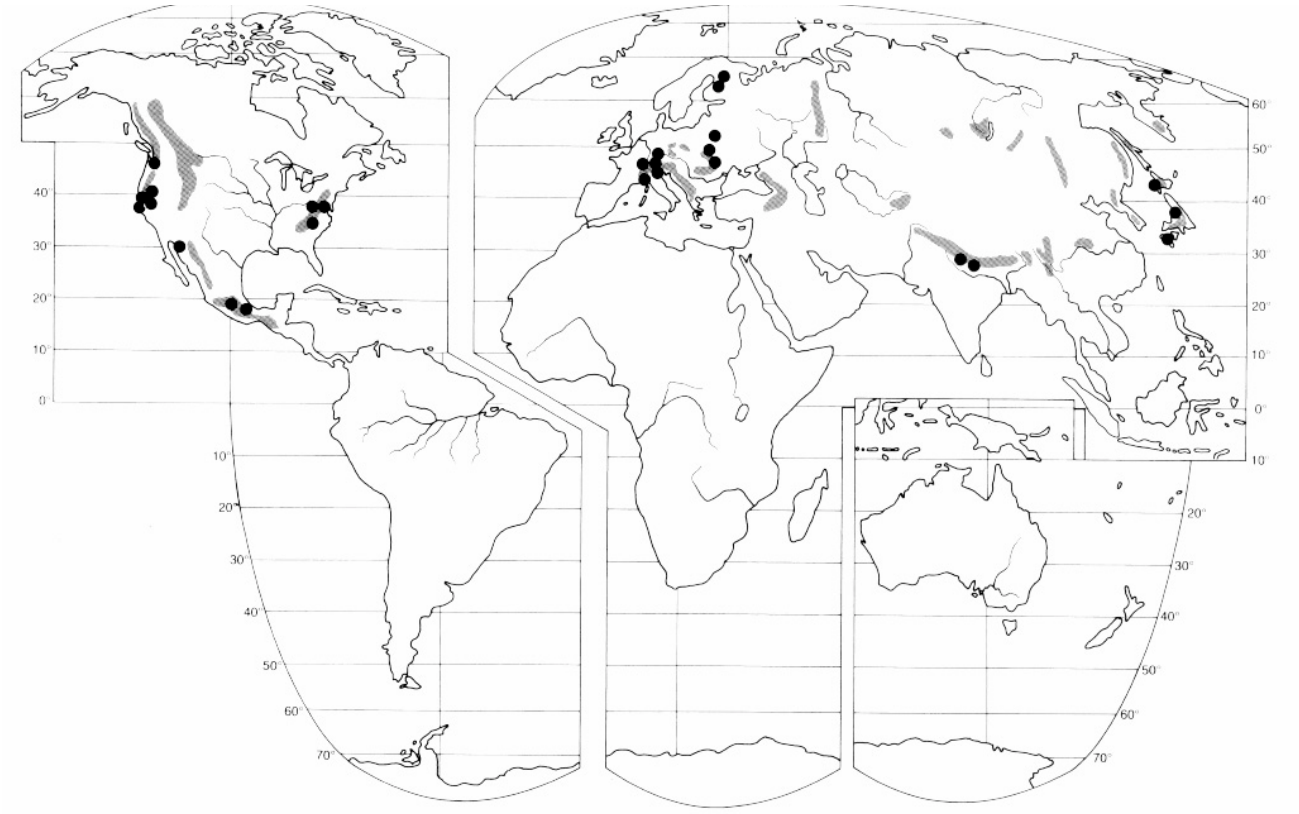


Fig. 5. Preliminary distribution map for *Barbeyella minutissima*. As an approach to determine the putative range of the species, montane areas (orobioms according to Walter & Breckle 1986) with spruce-fir forests are shaded.

lists the liverwort species observed in 25 records with substrata pieces large enough to allow their determination, and the liverwort data given by Meylan for the holotypus. Two genera of liverworts were registered for roughly one half of all specimens investigated: *Nowellia* with *N. curvifolia* (Dicks.) Mitt. (14 specimens) and *Cephalozia* (12 specimens). *Nowellia curvifolia* is described as almost completely restricted to moist decaying logs, often occurring as a pioneer species on decorticated logs, with a pH optimum between 4.6-5.2 (Schuster 1969, 1974). This liverwort, often forming almost pure mats, could well serve as an indicator species for *Barbeyella*. The species of the liverwort genus *Cephalozia* are more ubiquitous, with *C. lunulifolia* (Dumort.) Dumort., often associated with the American specimens of *Barbeyella*, also inhabiting peat bogs and moist rocks. In spite of the occurrence of *Colloderma oculatum* (C. Lippert) G. Lister in moss covers on rocks and boulders provided with trickling water (Schnittler & Novozhilov 1996), *Barbeyella* was never recorded from this microhabitat.

Stephenson & Studlar (1985) considered *Barbeyella* as strongly bryophilous. Observations and collections made in a narrow and cool valley system in the Northern Ammergauer Alps (Schnittler & Novozhilov 1998) appear to add yet another aspect to the ecology of this myxomycete – the association with unicellular algae, which form a slime layer providing continuous moisture as well as a microenvironment suitable for microbial growth. In five of seven collections of *Barbeyella*, algae were clearly visible, forming a thin, slimy layer on the wood surface. Most of the collections cited in the literature mention liverworts as a substratum, but none of these noted the much less conspicuous algae. Due to the often solid inner wood of the decorticated logs upon which the largest colonies tend to occur, we assume that the plasmodia live in the outermost substratum layer formed by a slimy cover of algae, perhaps feeding upon the algae or the bacteria living in association with the polysaccharide sheaths of the algae. With their leaves protruding from the layer of algae, liverworts provide a drier substrate for fruiting. Frequently, sporocarps were found to occur on such leaf tips.

Barbeyella often occurs in association with other myxomycetes. From the 41 collections studied, 29 had other species of myxomycetes present on the same piece of substratum. Species recorded more than once included *Lepidoderma tigrinum* (11 times), *Lamproderma columbinum* (Pers.) Rostaf. (10), *Colloderma oculatum* (6), *Diderma montanum* (4), and *Cribraria purpurea* Schrad. (3). The first three species also were mentioned also by Jarocki (1931) as 'often associated' with *Barbeyella*, but without providing data for single collections. *Lepidoderma tigrinum* is well-known for preferring a covering of liverworts on damp, coniferous logs (Ing 1994). These associations probably occur throughout the world range of *Barbeyella*. Accompanied by one or more of the first three species mentioned above, *Barbeyella* has been recorded from Germany, Poland, eastern North America, India, Mexico, and Japan. When herbarium collections of the myxomycete species mentioned above were checked, in several cases overlooked sporocarps of *Barbeyella* were found, as for example in two boxes of Brandza's exsiccate series.

The pattern of occurrence during the year (Fig. 6) shows

Table 1. Liverworts recorded from collections of *Barbeyella minutissima* examined in this study. The locality number cited in column „Loc." corresponds with the numbers given in the locality descriptions.

		Species of liverworts															
Collection	Loc.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
ne2156	4							x									
sc5404	5		x	x										x	x	x	x
sc5442	5		x	x			x				x			x		x	x
yy11686	9								x					cf			
gf1252	11							x									
LAU	16		x									x	x				
FWVA546	22													x			
FWVA1557	22									x							
FWVA2399	22													x			
FWVA2404	22									x							
FWVA3634	22					x											
FWVA3645	22					x								x			
FWVA3649	22													x			
FWVA3657	22													x			
FWVA3651	22	x												x			
FWVA3663	22													x			
FWVA3677	22					x				x							
FWVA3679	22													x			
FWVA3686	22													x			
FWVA3688	22					x											
FWVA3692	22					x											
FWVA3867	22							x									
FWVA3608	24				cf												
FWVA2394	27													x			
sc11300	27							x						x			
FWVA2299	28					x											

The following liverworts were found associated with *Barbeyella* (x, occurrence, cf, material too scanty to allow a definite determination): 1, *Anastrophyllum michauxii*; 2, *Blepharostoma trichophyllum;* 3, *Calypogeia* sp.; 4, *Cephalozia bicuspidata*; 5, *Cephalozia lunulifolia*; 6, *Cephalozia lacinulata*; 7, *Cephalozia* sp., 8, *Jungermannia* sp., 9, *Lepidozia reptans*; 10, *Lophocolea heterophylla*; 11, *Lophozia longidens*; 12, *Lophozia ventricosa*; 13, *Nowellia curvifolia*; 14, *Plagiochila asplenioides* ssp. *porelloides* ; 15, *Riccardia palmate*; 16, *Tritomaria exsecta*.

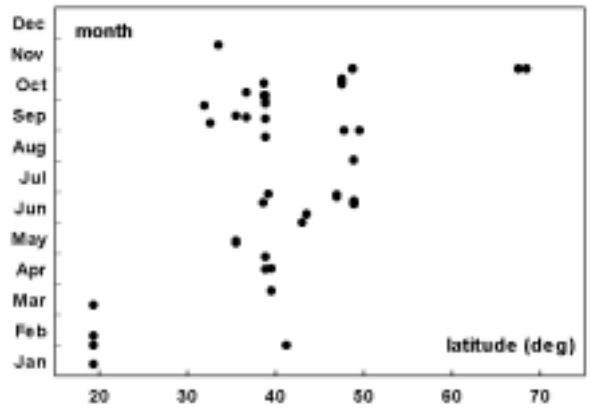


Fig. 6. Phenology of *Barbeyella minutissima*, showing latitude and collection data for 58 records.

that in southern regions *Barbeyella* fruits in the winter, whereas in more northern regions the fructification peak occurs in September to early October (eastern North America) or mid-October (Germany). Observations from the German Alps (Schnittler & Novozhilov 1998) provide evidence that *Barbeyella* can develop at temperatures between 0 and 10 °C. These collections were made after a first period of frost in the year, followed by a couple of warmer autumn days. Only the most cool and shady parts of the narrow ravines investigated in this study harboured *Barbeyella*. In summary, *Barbeyella* seems to have the following environmental requirements: (1) a shady coniferous woodland occurring in a habitat with continuously high air humidity and (2) a locality characterised by a humid climate providing at least one cooler period in the year.

Due to the difficulties in elucidating the true distribution and ecology of such a minute organism as *Barbeyella minutissima*, the distribution map given herein provides only a rough picture. However, even with the few known localities, it at least demonstrates that not all species of myxomycetes are ubiquists. Instead, some species may inhabit rather narrow ecological niches. Since microclimatic factors and availability of microhabitats, rather than macroclimate, will limit their distribution, only careful examination of microhabitat requirements can elucidate world-wide distribution patterns in myxomycetes.

ACKNOWLEDGEMENTS

Field work was supported by the German Academic Exchange Service (DAAD) for the third author, and laboratory work by a further DAAD scholarship for the first author. For loans of

specimens we are indebted to A. Rossman (BPI, Beltsville), A. Estrado-Torrez (Mexico), and Y. Yamamoto (Japan). For determination of liverworts we wish to thank S. Studlar (West Virginia University, USA), H.-J. Zündorf (Herbarium Haussknecht, Jena) and A. Potemkin (Komarov Botanical Institute, St. Petersburg).

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Corresponding Editor: B. Senn-Inlet

Chapter 14. Ecology of myxomycetes of a winter-cold desert in western Kazakhstan

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Mycologia (in review)

Abstract: The moist chamber culture technique was used to study the ecology of myxomycetes from a winter-cold desert of the Mangyschlak Peninsula (western Kazakhstan). A rather species-poor community of 27 myxomycete taxa, two protostelids and some undifferentiated myxobacteria was found. The rank-abundance plot is described best by a log series or a geometric model. The species that developed formed a successional sequence that correlated well with morphological features of the fructifications. Using canonical correspondence analysis, environmental parameters recorded within substrate sampling were related to species abundances. Substratum type and pH accounted for most of the variance in species distribution. Using five environmental parameters and development time as resource states, niche breadths were calculated for the 18 most common species in the study. Bark-inhabiting species were found to be more specialized than those inhabiting litter. Members of the first group tend to develop rapidly, have small, usually stalked sporocarps without a peridium and possess protoplasmodia or minute aphanoplasmodia. Members of the second group tend to have a phaneroplasmodium and develop more slowly into larger, usually sessile fructifications with often well-developed peridia. A plot of niche overlap vs Cole index of association for the most common species revealed frequent associations among species with small sporocarps and proto- or aphanoplasmodia. In contrast, litter-inhabiting species with phaneroplasmodia seem to avoid each other. Myxomycetes in the investigated winter-cold desert behaved as rather opportunistic k-strategists, quickly using all temporally and spatially changing microhabitats.

Key Words: myxomycetes, protostelids, myxobacteria, ecology, microhabitat, desert

Introduction

Myxomycetes (plasmodial slime molds) are a group of phagotrophic eukaryotes comprising about 1000 legitimately described subgeneric taxa (Mitchell 1999). The first of the two trophic stages in the life cycle is a true microorganism and consists of uninucleate amoeboid or flagellate cells. The second stage is a distinctive multinucleate structure, the plasmodium, that can achieve macroscopic dimensions (Martin et al 1983). Plasmodium types among myxomycetes range from microscopic structures (protoplasmodia) that form only one fructification, to larger aphanoplasmodia and phaneroplasmodia. The latter are very mobile, achieve macroscopic dimensions and give rise to often several hundred fructifications (Alexopoulos 1969). The spores complete the life cycle by germinating to produce the uninucleate amoeboflagellate cells. Remarkable is the presence of three different dormant stages in the life cycle. Myxamoebae can convert into microcysts and plasmodia into sclerotia. Finally, very durable spores are produced (Erbisch 1964).

Compared with the recent progress in taxonomy (Schnittler and Mitchell 2000), the ecology of the myxomycetes is still poorly understood. Comprehensive ecological studies have been done only for field-collected myxomycetes in woodland ecosystems (Drozdowicz 1977; Maimoni-Rodella and Gottsberger 1980; Eliasson 1981; Stephenson 1988, 1989). For myxomycetes from desert ecosystems, the papers of Blackwell and Gilbertson (1980a, 1984) from the Sonoran desert, Arizona, are the only significant contributions to ecology.

This study presents data about the ecology of a community of myxomycetes and myxomycete-like organisms in a winter-cold shrub desert with a vegetation cover similar to that of the American Great Basin. In addition to the plasmodial slime molds (Myxomycetes), protostelids (Protosteliales) and the gliding, fruiting bacteria (Myxobacteriales) were included, since members of all three systematic groups share important features such as (i) unicellular vegetative stages that prey on bacteria and (ii) fruiting bodies that provide spores or spore-like cells for dispersal through the air. In contrast to most other papers that compare species assemblages within vegetation units (habitats), this study focuses on the microhabitat as the primary environment for the trophic stages of myxomycetes, with the goal of defining niches for individual species. Due to the virtual absence of colonies of myxomycetes in the field during the time of the survey, the moist chamber culture method (Gilbert and Martin 1933) was employed throughout. All taxa found in this survey are described in Schnittler and Novozhilov (2000).

Materials and Methods

Study area.—Field work was carried out in April and May 1995 during a journey extending over 1500 km through the Mangyschlak Peninsula, located in western Kazakhstan (ca 52°13'E 44°01'N) on the eastern shore of the Caspian Sea. The region consists of stony badlands, inhabited by scattered shrubs and numerous perennial and annual plants that form a very sparse vegetation cover. Due to the very continental climate with cold winters and hot summers, trees as well as succulent plants are absent. Sand dune areas scattered throughout the region tend to have a richer vegetation, with up to 3 m tall shrubs of *Calligonum* spp. and *Haloxylum aphyllum.* Together with *Atraphaxis replicata*, a common shrub of the stony badlands, these woody plants can easily reach ages of 100 years and more, as indicated by ring counts of wood samples. A detailed description of the region, its climate and habitats is given in Schnittler and Novozhilov (2000).

Substratum sampling and microhabitat descriptions.—All substrata were sampled within plots of homogenous vegetation covering 500–1000 m^2. Vegetation coverage as well as species composition and abundance of all vascular plant species were recorded. Within a sampling plot, all microhabitats suitable for myxomycete growth were classified and sampled. The term 'microhabitat', herein used *sensu* Stephenson (1988), refers to a small section of a habitat that is spatially homogeneous in both biotic and abiotic factors, i.e., a section of the trunk of a shrub, or small, shaded patches of litter with relatively the same thickness, moisture, etc. For each substratum sample, a set of environmental parameters was measured or classified into 4–10 predefined states. An effort was made to keep these parameters as constant as possible for the 5–10 individual substratum samples from one microhabitat in a given plot (e.g., 2–3 scales 1–3 cm long of dead outer bark of 5–10 shrubs of comparable age and trunk diameter), which were pooled for one moist chamber. Three main groups of myxomycete substrata were sampled: bark, litter and droppings of herbivorous animals. Bark as the most diverse substratum was further subdivided in five 'texture groups' according to its physical features (TABLE II). These were smooth and thin bark not furrowing with age (texture group b1); smooth bark that breaks into flakes rolling outward in aging twigs, sometimes forming curls on dying twigs (b2); smooth bark peeling in long, more or less loose strips like that of juniper, in older trunks often forming a sheath of 2–5 layers (b3); solid and often deeply furrowed bark with an appearance like that of an oak (b4); and fibrous bark with a fur-like surface of fine fibers (b5). Litter was classified into leafy litter (ll) consisting of small (1–2 cm), often leathery and slowly decaying leaves, sometimes forming 1–2 cm thick, dry and loose mats under shrubs (e.g., *Rhamnus sintenisii* and *Ammodendron eichwaldii*); grass litter (gl) mostly formed by *Agropyron fragile* and *Stipagrostis pennata* growing in narrow ravines or dune depressions with dense mats or tussocks of shoots from the previous year up to 10 cm thick; and herbaceous litter (hl) from small, still herbaceous and slightly succulent twiglets of shrubs with scale-like leaves, typically 1–3 diam. Such herbaceous litter included all species of *Haloxylon* and *Calligonum*, where twiglets can accumulate over years to 1–2 cm thick mats. Dung ranging from 2 x 3 cm (camel) to 0.5 x 1.5 cm (rodents of the genus *Citellus*) was not further differentiated.

Environmental parameters included sampling height above the ground, light intensity, wind exposure, water retention and pH of the substratum. Omitted from further analyses were substratum moisture (all substrata had

dried out completely at the beginning of the short spring season), the diameter of shrub trunks and its exposure. All desert shrubs had stems with diameters hardly exceeding 10 cm, thus forming no pronounced rain-sheltered sides as it is often the case for larger, free-standing trees. Also, the sparse flora of epiphytic lichens showed an equal dispersion around the stems. Sampling height was recorded in 5 cm-intervals, but for further data evaluation classified into five categories: 0–5, 5–10, 10–20, 20–50 and higher than 50 cm. Light intensity was estimated using five categories ranging from complete darkness (e.g., under stones) over various degrees of shade to full sunshine. Wind exposure was described using a scale of four categories reaching from fully sheltered to strongly exposed. To estimate the water retention of bark, sticks about 8 cm long were removed from the trunks of all sampled species of shrubs. Two, sometimes 3–6 sticks with typical bark structure were collected within the diameter range used for substratum sampling. Their ends were covered with nail polish to prevent water from soaking through wood pores. Sticks were weighed dry, then watered for two hours, simulating strong rainfall, and weighed again. The differences between dry and wet weight, and diameter and length of the sticks were used to calculate water retention in mL/dm^2 bark surface. For litter, a 5 x 5 cm piece from each substratum collection with approximately the same density and thickness as the litter mat observed in the field was prepared, placed on a fine sieve and treated as described for bark. In a similar way, animal droppings were analyzed, calculating their approximate surfaces by assuming a globose or half-globose shape. pH values were measured twice for each moist chamber culture (day 3 and day 20 after starting the culture) on three wet substratum pieces with a solid state probe pHuture and an Orion model 610 pH meter. Fluctuations of 0.1–0.2(–0.4) units were found between individual substratum pieces, but the pH remained stable between day 3 and day 20 (paired t-test, $P < 0.05$). Therefore, the mean value of the measurement at day 3 was used in all further analyses. Average pH values were calculated with delogarithmated values, and optimum pH was determined by weighting of these values with the respective absolute abundances of a species in a moist chamber (as described below).

Moist chamber cultures.—For the 146 moist chamber cultures prepared in this study, 5–10 substratum samples from the same microhabitat in one plot were pooled to prepare one culture, having the whole surface of a disposable plastic petri dish (63.6 cm^2) evenly and densely covered with substratum pieces. All cultures were started simultaneously as described by Härkönen (1977) by moistening with distilled water adjusted to pH 7.0 and kept for two months at room temperature (ca 22–23 C) in a bright room sheltered from direct sunlight. Cultures were checked five times (2, 6, 11, 21, and 40 d after start) under high magnification with a dissecting microscope. For each culture, the number of sporocarps observed for each myxomycete species was counted (for species with up to several hundred sporocarps per colony) or estimated, counting a part of the colony and using the surface area covered by this part as a counting unit to estimate the total sporocarp number (species with minute fructifications in colonies of several thousand sporocarps). Plasmodiocarpous myxomycetes such as *Perichaena vermicularis* were counted by assuming a plasmodiocarp would consist of a row of circular sporocarps with the same diameter as the plasmodiocarp width. The control day with the highest sporocarp number was used to calculate weighted abundances (see below).

Species identification.—Names of vascular plants are as given in Czerepanov (1995), following a regional checklist compiled by Safronova (1992). For all other organisms of this study, nomenclature and taxonomic descriptions are given in detail in Schnittler and Novozhilov (2000). For the ecological analysis presented herein,

species complexes that could not be clearly separated taxonomically were treated as aggregates. These were the closely related taxa *Didymium anellus* and *D. inconspicuum*, the forms of *Physarum notabile,* and at least five undifferentiated myxobacteria. Ten myxomycete records from the field (all represented by *Didymium squamulosum* or *Physarum notabile*) were omitted from this study.

Data analysis.—To estimate the extent to which the survey was exhaustive in terms of recorded species, a bootstrap analysis, modified from the procedures given in Efron (1982) and Krebs (1999), was carried out. The sequence of samples (moist chamber cultures) was permutated randomly and the cumulated number of records was plotted against the number of samples. After 100 repetitions of this procedure, the mean cumulated number of records increased in an almost linear manner with the number of samples, indicating that 100 runs are sufficient for the analysis. The corresponding plot of the mean cumulated number of species vs 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 expect. The rank-abundance plot of all myxomycete species was used to test four species abundance models (geometric series, log series, log normal and broken stick) according to the procedures described in 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 in log2 (doublings of the number of individuals) as a parameter. The procedure described by Pielou (1975) for fitting a truncated log normal distribution gives an additional estimate of the number of species to be expected.

For all ecological analyses, one or more of the following measures were applied: (i) number of records per species, with the occurrence of a species in one culture constituting a record, (ii) absolute abundance based on the number of sporocarps for a species in one culture or (iii) weighted abundance. The latter was calculated by dividing the absolute number of sporocarps recorded in a particular culture by the mean value for all cultures yielding this species. Consequently, the sum of all weighted abundances for all cultures with a particular species is equal to the number of records for this species. This measure was used for all comparative analyses, since it equalizes the very different fructification numbers of the species (for an *Echinostelium*, 200 sporocarps were still a small colony, but for a *Physarum* this would represent a rather large colony).

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). As abundance measures, numbers of records or the total abundance were used. As niche dimensions, the following parameters were taken: substratum type (9 resource states), pH (8), sun (5), wind (4), height (5) and development time (5). For development time, the five control days of the moist chamber cultures (2, 6, 11, 21 and 40) were chosen as resource states. The pH value, ranging from 4.5 to 8.5, was subdivided into classes of 0.5, whereas resource states for the other parameters were defined as explained above. In the same manner, niche overlap (NO) was computed, using the symmetrical index $NO_{ik} = \sum P_{ij} P_{ik} / \text{sqrt} (\sum P_{ij}^2 \sum P_{ik}^2)$, with P_{ij} and P_{ik} as the proportions of the *i*th resource state by the *j*th and *k*th species, respectively (Levins 1968, modified by Pianka 1973). Values for niche breadth and niche overlap range from 0 to

1. Since not all environmental parameters recorded in the present study are completely independent from each other, overall values for niche overlap were calculated as the arithmetic mean of the overlaps for each niche dimension (May 1975).

For analysis of myxomycete associations (here used in the sense of co-occurrence), the Cole (1949) index of interspecific association and its standard error was computed. This index is based on a 2 x 2 contingency table for presence and absence of a pair of species in one moist chamber, ranging from -1 (the species never occur together) to 1 (the species always occur together). The significance level of deviations between observed association frequencies and those expected by chance was determined with a chi-square test. To calculate indices for species diversity H' on various substrata, Shannon's formula $H' = - \sum (P_i \ln P_i)$ was used (Shannon and Weaver 1963), with P_i as the proportion (in terms of weighted abundance) of all records represented by species *i*. A range varying from 0 to a certain maximum is obtained, reflecting both species richness and eveness of their distribution.

Canonical correspondence analysis (CCA, Ter Braak 1986, 1987a) was used to determine the response of the myxomycete community to environmental factors. Each moist chamber culture, representing one microhabitat from one sampling plot, was coded in the environmental dimensions according to the states classified for each parameter (or numerical values for pH and height). The untransformed weighted abundance values for each record in the 132 positive moist chambers were used for this analysis. The given eigenvalues, ranging between 0 and 1, are a measure for the degree in which species distribution can be explained by the respective ordination axis (Ter Braak 1987b). Calculations were carried out with the program Canoco (Ter Braak 1988). For biplots, species scores and these of the environmental variables on the canonical axes were symmetrical scaled to mean 1 and sd 1. The centroids of the environmental variables were associated with species by an Euclidian distance matrix. To reveal preferences of the myxomycetes for bark texture types, a second CCA including only species recorded from bark was performed (74 cultures, 25 species).

Results

Twenty-seven taxa of myxomycetes, two protostelids and five morphologically distinct forms of myxobacteria were identified from 513 records (328 myxomycetes, 53 protostelids, 132 myxobacteria).Three myxomycetes (*Physarum notabile*, *Echinostelium colliculosum*, and *Perichaena vermicularis*) accounted for 52% of all myxomycete records (TABLE I). The mean number of species per culture was 3.5.

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. 1). According to a fit with a saturation function extended by a linear term, 21 species can be expected to occur regularly (plus an indeterminate number of very rare species increasing slowly but unlimited with sample number). In reality, from the 30 species recorded in total (including two protostelids and the undifferentiated myxobacteria), 19 were represented by more than two records.

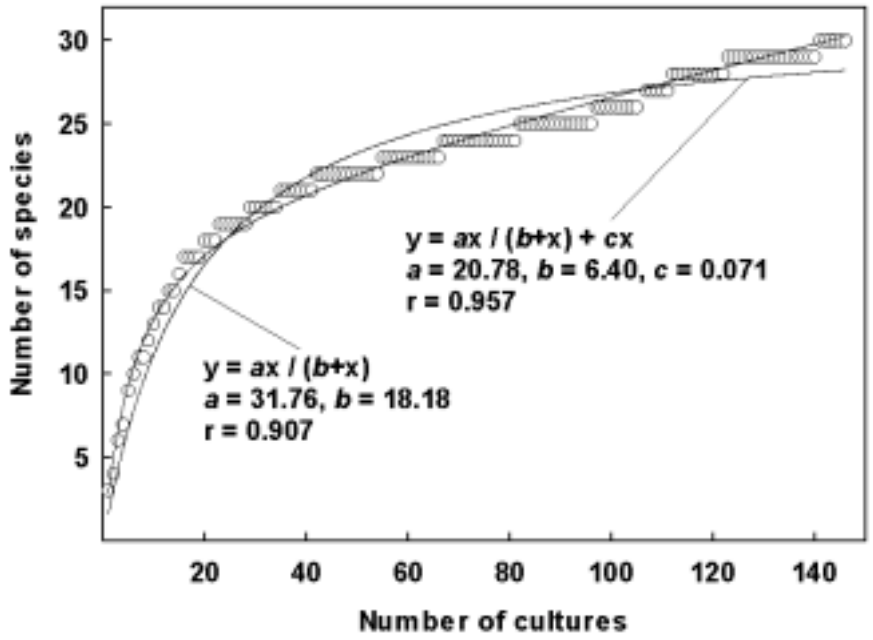

FIG. 1. Bootstrap analysis of the randomly permutated sequence of samples (moist chamber cultures) vs cumulated species numbers (open circles). The presented values are the means of 100 runs. The solid lines show the results of an regression analysis using a saturation function with and without an additional linear term. In this model, *a* is the maximum number of species to be expected, with an additional number of *c* * [sample number] of very rare species for the second model.

From the four rank-abundance models tested, the myxomycete community is described best by the log series distribution (FIG. 2, sum of chi squares = 0.73), followed by the geometric (1.61) and the log normal model (1.87), all three with $P > 0.95$. The broken stick model did not fit the data (sum of chi squares = 22.02, $P < 0.01$). The estimate for the total number of species to expect as derived from the log normal model is 33.53.

Development time.—FIG. 3 shows the time spectra of the 18 most common species (represented by at least three records) based on their weighted abundance during the respective control days. Rapidly developing species tend to have proto- or aphanoplasmodia which give rise to small and stalked sporocarps with evanescent peridia. Species appearing late develop most often from phaneroplasmodia and form larger, often sessile sporocarps with a well-developed peridium.

Environmental parameters.—From the three main substratum types, bark was cultured most often (81 moist chamber cultures, yielding 368 records and 26 species, H' = 1.10). It had the richest myxomycete flora (23 species from 242 records, H' = 1.10). Up to 8 species per culture were observed. Occasionally, very smooth bark (especially the thin bark of *Haloxylon* spp.) yielded only myxobacteria (TABLE II). Litter (35 cultures prepared) was less productive than bark, yielding 100 records and 14 species (H' = 0.78, myxomycetes only: 63 records, 11 species, H' = 0.67). The average species yield was lower than

for bark; only two species (*Physarum notabile* and *Perichaena vermicularis*) occurred regularly. The least productive substratum was dung (29 cultures prepared), resulting in 45 records with 9 species (H' = 0.64, myxomycetes only: 23 records, 8 species, H' = 0.56). Only two myxomycetes, *Didymium annulisporum* and *Licea* sp., were found exclusively on dung, but each occurred only once. The very small droppings of rodents (mostly the genus *Citellus*) were less productive than the dung of larger herbivorous animals (camel, sheep and horse), which correlated with the better water retention of the latter. Both protostelids were common on bark and litter, but were never observed on dung. The myxobacteria as a group behaved as ubiquists.

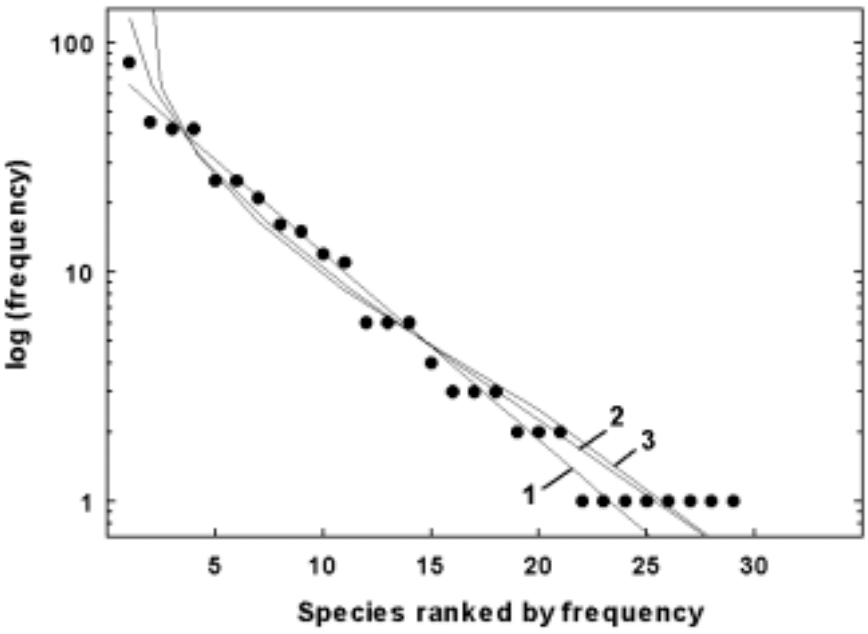

FIG. 2. Rank-abundance plot for the observed myxomycetes and protostelids. The straight line (1) shows the best fit according to a geometric frequency distribution (r = 0.961), line 2 the best fit for a log series model, and line 3 for a log normal model.

The relative importance of the seven environmental parameters recorded (substratum type, water retention, pH, sampling height, wind exposure, light intensity) is shown in the CCA biplot of FIG. 4 which results from a total of 513 records obtained from 132 positive moist chambers. The four extracted axes accounted for 86.8% of the species variance, with 59.5% for the first two axes. Axis 1 is correlated with pH (r = -0.74), axis 2 with the height of sampling (r = 0.54), and axis 3 with the substratum type bark (r = -0.49). An agglomerative cluster analysis of the species scores for the four main axes revealed seven clusters; four of these are markedly separated (dotted circles in FIG. 4). Most of these clusters correlate with ecological groups of species. As to be expected, the three substratum types explain most of the species variance. Litter and dung are positively and bark is negatively correlated with the parameter water retention. The scores for the parameter bark and wind exposure lie in the same direction

from the origin of the axes (bark was the only substratum type sampled on wind-exposed structures above ground); and both are correlated with the parameter sampling height. Independent is the pH value, ranking as the second most important environmental parameter. As confirmed by their pH optima (TABLE I), only a few species cluster in the opposite direction of the parameter pH. Almost all substrata had pH values higher than 7 (TABLE II). The average pH values and ranges (in brackets) were 7.6 (6.5–8.8) for litter, 8.0 (7.5–8.6) for dung and 7.6 (6.5–8.3) for bark (without *Tamarix*), but 5.3 (4.6–7.2) for bark of *Tamarix*. Two of the more common species (*Comatricha laxa* and *C. pulchella*) showed a preference for the acidic bark of *Tamarix*.

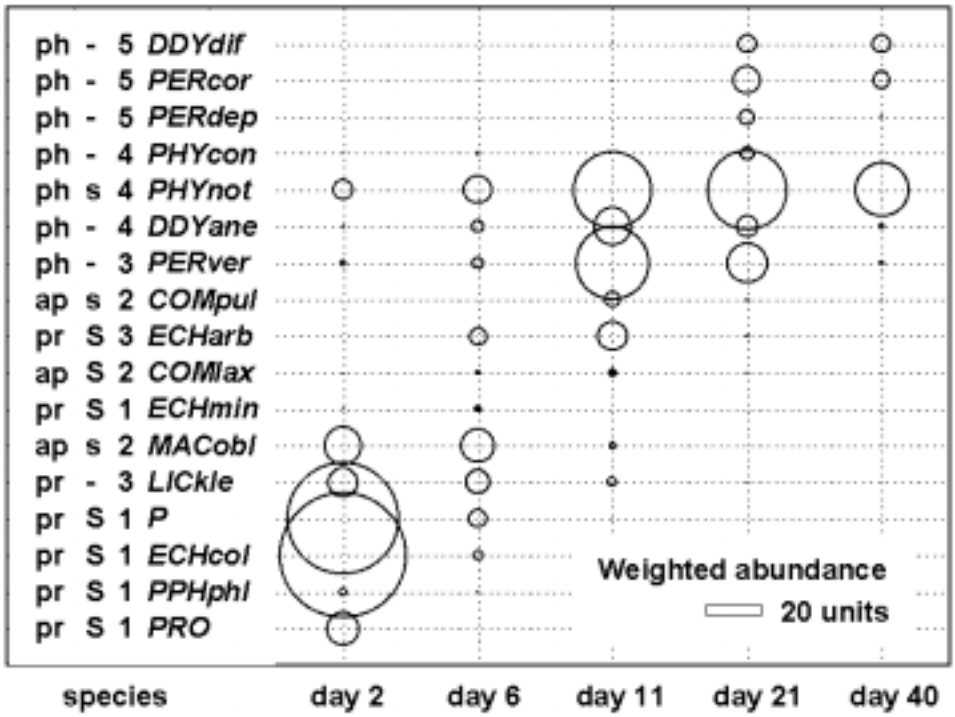

FIG. 3. Development times recorded for the 18 most common species. Circles represent the sum of the weighted abundances for all moist chambers with the respective species present on days 2, 6, 11, 21 and 40. Species names are abbreviated as explained in TABLE I. Letter symbols preceding the species names indicate the plasmodium type: pr = protoplasmodium, ap = aphanoplasmodium, ph = phaneroplasmodium; and the degree of stalk development: S = stalk longer than the sporotheca diameter, s = stalk shorter than the sporotheca diameter, - = 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, covered with lime or amorphous material, 5 = persistent and shell-like, covered with a dense crust of lime or amorphous material.

Corticolous myxomycetes.—Since a high proportion (85%) of the 81 cultures prepared with bark yielded myxomycetes, a second CCA was carried out to reveal preferences of myxomycetes for the five differentiated texture groups (FIG. 5). The texture groups b4 (fissured bark) and b3 (peeling bark) showed the most distinctive flora, with sharply contrasting species preferences and clearly associated

common species. The remaining three texture groups b1 (smooth), b2 (smooth but breaking with age), and b5 (fibrous) cluster together and have no clear associates among the more common species. The relative length of the bars for each texture group correlates roughly with the number of myxomycete records obtained for each group.

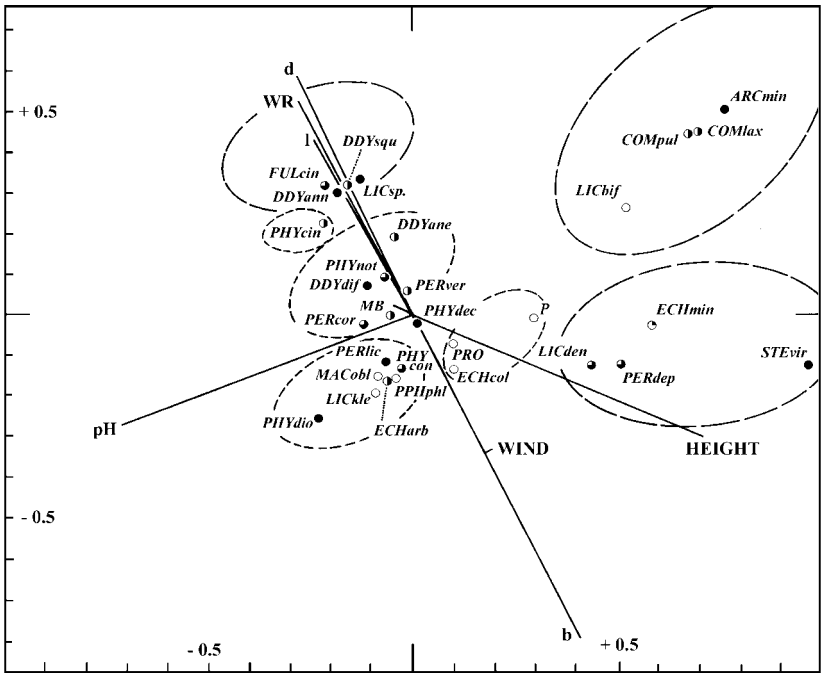

FIG. 4. Biplot of the CCA analysis for 30 species with eight environmental parameters. Abbreviations for the species are as explained in TABLE I. Environmental parameters are labeled with b, l, and d for the substratum types of bark, litter and dung, WR for water retention, HEIGHT for sampling height, and WIND for wind exposure. Light intensity is represented only by a very short line pointing from the origin of the axes to the upper left. The points for the species are coded according to their peaks in development time: open circle = day 2, one quarter filled = day 6, half filled = day 11, three quarters filled = day 21, completely filled = day 40). Eigenvalues for the first four axes are 0.55, 0.36, 0.27 and 0.15. Dashed lines indicate deeply separated clusters (rescaled distance >10) of a cluster analysis of the species scores (Ward method, program SPSS).

Ecological niches.—Niche breadths were calculated for the 18 most common species, based on record numbers (as in Stephenson 1989) or on total abundance values (sporocarp numbers) of the species. With the second approach, except for a few obvious ubiquists (e.g., *Didymium difforme*), the resulting indices were smaller due to the down weighting of scanty records occurring under less optimal conditions. FIG. 6 gives a graphical representation as a niche space, obtained by using abundance values. None of the species used the whole breadth of a niche dimension, and mean values for all niche dimensions were below 0.6, with particularly low ones for the dimensions pH and substratum type.

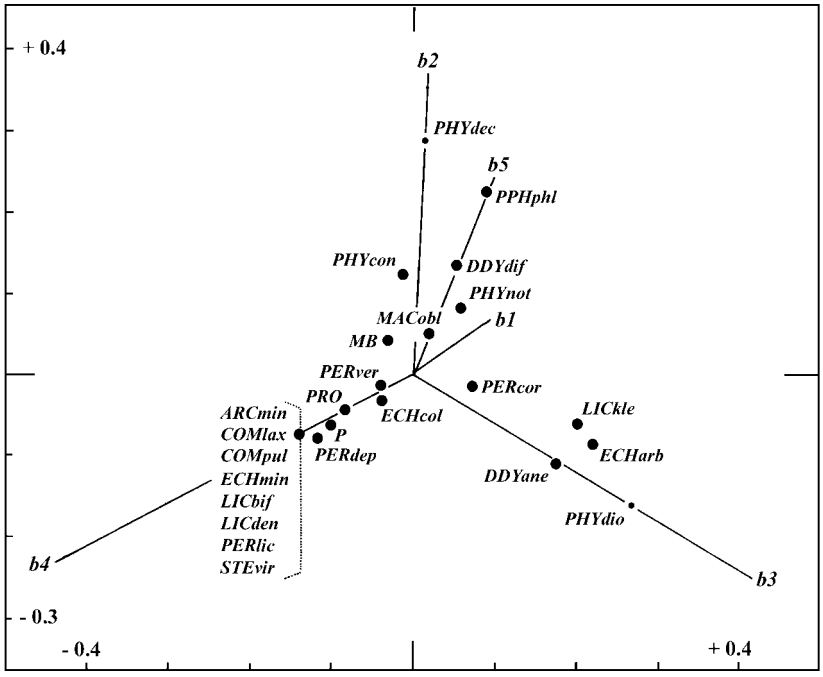

FIG. 5. Biplot for a CCA analysis of all myxomycete occurrences on bark, encompassing 25 species. The bark texture groups b1–b5 were chosen as environmental parameters. For abbreviations of the species see TABLE I. Species with more than two records on bark are represented by large points, rare species by small points. Eigenvalues for the first four axes are 0.34, 0.17, 0.12 and 0.03.

Myxomycete associations.—For all common species the number of observed associations between two species (records in the same moist chamber) was recorded and compared with those expected by chance. The respective deviations are expressed by the Cole index. Five pairs of myxomycetes were associated significantly more often than to be expect by chance ($P > 0.05$). These are all combinations of corticolous myxomycetes with small fructifications and proto- or aphanoplasmodia. In the plot of mean niche overlap vs Cole index of interspecific association (FIG. 7), species above the dotted line show a positive association in relation to their degree of niche overlap; those below the line occur less often together than it would be expected from their niche overlap values. From species combinations where both partners have no (the myxobacteria) or microscopically small plasmodia, 10 combinations are above the dotted line (indicating positive association), and 7 below. In contrast, only 2 of the combinations of species having both macroscopically visible phaneroplasmodia were found above the line, but 11 below (in both cases, combinations of species never found together and represented by the line of points with association indices of -1 were not counted). The relationships between niche overlap and Cole index for the three most common species with phaneroplasmodia (*Physarum notabile*, *Didymium anellus* and *D. difforme*) indicate possible competition behavior. An analysis of the numbers of sporocarps produced in moist chamber cultures yielding *Physarum notabile* and *Didymium anellus*

provides further evidence for competition: moist chambers with *P. notabile* alone produced 148 ± 29 sporocarps of this species (67 records), those with both species 94 ± 23 sporocarps (15 records). The same relationship holds true for *D. anellus*: cultures yielding this species only have 53 ± 16 sporocarps (10 records), those with both species 20 ± 9 sporocarps (15 records). The latter difference is statistically significant (rank sum test, $P < 0.01$). This phenomenon of lower sporocarp numbers in mixed cultures was not observed for combinations of *P. notabile* or *D. anellus* with the much more slowly developing *D. difforme*.

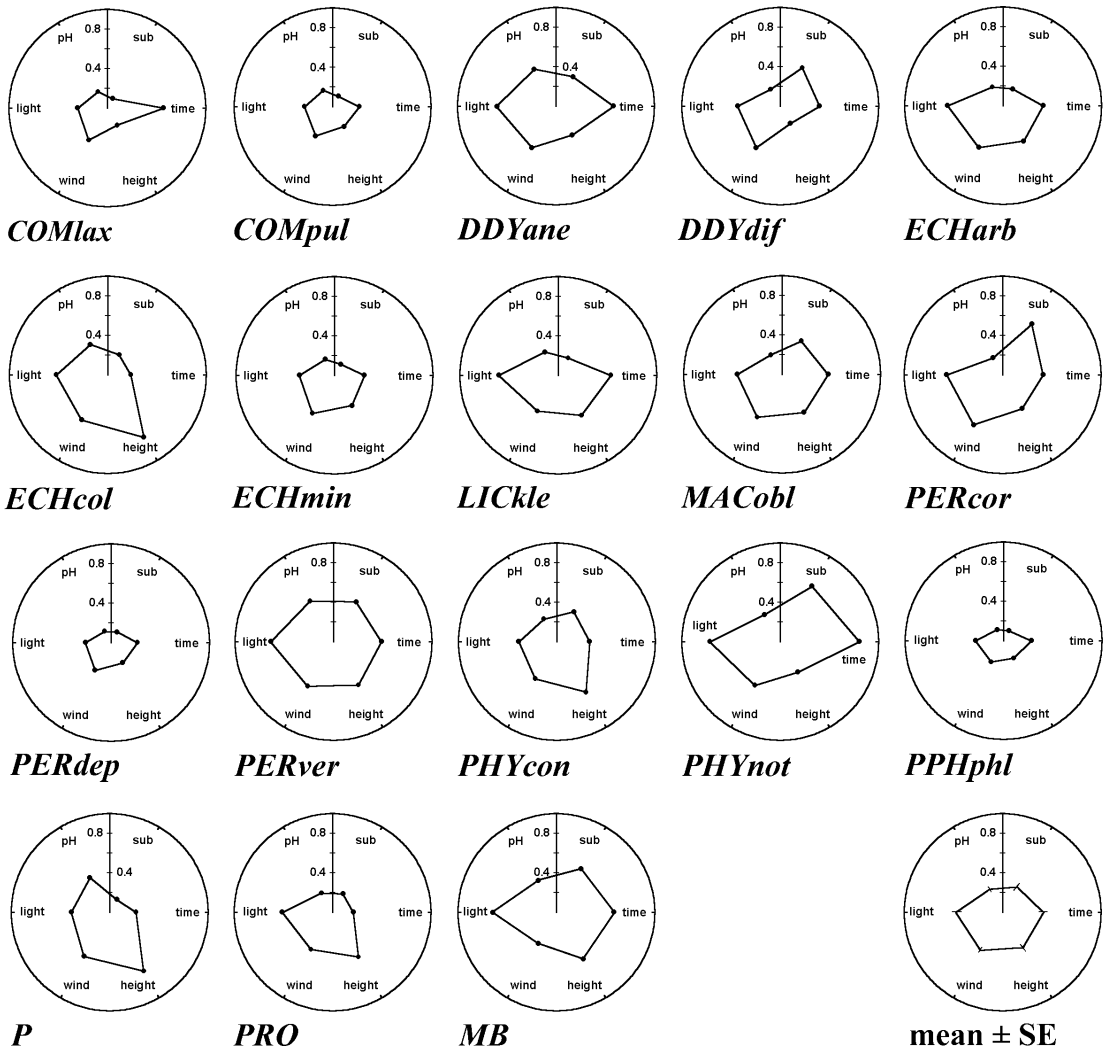

FIG. 6. Graphical visualization of niche breadths for six environmental parameters (substratum type, development time, sampling height, wind exposure, light intensity and pH) for the 18 most common species (see TABLE I for abbreviations of species names). Mean niche breadths ± standard error (S.E.) for all species are given in the last diagram (lower right).

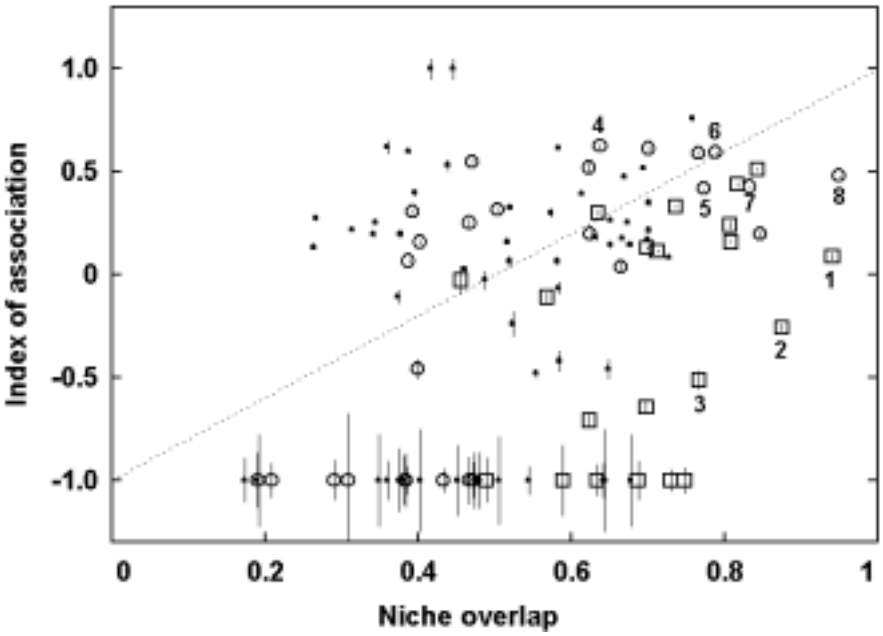

FIG. 7. Diagram of mean niche overlap values vs Cole index of association for all 105 combinations of the 18 most common species. A dotted line marks the boundary between association behavior (upper left) and competition behavior (lower right). Rectangles represent combinations of species having both larger sporocarps (>0.3 mm diam.) and phaneroplasmodia, circles those of species having both small sporocarps (<0.3 mm diam.) and proto- or aphanoplasmodia, and dots combinations of species with large and small sporocarps. Three combinations between the most common species of Physarales show competition behavior (for abbreviations of names see TABLE I): *PHYnot* x *DDYane* (1), *PHYnot* x *DDYdif* (2), and *DDYdif* x *DDYane* (3). Five positive associations of species are statistically significant ($P < 0.05$): *ECHarb* x *MACobl* (4), *ECHarb* x *LICkle* (5), *ECHcol* x *MACobl* (6), *LICkle* x *MACobl* (7), and *COMlax* x *COMpul* (8).

Discussion

Compared with data from other vegetation zones, the myxomycete community observed in the desert of the Mangyschlak peninsula is species-poor but constitutes one of the most distinctive assemblages on Earth, showing similarities only with communities from Mediterranean areas (Schnittler and Novozhilov 2000). The resulting rank-abundance plot (FIG. 2) follows best a log-series or a geometric model. This can be expected for communities inhabiting extreme environments with one limiting resource (Whittaker 1965). In the surveyed desert, this limiting factor is most probably the availability of water.

Completeness of survey.—Two independent methods were used to estimate the number of species to be expected in this survey. The fit of the bootstrap curve with a saturation function (resulting in 31.8 species) agrees well with the results from the truncated lognormal model (33.5 species, 35.3 when including the myxobacteria). These numbers indicate a survey complete to 86–94% when comparing with the 27 myxomycetes, 2 protostelids and the undifferentiated myxobacteria observed.

A fit of the bootstrap curve with a saturation function extended by a linear term can be used to differentiate between common and randomly occurring rare species. Considering the possibility of long-term dispersal for air-borne myxomycete spores, under exceptional weather conditions (in a certain degree simulated by moist chambers) records of species outside their true range can not be ruled out. In accordance with this assumption, a saturation function with an additional linear term showed a better fit than a saturation function alone (FIG. 1). Here, 20.8 species can be expected as common (19 were found more than twice in reality).

Development time.—A clear successional sequence of the common myxomycete species is evident from the time peaks (FIG. 3). Only a few species with phaneroplasmodia, such as *Physarum notabile*, appeared throughout the entire period the cultures were maintained. A possible explanation would be that these species develop regularly sclerotia, which may have been collected with the substrata and developed rapidly into fructifications. Short development times in moist chambers are not uncommon for members of the Physarales from deserts, as shown for *Badhamia gracilis* (Macbr.) Macbr. and *Physarum straminipes* Lister from the Sonora desert (2–7 days, Blackwell and Gilbertson 1984).

The position of the species within the successional sequence shown in FIG. 3 corresponds well with morphological characters such as plasmodium type, stalk development, and presence or absence of a peridium. From these correlations, two life strategies are conceivable. The first is to develop rapidly fructifications from proto- or very small aphanoplasmodia. Typically, these are tiny unsheathed sporocarps which develop on the wet substratum still covered with a water film. In this case, a stalk is indispensable to allow the spores to dry out and become airborne. Species using this strategy are probably able to fruit after a single heavy rainfall and repeatedly during the year. Here, drying out during sporocarp formation destroys the fructifications, as observed by removing immature sporocarps from a moist chamber. Slow-developing species with larger fructifications represent the second life strategy. Typically, a macroscopically visible phaneroplasmodium gives rise to robust, often sessile fructifications covered by a well-developed peridium. As a consequence of developing a peridium first, these species can survive moderate periods of desiccation during development. Moreover, a firm peridium should lower the probability of sporocarps to become infected with parasitic fungi. Eventually, the peridium dehisces to release spores when the substratum dries out. In the desert habitat investigated, such species probably fruit only once or twice (in spring and in autumn) during the year. Whereas small corticolous species tend to realize the first strategy, species on litter and dung more often follow the second. Even more than the development of a stalk, a firm peridium leads to an allocation of resources into non-reproductive structures, which may be easier to afford for species with larger plasmodia.

Environmental parameters.—The very basic pH, as recorded for most substrata in this study, accounts probably for the distinctive myxomycete flora of deserts. Still higher pH values (8.7–10.4) were recorded from the dead pith of cacti from the Sonora desert (Blackwell and Gilberson 1984). Humid regions, especially with coniferous trees, possess more substrata with low pH values, as preferred by most members of the Stemonitales, or species of *Licea* (Stephenson 1989, Härkönen 1977). Only one member of the Stemonitales, *Macbrideola oblonga*, was common during the present study, and this was the only species of its order with an apparent optimum for higher pH values (TABLE I). Similarly, the species of *Perichaena* are probably an exception among the order Trichales, where most of the species inhabit decaying wood with low pH values. All three species of *Perichaena* reported herein were found on substrata with high pH values. Reports for *P. chrysosperma* (Stephenson 1989) seem to fit this picture, as is also the case for the records of *P. corticalis* in the study of Blackwell and Gilbertson (1980a).

The basic pH of the majority of substratum samples causes most of the species scores to clump together in the CCA biplot of the first two axes. A cluster analysis of the species scores from all four axes resulted in seven clusters that can be correlated to ecological groups of species (FIG. 4). The most distant cluster (upper right) consists of corticolous species preferring low pH values. Shrubs of *Tamarix* spp., the only bark substratum with an acidic pH, were found only locally on the margins of small, salty depressions or salt springs. For *Comatricha pulchella*, four of the six records were from bark (3) or litter (1) of *Tamarix*, with only two additional records from other shrubs. Also two of the four records from *Comatricha laxa* came from *Tamarix* bark. For both species, 98% of all sporocarps recorded grew on this substratum. It seems that in species-poor ecosystems such as the investigated desert, survival of a number of myxomycete species can be highly dependent upon the presence of only one substratum type, in this case *Tamarix*. The second cluster in the CCA is correlated with the environmental factor height and includes also corticolous myxomycetes (middle right in FIG. 4). Except one record each of *Licea denudescens* (on *Calligonum densum*) and *Perichaena depressa* (on *Atraphaxis replicata*) all records came from trees planted around wells or from *Crataegus ambigua*, the only native tree occurring in deep-cut valleys of the Karatau Mountains, which can be seen as the southernmost steppe island (Schnittler and Novozhilov 2000). Judged by the occurrence of the plants providing the substrata, this group of species does not form a part of the true desert flora. The third distant cluster (upper middle in FIG. 4) is correlated with water retention and supports a group of mostly rare dung inhabitants (TABLE I). *Physarum cinereum*, found only once, forms a cluster on its own. The three clusters around the origin of the axes comprise all common myxomycetes preferring basic substrata. The one above the origin of the axes unites species preferring litter substrata, the two below the origin consist of mostly common corticolous myxomycetes. Interestingly, three of these (the two protostelids and *Echinostelium colliculosum*) form a cluster on its own that is associated with sampling height. Only these rapidly

developing species with minute fructifications are able to complete their life cycle on bark substrata higher than 10 cm above ground (compare FIGS. 3, 6). Seemingly, this ability frees them from competition in this habitat; all three species were common, together accounting for 98 records (26% of all records on bark).

The high eigenvalues of the four CCA axes (sum = 1.33) indicate that the recorded environmental parameters explain most of the variance in species distribution. Light intensity is of negligible influence, since shaded microhabitats do not exist in the open desert landscape. From the remaining parameters, pH and substratum type are most important. The parameter pH was found to be correlated with the first axis, as it was the case in the detrended correspondence analysis of tree species based on records of corticolous myxomycetes carried out by Stephenson (1989). Although pH accounts for a considerable amount of variance in species distribution, its resolution power is limited by the fact that most of the substrata exhibit rather high pH values. Water retention is correlated with the substratum types litter and dung, which have 2–3 times higher water retention values than bark (TABLE II). As predetermined by the sampled substrata, with litter and dung on the ground and bark above ground, sampling height as well as wind exposure are correlated with the parameter bark.

Corticolous myxomycetes.—Eighty-five per cent of the 81 moist chamber cultures prepared with bark were positive for myxomycetes, which is one of the higher percentages reported (boreal forests, Finland: 48%, Härkönen 1977; deciduous broadleaf forests, eastern North America: 59%, Peterson 1952; 75%, Pendergrass 1972; 90%, Stephenson 1989; deciduous forests, Austria, selected trees: 90%, Nowotny 1986). The only exception was the very thin and smooth bark of shrubs belonging to the family *Chenopodiaceae* (texture group b1 in TABLE II). In the CCA shown in FIG. 5, this bark type had an average yield of only one record per moist chamber, with no species clearly associated with it. Interestingly, Saksaul (*Haloxylon aphyllum*) as one of the largest and most common shrubs belongs to this texture group. It accounts for a considerable amount of wood and litter biomass especially in sand dune areas (Miroshnichenko 1974). As already shown on the example of *Tamarix* spp., the abundance of a particular shrub is not at all correlated with the diversity and abundance of corticolous myxomycetes. Texture group b2 (smooth bark fissuring with age) yielded about four records per culture and was represented by two shrubs, *Rhamnus sintensii* and *Caragana grandiflora*. Both are common, especially in the western parts of the Mangyschlak Peninsula near the Caspian Sea. Clearly separated in the CCA were the texture groups b3 (layered, peeling bark) and b4 (deeply furrowed bark), both yielding 5–6 records per culture. Group b3 was represented primarily by two shrubs, *Atraphaxis replicata* (common throughout the region) and *Calligonum eriopodum* (occurring in sand dune areas). This bark type seems to provide a niche for rapidly developing myxomycetes with small sporocarps. *Echinostelium arboreum* and *Licea kleistobolus*, with 74% and 72% of all sporocarps recorded from this

substratum type, are probably the most specialized species. Most of the shrubs were classified as texture group b4 (e.g., *Calligonum densum* in sand dune areas, and *Crataegus ambigua* from the Karatau Mountains). This bark type had the highest species diversity, and most of the common corticolous myxomycetes and the two protostelids had an affinity for this substratum type. Texture group b5 (fibrous bark) was represented by three species of *Astragalus* and sagebrush (*Artemisia* spp.), thus occurring throughout the region but represented only by shrubs with small trunk diameters. However, except for *Protophysarum phloiogenum* with three records only, no clear specialists were found for this bark type. In general, all of the more common corticolous myxomycetes were found on several different species of shrubs. As such, bark probably determines the myxomycete flora not as a result of the particular plant species providing the substratum but mainly because of its physical and chemical properties, with pH, texture and water retention as the most important factors.

The high percentage of bark cultures positive for myxomycetes, together with the finding that even slightly fissured bark (cultures from dying twigs of *Haloxylon* with ruptured bark were successful) seems to work as spore traps, suggest a high dispersal potential of myxomycetes. Deeply fissured bark provides more surface area per square centimeter, and opens, through better water retention, a prolonged time window for bacterial growth and myxomycete development. If existing at all, the minimum surface area for corticolous myxomycetes seems to be very small. All five cultures set up with bark from sagebrush dwarf shrubs (*Artemisia* spp.) produced myxomycetes, with up to five species in one culture dish. The shrubs were lower than 20 cm, with trunks barely reaching 1 cm in diameter and only a few cm in length.

Ecological niches.—As already indicated by the CCA analysis, for most myxomycetes the average niche breadths were lower for states describing microhabitat features (pH, substratum type) than for those reflecting climatic parameters (light, wind, FIG. 6). This may express difficulties in estimating the latter parameters for a very small space, but more probably it shows the generally higher importance of microhabitat features in comparison to habitat-describing parameters. Development time of the myxomycete species was treated also as a niche state, since the species showed a clear successional sequence (thus probably avoiding direct competition, FIG. 3). It is possible that they prey on different taxa of bacteria and yeasts, which may show a similar successional sequence as the myxomycetes themselves. Several tendencies are apparent from the diagrams in FIG. 6: (i) rare species tend to be specialists, having smaller niche spaces than common species, (ii) small corticolous species such as *Echinostelium colliculosum* or the protostelids have very wide niches for the parameters of wind exposure and sampling height, and (iii) corticolous myxomycetes tend to have smaller niche breadths than lignicolous species, especially for the parameter substratum type. As such, bark myxomycetes seem to be more specialized than litter forms. From the 21 species (including the two protostelids) preferring

bark, 14 were found exceptionally on this substratum. In contrast, from the 7 species found predominantly on litter, only 2 rarer species inhabited this substratum exclusively. The high indices for niche breadths of species frequently found on litter (*Didymium difforme*, *Perichaena corticalis*, *P. vermicularis*, *Physarum notabile*, and the myxobacteria) confirm this. Defining preference as occurring more often on the respective substratum type (regardless of abundance), from the common species shown in FIG. 6 only *Didymium annellus* agg., *Perichaena vermicularis*, *Physarum notabile* and the myxobacteria prefer litter. But, if preferences were expressed by counting sporocarp numbers (abundances) for the respective substrata, three of these species grew better on bark (preference factors of 1.12 for *P. vermicularis*, 1.62 for *P. notabile*, and 6.27 for the myxobacteria, respectively). In contrast, preference factors for the 21 bark species when compared to litter were always higher than 10, or the species grew exclusively on bark. The only exception was *Perichaena corticalis* (2.3). It can be stated that litter species can well grow on bark, but bark species seem mostly unable to utilize litter substrata. However, the long development times of litter-inhabiting species restrict these in nature probably to litter, since bark dries out too quickly. Dispersal barriers between the two substrata are hardly conceivable, since the frequently occurring dust storms should carry spores from litter to the low trunks of the desert shrubs. Bark samples were often dusty and covered with sand grains. *Physarum notabile* and the myxobacteria, the most common taxa on dung, were also the least specialized, occurring on all substratum types with roughly the same frequency. Only *Didymium anellus* agg. grew best on dung, although it was more often recorded on litter and bark (TABLE I). *Didymium annulisporum*, found once on dung, is too rare to draw conclusions towards substratum preferences. Nevertheless, it is remarkable that all species of *Didymium* preferentially inhabited dung. Of all other environmental parameters, pH had the lowest average niche breadth. However, due to the limited supply of acidic substrata, the calculated niche breadths may be more narrow than the true physiological limitations of the species. As to expect from the CCA, the climatic parameters of light intensity, wind exposure and sampling height had the highest average niche breadths.

The corticolous myxomycetes in particular show a considerable degree of niche overlap. Here, limitations of the moist chamber method should also be considered. Species found together in a moist chamber do not necessarily develop together in the field. As strongly indicated by their development times, they may have a different phenology. Conceivable are quick-developing species occurring after rare summer rains (thunderstorms) at high temperatures and slow-developing species appearing in autumn at lower temperatures. Furthermore, the continuously wet conditions in a moist chamber tend to obscure the influence of a factor such as water retention, which acts probably much more strikingly in nature. On the other hand, moist chamber cultures seem to reflect properly the myxomycete assemblage actually present for a particular microhabitat and do not work like air spore traps showing presence of propagules only. Field records combined with moist chamber studies from the Sonoran desert resulted in

very similar myxomycete assemblages (Blackwell and Gilbertson 1980a). Probably, many species of myxomycetes can not complete their whole live cycle under constant moisture and must be present in the form of microcysts or sclerotia to appear in a moist chamber culture. In the present study, with exception of a very weak second appearance of the smaller protostelid species, a second fructification peak was never observed (FIG. 3). This confirms the observations of Alexopoulos (1964) and supports his hypothesis that microcysts play an important role as dormant stages, especially in arid environments. On the other hand, life cycles of desert myxomycetes can be surprisingly short, as demonstrated for *Didymium eremophilum* Blackwell & Gilbertson (3–7 days in agar culture, Blackwell and Gilbertson 1980b). Further evidence for the value of the moist chamber method in detecting myxomycetes can be derived from the fact that even very common species (e.g., *Echinostelium colliculosum*) exhibited clear substratum preferences, although it may be assumed that spores are present on almost all substrata.

Myxomycete associations.—From the plot of myxomycete associations versus niche overlaps (FIG. 7), several conclusions can be drawn. (i) Due to the plasmodium, a naked mass of protoplasm covered by a cell membrane and a slime layer, myxomycetes can use only a narrow range of environmental conditions for active life. Therefore, differing development times may be the most effective way to avoid spatial competition. In 40 of the 105 combinations analyzed, development time showed the lowest niche overlap values. (ii) Regarding the generally low utilization of space (also in the most productive moist chambers, not all substratum pieces had myxomycete colonies), a low niche overlap in already one dimension seems to allow the coexistence of two species. After the development time, substratum type exhibited the lowest niche overlap in 26 of the 105 combinations, followed by pH (22), sampling height (13), sun intensity (4) and wind exposure (0). (iii) Environmental conditions seem to control myxomycete growth in a desert more than the availability of food organisms. Even species with high niche overlap values (>0.6) showed association rather than competition phenomena. (iv) Only myxomycetes with large sporocarps (>0.3 mm) and phaneroplasmodia seem to be an exception. Here, competition is indicated by mostly high niche overlap values combined with low indices of association (FIG. 7). As observed frequently during the time of cultivation, species with mobile phaneroplasmodia utilized a larger part of the moist chamber than those with proto- or aphanoplasmodia. Often, fructifications were formed on the lid of the Petri dish. (v) In contrast, small myxomycetes with proto- or aphanoplasmodia (mostly corticolous forms) often occur together. For this group, no limitation with respect to food resources can be assumed. (vi) A more pronounced competition between closely related species, as reported by Stephenson (1988), was not observed. For instance, the highest niche overlap, but also a statistically significant association behavior was found for the pair *Comatricha laxa* x *C. pulchella*.

In general, the results of this study suggest that microhabitat parameters determine myxomycete distribution to a higher degree than climate factors. However, climate is the most limiting factor for myxomycete development, as it is indicated by the rank-abundance plot of the species which can be described by a geometric model. As to be expected in this context, myxomycetes and myxomycete-like organisms in the desert community behave as r-strategists *sensu* Pianka (1970). Due to the dormant stages accompanying each part of the life cycle and the longevity of the spores (Erbisch 1964), high sporocarp numbers can develop in a short time on a small amount of substratum, as demonstrated by the sporocarp numbers for the moist chamber cultures (TABLE I). This results in a high dispersal potential especially for the myxomycetes and allows these organisms to invade quickly and utilize almost all available resources of decaying plant material in the desert. The high proportion of moist chambers cultures positive for myxomycetes (82%, 120 of 146) confirms this. Very probably, these organisms constitute a rather important element of the detritus food chain in the desert, perhaps representing the single most important group of bacterial predators. Various adaptations for successful growth in rather short humid periods cause myxomycetes to be an important cryptogram group in the investigated winter-cold desert, in contrast to woodland ecosystems much richer in mosses, lichens and fungi. As shown for the more common myxomycetes, ecological niches are determined primarily by substratum features, with pH, texture and probably water retention as the most important factors. By establishing succession sequences of species with different development times, interspecific competition is avoided or, if occurring in nature at all, restricted to a few species with large phaneroplasmodia. Myxomycete abundance is not necessarily correlated with the abundance of the plants providing the respective substrata (bark, litter). Among the ecological groups of myxomycetes, corticolous forms are more specialized than litter or dung inhabitants, which correlates with the fact that the respective microhabitats (shrubs and trees) are stable for a much longer period of time than litter accumulations. Most of the dung-inhabiting myxomycetes are also able to utilize undigested plant litter, thus confirming the report of Eliasson and Keller (1999) that only a very limited number of coprophilous myxomycetes is restricted to dung as a substratum.

To elucidate more completely the ecology of such hidden organisms as myxomycetes, a standardized, comprehensible description of microhabitat features has to be developed. Applying current techniques of statistical analysis, the moist chamber method developed by Gilbert and Martin (1933) should be developed further, to simulate more precisely the natural conditions of the studied region. However, the largest challenge for further studies remains untouched – to include the „missing link“, the bacteria or algae upon which the trophic stages of myxomycetes feed, into ecological investigations.

Acknowledgements

The field work for this study was kindly supported by a travel grant (40095/705.6.168) from the Stifterverband für die deutsche Wissenschaft. For discussions and proofreading of the manuscript I am indebted to Dr. S.L. Stephenson, Fairmont, WV. For further helpful comments I want to thank D.W. Mitchell, Sussex, UK, Dr. Y.K. Novozhilov, Komarov Botanical Institute, St. Petersburg, Russia, T. Stampfer, Santa Fe, NM and two anonymous reviewers.

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TABLE I. Abundance values, development time and pH preferences of myxomycetes, protostelids and myxobacteria from the Mangyschlak peninsula.

Species Name	Abbr.	Abundance total[a]	(mean ± SE)	Bark re[b]	Bark abu_w[c]	Litter re	Litter abu_w	Dung re	Dung abu_w	pH opt.[d] (range)	development time[e] (days)
Arcyria minuta	ARCmin	50		1	1.00	—		—		4.6	40.0
Comatricha laxa	COMlax	635	(159 ± 116)	4	4.00	—		—		4.9 (4.6–7.4)	11.0
Comatricha pulchella	COMpul	250	(42 ± 32)	3	5.76	3	0.24	—		4.9 (4.6–8.1)	22.3
Didymium anellus agg.	DDYane	829	(33 ± 9)	9	9.41	11	3.68	5	11.89	7.6 (4.6–8.3)	19.4
Didymium annulisporum	DDYann	20		—		—		1	1.00	8.2	40.0
Didymium difforme	DDYdif	385	(32 ± 9)	7	5.61	1	3.12	4	3.27	7.8 (7.2–8.2)	36.8
Didymium squamulosum	DDYsqu	45	(15 ± 3)	—		1	1.33	2	1.67	7.8 (7.7–7.9)	11.0
Echinostelium arboreum	ECHarb	5656	(354 ± 181)	16	16.00	—		—		7.8 (5.7–8.2)	9.4
Echinostelium colliculosum	ECHcol	4226	(3939 ± 330)	43	44.92	2	0.07	—		7.6 (6.8–8.2)	4.1
Echinostelium minutum	ECHmin	140	(47 ± 27)	2	2.79	1	0.21	—		7.2 (4.6–7.8)	4.7
Fuligo cinerea	FULcin	55	(28 ± 23)	1	0.18	—		1	1.82	8.2 (7.7–8.2)	21.0
Licea biforis	LICbif	250		1	1.00	—		—		5.8	2.0
Licea denudescens	LICden	305	(153 ± 147)	1	1.97	1	0.03	—		7.4 (7.3–7.4)	16.0
Licea kleistobolus	LICkle	2580	(123 ± 22)	21	21.00	—		—		7.9 (7.3–8.2)	7.4
Licea sp.	LICsp.	750		—		—		1	1.00	8.0	40.0
Macbrideola oblonga	MACobl	634	(25 ± 7)	25	25.00	—		—		7.7 (7.5–8.2)	6.5
Perichaena cf. *liceoides*	PERlic	100		1	1.00	—		—		7.6	40.0
Perichaena corticalis	PERcor	508	(34 ± 8)	11	9.68	4	5.31	—		7.8 (6.5–8.1)	31.7
Perichaena depressa	PERdep	1783	(297 ± 241)	6	6.00	—		—		7.5 (5.7–7.9)	32.0
Perichaena vermicularis	PERver	1417	(34 ± 6)	27	24.16	14	17.78	1	0.06	7.5 (5.7–8.2)	17.3
Physarum cinereum	PHYcin	250		—		1	1.00	—		7.7	11.0
Physarum cf. *confertum*	PHYcon	1115	(186 ± 75)	6	6.00	—		—		7.7 (7.4–8.0)	18.5
Physarum decipiens	PHYdec	84	(42 ± 38)3	2	2.00	—		—		7.1 (7.0–7.2)	30.5
Physarum didermoides	PHYdio	500		1	1.00	—		—		8.0	40.0
Physarum notabile	PHYnot	11360	(139 ± 24)	50	35.43	24	20.95	8	25.62	7.8 (4.6–8.2)	19.7
Protophysarum phloiogenum	PPHphl	122	(41 ± 30)	3	3.00	—		—		7.7 (7.6–8.2)	4.7
Stemonitis virginiensis	STEvir	100		1	1.00	—		—		7.3	40.0
Protosteliales sp. I	P	392500	(9345 ± 2415)	40	41.66	2	0.34	—		7.0 (4.6–8.0)	4.2
Protosteliales sp. II	PRO	17350	(1577 ± 867)	10	9.73	1	1.27	—		7.6 (7.0–8.1)	2.3
Myxobacteria	MB	57840	(438 ± 89)	76	91.26	34	14.92	22	25.80	7.6 (6.5–8.3)	10.3

[a] Sum of sporocarps recorded in all moist chamber cultures with the respective species.
[b] Number of records per substratum type.
[c] Sum of weighted abundances for this substratum type.
[d] Mean pH of all moist chamber cultures with the respective species, weighted by the number of sporocarps for each record.
[e] Mean of all days with the highest number of sporocarps for a particular record.

TABLE II. Substratum features and myxomycete yields for all investigated plants and plant remnants.

Substratum	Type[a]	pH[b]	WR[c]	diam.[d]	mc[e]	re[f]	sp[g]	H'[h]
Arthrophytum lehmannianum	b1	8.1	3–4	1–1.5	1	1 (1)	1	—
Convolvulus fruticosus	b1	8.0	4–5	1–2	1	2 (1)	1	—
Salsola arbuscula	b1	8.1 (7.8–8.2)	2–4(–5)	2–3	3	6 (4)	3	0.36
Salsola arbusculiformis	b1	7.9	2–4	2–3	1	0	—	—
Haloxylon aphyllum	b1	8.2	3–5	8–15	7	5 (4)	2	0.11
Total	**b1**	**8.1 (7.8–8.3)**			**13**	**14 (10)**	**5**	**0.57**
Caragana grandiflora	b2	7.8 (7.7–8.1)	3–5	1–2.5	4	21 (14)	7	0.71
Rhamnus sintenisii	b2	7.5 (7.0–8.1)	1–2	2–7	13	51 (26)	10	0.78
Total	**b2**	**7.5 (7.0–8.1)**			**17**	**72 (40)**	**12**	**0.90**
Atraphaxis replicata	b3	7.8 (7.6–8.1)	5–7	2–6	11	71 (49)	12	0.90
Calligonum eriopodum	b3	7.4 (7.3–7.5)	6–8	5–10	4	26 (20)	7	0.72
Total	**b3**	**7.7 (7.3–8.1)**			**15**	**97 (69)**	**12**	**0.91**
Ammodendron eichwaldii	b4	7.4	3–5	1.5–3	1	5 (4)	4	0.47
Calligonum densum	b4	7.4 (7.0–7.7)	4–6(–8)	4–10	6	41 (25)	9	0.75
Calligonum leucocladum	b4	7.9	1.5–3	4–5	1	3 (2)	2	0.29
Crataegus ambigua	b4	7.0 (6.5–7.5)	5–7	7–20	4	14 (6)	5	0.39
Eleagnus spp.[i]	b4	7.2	5–6	10–20	1	6 (3)	3	0.42
Halostachys caspica (= *H. belangeriana*)	b4	8.2	3–6	2–5	1	7 (5)	5	0.41
Salix alba[i]	b4	7.7 (7.6–7.9)	6–8	20–50	3	14 (9)	6	0.43
Tamarix spp.	b4	5.3 (4.6–7.2)	4–8	2–5	5	28 (20)	11	0.88
Ulmus sp.[i]	b4	8.0 (8.0–8.1)	6–9	20–40	2	5 (2)	3	0.30
Total	**b4**	**5.9 (4.6–8.2)**			**24**	**123 (77)**	**20**	**1.01**
Astragalus ammodendron	b5	7.6 (7.6–7.7)	12–18	2–4	3	23 (18)	9	0.81
A. brachypus	b5	7.8 (7.6–8.0)	6–10	2–4	3	14 (11)	6	0.61
A. karakugensis	b5	7.7 (7.6–7.8)	8–12	1.5–3	2	10 (6)	4	0.46
Artemisia spp.[j]	b5	7.7 (7.7–7.9)	4–5	0.5–1	3	15 (11)	6	0.61
Total	**b5**	**7.7 (7.6–8.0)**			**11**	**62 (46)**	**10**	**0.87**
earth lichens		7.7 (7.5–7.9)	?	—	2	0	—	—
Agropyron fragile and *Stipagrostis pennata*	gl	7.7 (7.4–7.9)	10–16	1–3	8	32 (19)	7	0.54
Anabasis brachiata	hl	8.7		0.03	1	1 (1)	1	—
Calligonum densum	hl	8.0 (7.8–8.1)	8–10	0.02–0.03	3	12 (9)	5	0.56

Substratum	Type[a]	pH[b]	WR[c]	diam.[d]	mc[e]	re[f]	sp[g]	H'[h]
Haloxylon aphyllum	hl	8.2	10–12	0.03–0.04	1	1 (1)	1	—
Mentha longifolia	hl	7.9 (7.7–8.1)	10–11	0.4–0.8	3	9 (5)	5	0.46
Salsola dendroides	hl	8.2	10–11	1.0–1.5	1	1 (1)	1	—
Tamarix spp.	hl	6.8 (6.5–7.5)	11–12	0.01–0.02	3	9 (8)	5	0.53
Zosima orientalis	hl	7.9	8–9	1–2	1	1 (0)	—	—
Total	**hl**	**7.5 (6.5–8.8)**			**23**	**51 (34)**	**8**	**0.62**
Ammodendron eichwaldii	ll	7.9	12–14	1–2	1	5 (4)	4	0.32
Caragana grandiflora	ll	7.8	12–14	1–2	1	4 (4)	4	0.38
Crataegus ambigua	ll	7.3	12–14	1–2	1	5 (2)	2	0.14
Rhamnus sintenisii	ll	7.9	12–14	1–2	1	1 (0)	—	—
Total	**ll**	**7.7 (7.3–7.9)**			**4**	**15 (10)**	**6**	**0.48**
camel	d	8.3 (8.1–8.6)	100–120	2 x 4	5	4 (1)	1	—
sheep or antelope	d	8.2 (8.0–8.4)	60–80	1 x 1,5	3	4 (2)	2	0.16
rodents: *Citellus* spp.	d	8.0 (7.5–8.3)	40–50	0.5 x 1.5	20	33 (18)	7	0.56
birds: *Lagopus* spp.	d	7.8 (7.8–7.9)	30–40	0.5 x 1.0	2	4 (2)	1	—
Total	**d**	**8.0 (7.5–8.6)**			**30**	**45 (23)**	**8**	**0.56**

[a] Bark texture groups (b1 = smooth, b2 = smooth but rupturing with age, b3 = peeling, b4 = furrowed, b5 = fibrous), kind of litter substrata (gl = grass remnants, hl = herbaceous but fleshy plants remants, ll = leaf litter) or dung (d).
[b] Average and range of pH values for all moist chambers prepared with material from this plant.
[c] Water retention in mL/cm^3.
[d] Trunk diameter or thickness of the respective substratum layer in cm.
[e] Number of moist chamber cultures prepared with material from this plant.
[f] Number of records for myxobacteria, protostelids and myxomycetes (in parentheses: myxomycetes only).
[g] Number of myxomycete species recovered from this substratum.
[h] Shannon-Weaver index of diversity.
[i] Planted trees found around artificial wells.
[j] Including the closely related species *Mausolea eriocarpa*.

Chapter 15. Ecology and evolution of the myxomycete fructification

Most of the preceding chapters of this thesis describe local assemblages of myxomycetes from surveys carried out in different vegetation zones world-wide. However, in comparison with other groups of cryptogams, the number of fairly complete local surveys allowing statistically significant conclusions towards myxomycete ecology is rather limited. On the other hand, over the last ten years of intensive field work on myxomycetes by the author, a large number of observations were made, resulting in a herbarium collection of more than 10 000 specimens. It is the purpose of this chapter to make these data on myxomycete ecology, which have been derived from personal experience in the field, available by means of a database that includes morphological traits of the fructifications together with observations on microhabitat preferences and distribution.

For the reason that the myxomycete fructification is usually the only indication of myxomycetes that one is able to observe in the field, morphological features of the fructifications were analysed herein. The hypothesis raised in this chapter is that the formation of the fructification is the major reason for the evolutionary success of myxomycetes. Evidence for this postulate is inferred from over 400 of the better-known species in the group. Advantages as well as biological limitations of this life strategy are discussed.

All species of myxomycetes develop more or less complicated fructifications, which can be classified into three groups. Here, the terminology used in Lado & Pando (1997) is followed. The most simple form is the plasmodiocarp, often in outline resembling the veins of the plasmodium prior to development. These plasmodial veins contract, resulting in short to worm-like elongated fructifications of fairly constant diameter but of variable length. When seen in cross-section, plasmodiocarps are most often spherical, but can be laterally compressed in some species. If these structures become globose, they can be regarded as sessile sporocarps, with a diameter and height which is relatively constant for a certain species. Many species produce stalked sporocarps, with a globose to cylindrical spore-mass, called sporotheca, at the apex of the stalk. The spore-mass is supported by internal thread-like structures, called capillitium, and is often protected by a peridium which can have additional layers of other materials, often consisting of amorphous or crystalline lime. Usually, larger plasmodia segregate upon fructification to form several dozens to hundreds of sporocarps, with a mean distance between them which is fairly constant in a certain species. But, in some species, the single sporocarps coalesce to build up massive structures called pseudoaethalia (where the single sporocarps still maintain their identity) or aethalia (where sporocarps are indiscernible) which are usually not stalked and can reach several centimetres in diameter and height.

Methods

Starting from taxonomic treatments such as Mitchell (1999), a set of morphological traits and ecological preferences was data-based for the described species. In detail, taxonomic descriptions available in the literature were searched for the following characters: type of fructification (plasmodiocarp, sporocarp, pseudoaethalium, aethalium), spore diameter, height of fructification, diameter and height of the sporotheca, and stalk length. Plasmodiocarps are very variable in length, thus the dimensions for the shortest possible fructification (which is equal to a sessile, globose sporocarp) were coded. Since myxomycetes show considerable variation in the dimensions of their fructifications due to environmental conditions, these dimensions were coded in ranges, and the respective means were used for all further analyses. Volumes of spores and sporothecae were calculated as for a sphere, or, if one axis was longer than the other, of an ellipsoid. From these data, the number of spores per fructification was estimated, assuming an arrangement of spores according to the densest possible package of spheres. This was regarded as a sufficiently good approach to natural conditions, since two sources of error counteract each other: (i) supporting structures such as capillitial threads, lime nodes or a columella disturb the arrangement of spores and occupy space, and (ii) spores are deformed by their mutual pressure, allowing a denser packaging than possible for perfect spheres. With these assumptions, the number of spores n per fructification can be calculated as $n = 0.74 * V_{spt} / V_{sp}$, with V_{spt} and V_{sp} as the respective volumes of the sporotheca and the spores. These estimated spore numbers correlated well with those counted directly from microscopic slides of several species of *Echinostelium*. For four species of myxomycetes with larger fructifications, all spores of a single sporocarp were mounted in 1 ml water (a small amount of Tween 80 was added to break the hydrophobicity of spores). After several steps of ten-fold dilutions, the spores present in a 10 µl of the final suspension were counted under the microscope. These calculated spore numbers were in the same order of magnitude as the respective values derived from the spore and sporocarp dimensions. To show trends in the development of fructification features more clearly, data for 17 species of Protosteliales and 11 species of Dictyosteliales were taken from the literature and included in the analyses as well.

Possible travel distances for myxomycete spores were calculated according to Stokes law (Gerthsen 1995). As outlined herein, this law applies for the calculation of the terminal fall velocity V_{term} of small spherical bodies in air, if they are too small to cause turbulences: $V_{term} = 2\ \rho\ g\ r^2 / 9\ \eta$. In this calculation, ρ is the density of the body, g the gravitation constant (9.81 m s^{-2}), and η the viscosity of air (1.84 x 10^{-7} Pa s). The following assumptions were made: (i) the spore under consideration is globose and (ii) smooth, and (iii) has a density that is equal to that of water (1 g cm^{-3}). At least the two latter assumptions may be quite often violated in reality, but act against each other. Many spores are ornamented and the resulting roughness slows down their fall. On the other hand, spores are more dense than water, since the specific weight of solid structures (e.g., the spore wall) is higher than that of water. This will increase the terminal fall velocity. With this parameter, the travel distance x of a spore per metre height loss (h) can be calculated for different horizontal wind speeds V_{wind} with the formula $x = V_{wind}\ h / V_{term}$ (Greene & Johnson 1993).

For the resource allocation model, developed to estimate the proportion of resources necessary for the development of a stalk of various length for a fructification of a certain size, the following assumptions were

made: (i) That the respective volumes of stalk and sporotheca gives an approximation for the resources necessary to develop the respective parts, (ii) that (from reasons of stability) the cross-sectional area of the stalk increases proportional with the volume of the sporotheca, which in turn corresponds with the weight of this structure, and (iii) a stalked sporocarp was assumed to have a spherical sporotheca and that, for stability reasons, the stalk forms a conical cylinder, with a diameter decreasing upwards at 1 µm per 10 µm of stalk length. A function of 0.2 * V_{spt} was found to give values for the cross-sectional area of the stalk that are in the observed range for myxomycete fructifications (compare Fig. 4a). With these assumptions, an iteration algorithm was programmed to calculate the volumes for stalk and sporotheca for any combinations of stalk length and sporocarp volume.

Table 1. Microhabitat groups defined for the myxomycete database.

Micro-habitat	Explanation
cor	Corticolous species from bark of living trees.
wood1	Dead, but still not decayed wood, often from still erect or freshly wind-thrown trees, bark firmly attached (especially for *Stemonitales* with plasmodia living in solid, perhaps living wood).
wood2	Slightly decayed wood, bark still attached, but cambium already rotten, wood ± solid.
wood3	Moderately decayed wood, bark already loose or fallen off, wood still in form, but appearing softer and often with abundant fungi infestation.
wood4	Strongly decayed, partly destroyed wood, mostly (with exception of *Betula*-logs) without bark, wood soft and of spongy consistency, easily broken by hand, often from thicker logs.
wood5	Very soft, spongy wood remnants which have lost their form already, last stage of wood decay.
woodA	Decorticated, slightly to medium decayed wood of logs thicker than 15 cm, lying very moist (water-saturated air) and shady, covered by a thin slimy layer of algae and liverworts.
rockA	As previous, rocks and boulders.
woodM	Mostly decorticate wood of decaying stage 2–4 but covered with thicker (> 1 cm) moss tussocks, seldom with liverworts (*Mylia* spp.) which are enriched with detritus.
rockM	As previous, but on rocks and boulders.
little	Leaf litter from trees of forests with a fairly closed canopy.
littW	As previous, but small woody litter, twigs and woody plant bases less than 5 cm in diameter.
littG	Litter of grasses on open ground in summer and autumn, lower altitudes.
littK	Litter of fleshy parts, especially stems, of herbaceous plants, shaded by tall perennials or in woodlands.
niv	Nivicolous species, mostly grassy plant litter on open slopes with intensive sunlight near to melting snow banks.
cop	Coprophilous species, older dung and droppings of plant-eating animals, lying on ground, see Eliasson & Keller (1999).
epi	Living leaves covered with liverworts, lichens and algae, predominantly in rainforests (epiphyllic species, see Schnittler 2001).
suc	Succulenticolous species in the sense of Lado et al. (1999), occurring on decaying parts of succulent plants infected with yeasts.
inflo	Parts of living inflorescences quickly decaying between the still alive bracts, mostly with a very basic pH (Schnittler & Stephenson 2001), ”epiflorous” species.

All described taxa were classified into three categories as described in chapter 2: those known only from the type locality as one or more collections, those reported from 2 to 20 localities, and those reported from more than 20 localities. In a second part of the database, each species was assigned to one of the orders of myxomycetes, using the taxonomy of Martin & Alexopoulos (1969). Based on the information given in the literature, but also from own experience, the microhabitats preferred by the respective species were classified according to the definitions given in Table 1. One or two additional microhabitats, where the respective species can be found fairly common as well, were allowed. However, when a species was assigned to more than one microhabitat, only the preferred microhabitat was considered.

For the microhabitat data, only species which are fairly common (category three) were included, since only for those a considerable number of collections and observations is available for the determination of microhabitat preferences. If no citation of the protologue is given, the names of myxomycete species mentioned in this chapter follow the nomenclature of Martin & Alexopoulos (1969).

Results

As of July 2000, 1008 subgeneric myxomycete taxa (for the sake of simplicity furthermore referred as species) have been validly described. Except for 13 members of the genus *Ceratiomyxa*, traditionally regarded as myxomycetes but belonging to the Protosteliales, 20 (2%) are members of the order Echinosteliales, 160 (16%) of the Liceales, 169 (17%) Trichales, 403 (40%) Physarales, and 243 (25%) Stemonitales. For 959 of these 1008 species, the whole set of morphological characters was available from the literature. The remaining 49 taxa were described validly according to the code of botanical nomenclature (Greuter et al. 1994) but not all measurements necessary for this evaluation were given. A total of 439 species was regarded as better known and included in the ecological analyses.

Morphology of fruiting bodies.—Of the 1008 described species (excluding the genus *Ceratiomyxa*) 73 fruit predominantly as plasmodiocarps and the same number form aethalia or pseudoaethalia. The majority (849 species, or 85%) have sporocarps. Of these, 561 (about two thirds) are stalked and 288 are sessile. The stalked sporocarp is the most common form of the myxomycete fructification, occurring in 56% of the 1008 described species and 58% (253) of the 439 better-known species.

Almost all species (933 of 959) have globose spores; in 26 species ellipsoid spores occur regularly, and only one (*Badhamia ovispora*, Keller 1975) possesses strongly ellipsoid spores. The spore diameter of the globose-spored species ranges from ca. 5 to 15 µm (Fig. 1a), with only a limited

number of species having larger or smaller spores. Spore size ranges most often between 7 and 12 µm. The respective numbers of spores per sporocarp range from two (*Echinostelium bisporum* (L.S. Olive & Stoian.) K.D. Whitney & L.S. Olive, Mycologia 74:680.1982), over 4–8 (*E. lunatum* L.S. Olive & Stoian. Mycologia 63:1051.1971), 40–60 (*E. colliculosum* K.D. Whitney & H.W. Keller, Mycologia 72:641.1980) to more than one million per sporocarp (members of the genera *Arcyria* and *Stemonitis*). The majority of species (652 of 933, or 70%) have between 10^4 and 10^6 spores per sporocarp, with 69 species having more than 10^6 spores, and only four exceeding the number of $5x10^6$ spores (Fig. 1b).

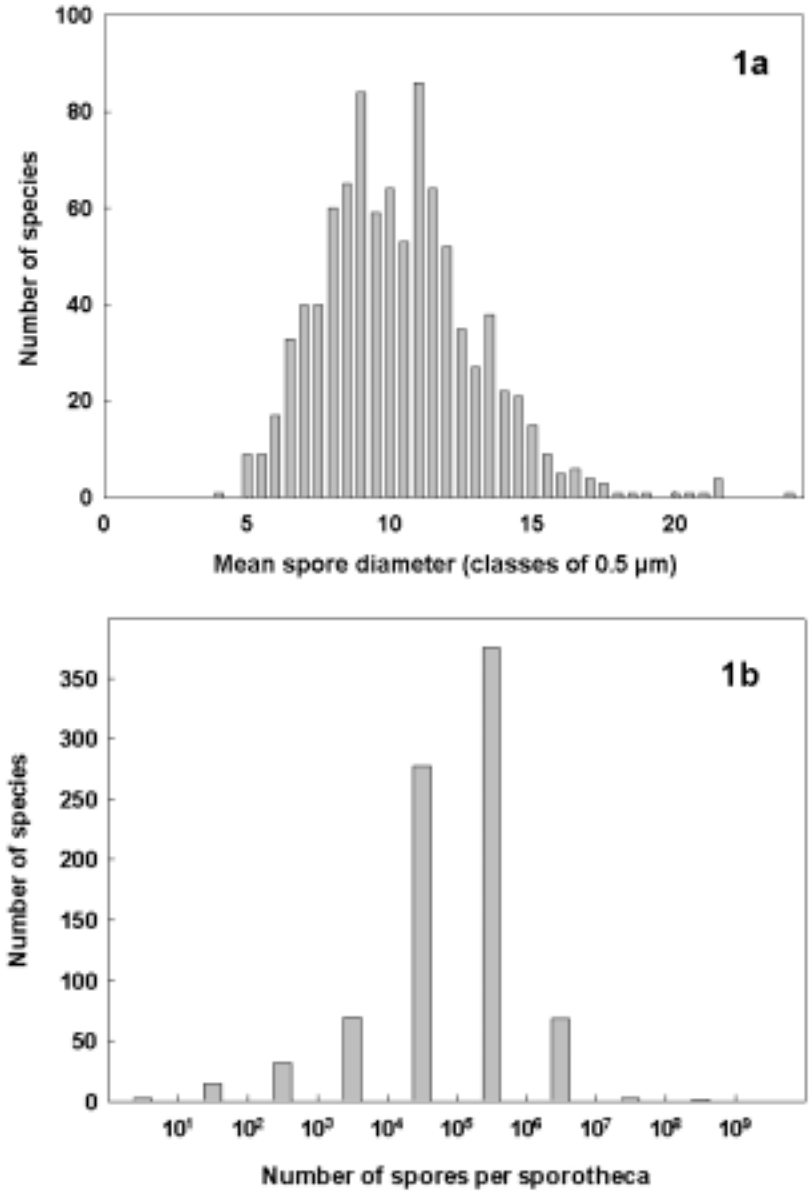

Fig. 1a. Histogram showing average spore diameter for 933 species of myxomycetes with globose spores. 1b. Numbers of spores per sporocarp for this set of species (except for 73 species forming aethalia or pseudoaethalia).

Fig. 2a shows the dependency of the terminal fall velocity on the spore diameter for the range occurring within myxomycetes. In reality, the shape of the parabola may vary slightly, since spores are more dense than water and are often ornamented with warts, ridges or spines; but these two effects counteract each other. Spores with 10 µm diameter should reach a terminal fall velocity of about 300 m per hour, but large ones with a diameter of 20 µm achieve a threefold speed (about 1 km per hour). The terminal fall velocity is the crucial parameter for the estimation of the distance that spores can travel in a lateral air current of a given velocity (Fig. 2b). The travelling distance per meter height loss

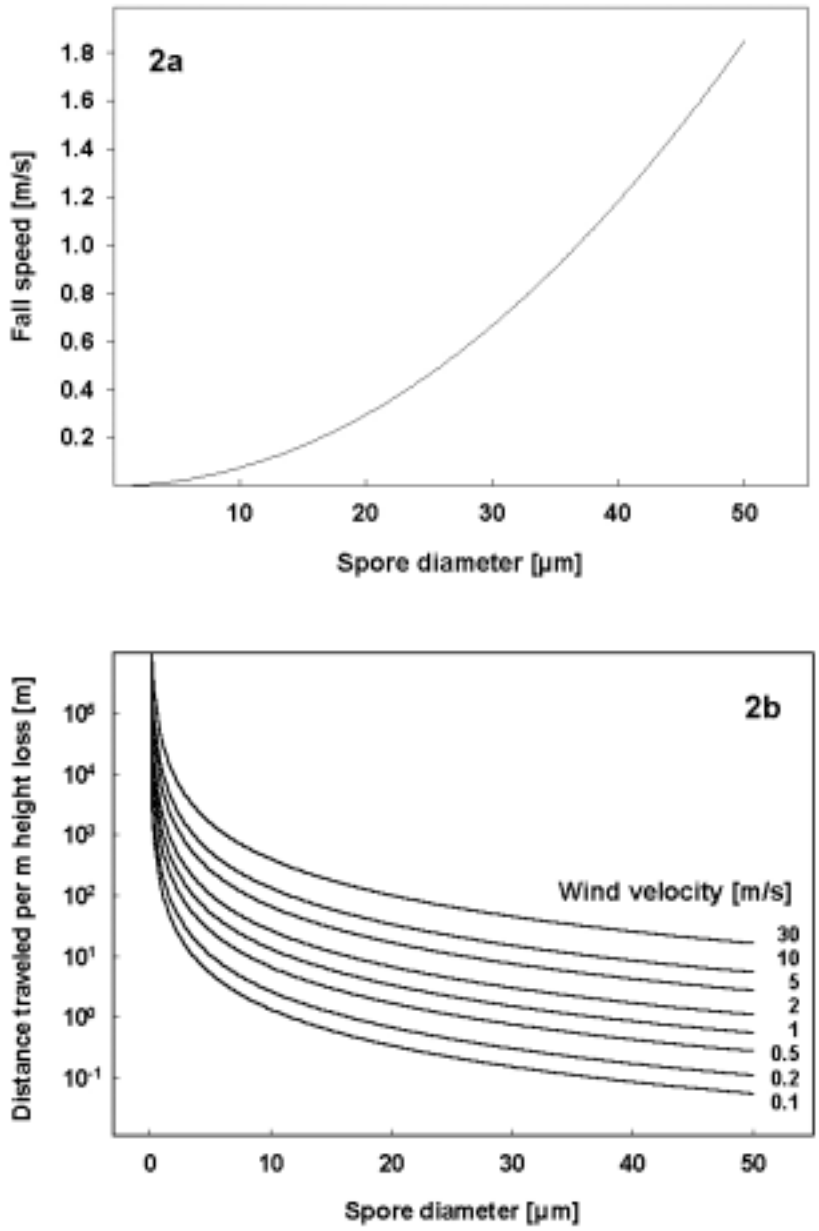

Fig. 2a. Terminal fall velocity calculated for myxomycete spores in dependence of the spore diameter.
Fig. 2b. Possible travel distances per metre height loss with different wind velocities.

decreases in a non-linear manner with the spore diameter, and with horizontal winds of 0.2–5 km/h, as to assume for a more or less dense vegetation, spores between 7 and 12 µm diameter can travel average distances between 1 and 50 metres.

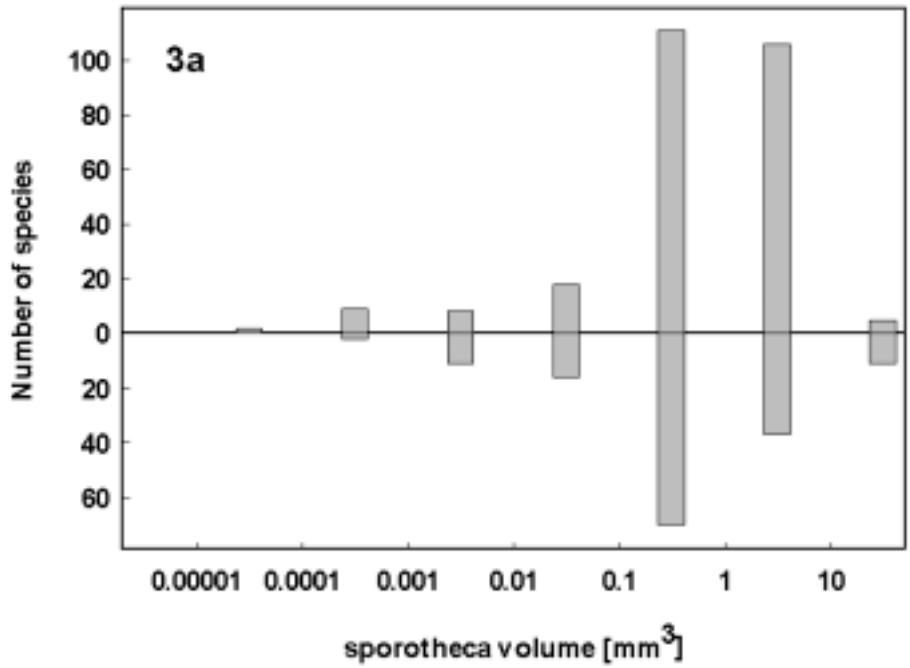

Fig. 3a. Numbers of stalked (upper part of the diagram) and sessile species (lower part) among 387 species of myxomycetes plotted against sporotheca volume.

Regarding the 387 better-known species of myxomycetes that have plasmodiocarps or sporocarps as fructifications, the volume of these structures covers five orders of magnitude, with almost two more orders added by the protostelids and dictyostelids included in the analysis. Of the 387 myxomycete species, 147 have sessile sporocarps (Fig. 3a). Sessile sporocarps occur within almost all orders of magnitude recorded for sporotheca volumes, although the relative proportions of the latter seem to increase with increasing sporotheca size. For the remaining 240 species with stalked sporocarps (including the members of the Protosteliales and Dictyosteliales), the respective stalk lengths depend on the sporotheca size until a volume of about 0.1 mm^3 is reached (Fig. 3b). The majority of stalked myxomycete species possess sporothecae of this size, which corresponds to a stalk length of between 0.4 and 1 mm. For larger volumes, the respective stalk length decreases again. A plot of the quotient stalk length by sporotheca volume versus sporotheca volume shows an almost linear relationship until the maximum sporotheca volume is reached (Fig. 3c). A comparison of Figs. 3b and 3c reveals that species with small fructifications (such as the usually single-spored Protosteliales) have short stalks, but these are long in relation to the sporotheca volume. The quotient stalk length by sporotheca

volume decreases continuously with sporocarp size, but the respective stalk length increases until a threshold is reached with sporocarp volumes of about 0.1 mm^3. As indicated by the cloud of dots in Fig. 3b, most of the stalked species seem to realize sporocarp volumes which enable them to reach the maximum possible stalk length.

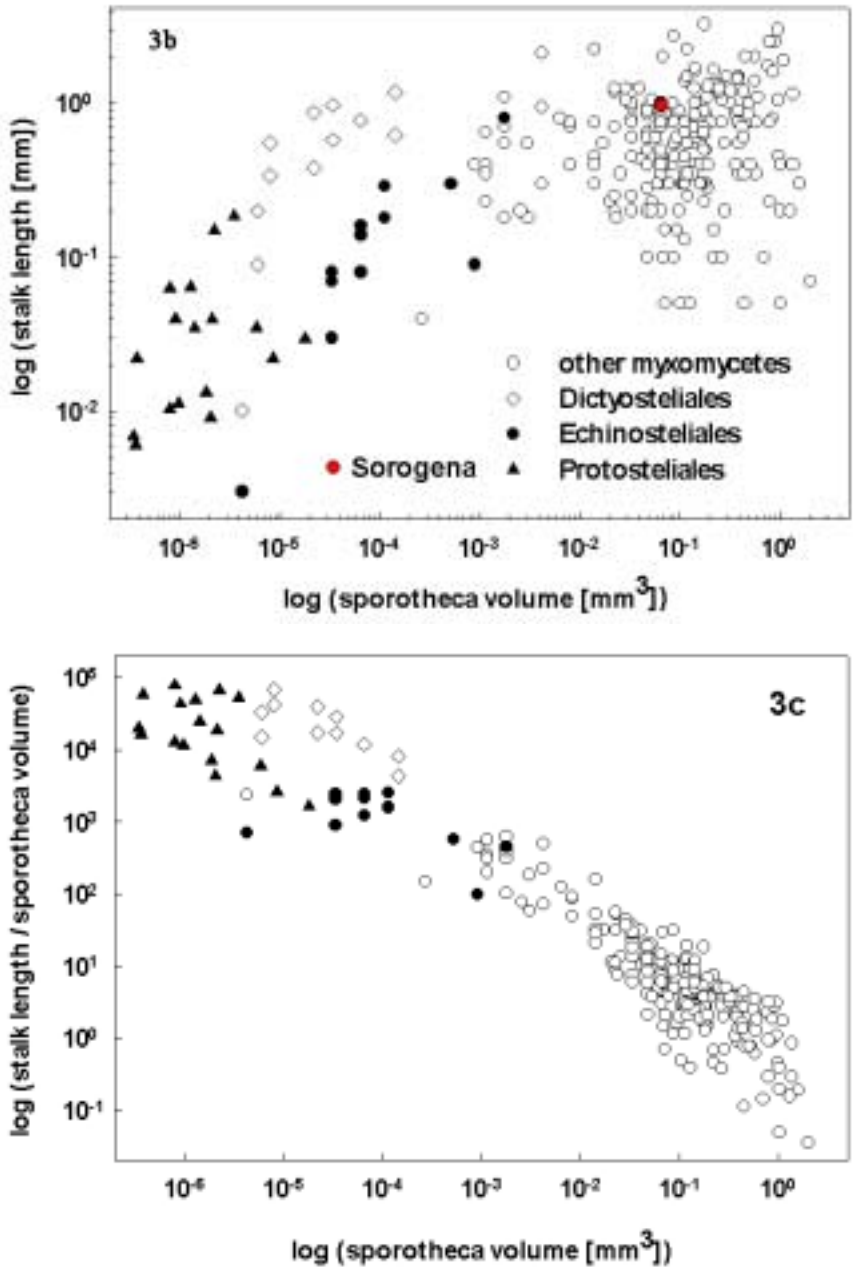

Fig. 3b. Relationship between sporotheca volume and stalk length for 240 myxomycetes and additional members of the Protosteliales (black triangles) and Dictyosteliales (open diamonds). Filled circles indicate members of the Echinosteliales, and open circles the remaining three orders of myxomycetes. Fig. 3c. Plot of the quotient stalk length by sporotheca volume versus sporotheca volume. Symbols are the same as in Fig. 3b.

Ecological species groups.—For 439 better-known species of myxomycetes, microhabitat preferences were assessed (Table 2). Five main groups of microhabitats can be differentiated (compare Table 1). Among these, wood is clearly the most specious habitat, followed by litter. Members of the Ceratiomyxales, Liceales and Trichales prefer most often wood, Physarales most often litter, whereas the Stemonitales are relatively evenly distributed among the microhabitat types. Orders with a high proportion of species that form small fructifications (Echinosteliales and Liceales) have many corticolous but no nivicolous myxomycetes. Litter-inhabiting myxomycetes are mostly Physarales, Trichales or Stemonitales.

Table 2. Microhabitat preferences of the better known species in the genus *Ceratiomyxa* and five orders of myxomycetes. Shown are absolute numbers and percentage of the total number of species considered for each order. Microhabitat abbreviations are as explained in Table 1, with "wood" comprising all stages of wood decay and "litt" including all four litter microhabitats.

Micro-habitat	total[a]	Cer[b]	Ech	Lic	Tri	Phy	Ste
wood	183	5 (83%)	3 (21%)	42 (60%)	53 (69%)	48 (30%)	32 (38%)
cor	69	—	11 (79%)	24 (34%)	4 (5%)	12 (7%)	18 (21%)
niv	33	—	—	—	5 (6%)	14 (8%)	14 (17%)
cop	5	—	—	2 (3%)	2 (3%)	1 (1%)	—
litt	123	1 (17%)	—	2 (3%)	13 (17%)	87 (54%)	20 (24%)
total	413	6 (100%)	14 (100%)	70 (100%)	77 (100%)	162 (100%)	84 (100%)

[a] A small number of microhabitat specialists (see Table 1) was excluded from this analysis.

[b] Abbreviations used for the orders of myxomycetes are Cer = Ceratiomyxales, Ech = Echinosteliales, Lic = Liceales, Tri = Trichiales, Phy = Physarales, and Ste = Stemonitales.

The majority (74%) of the better-known species of myxomycetes form sporocarps, and most of these (75%) are stalked (Table 3). However, in most microhabitat groups, there exist plasmodiocarpous species also. Aethalia and pseudoaethelia occur almost exclusively among species preferring wood or litter. The percentages of species with stalked versus sessile sporocarps differ among the substrata, ranging from 64% (wood) over 59% (bark), 55% (litter), 48% (nivicolous myxomycetes) to 20% (coprophilous forms). The number of truly coprophilous myxomycetes is too small (Keller & Eliasson 1999) for such conclusions. The volume of the sporotheca differs even more greatly: on average, coprophilous and corticolous species have 25-fold smaller volumes than those on wood and litter, and

Table 3. Features of the main ecological species groups in myxomycetes.

	number of species						mean figures (± standard errors) for			
Micro-habitat	total	aet[a]	pdc	spc	sessile	stalked	sporotheca volume $mm^3 \times 10^{-3}$	number of spores $\times 10^3$	stalk length[b] mm	spore diameter µm
wood	183	32	6	140	65	118	228±21	659±100	1.04±0.08	8.79±0.23
cor	69	1	6	62	28	41	4±9	76±34	0.36±0.05	10.49±0.39
niv	33	—	7	26	17	16	608±91	499±92	0.39±0.09	12.31±0.41
cop	5	—	—	5	4	1	4±28	93±81	0.75	9.64±1.44
litt	123	10	21	91	55	68	126±23	173±23	0.52±0.03	9.68±0.21
total	439	43	40	324	169	243	118±15	369±42	0.69±0.03	10.34±0.09

[a] Type of fructification: aet = aethalium or pseudoaethalium, pdc = predominantly with plasmodiocarps, spc = predominantly with sporocarps.

[b] Calculated for stalked species only.

the nivicolous forms have 6-fold larger volumes than those. However, due to their larger spores, the nivicolous species have not the largest spore numbers per sporocarp, this being superseded by the wood-preferring myxomycetes. Wood-inhabiting species tend to have many but relatively small spores, corticolous ones fewer and larger spores; coprophilous and litter-inhabiting species are in-between. Wood-inhabiting species have on average the longest stalks, followed by litter species. But when comparing the index stalk length versus sporotheca volume, due to their mostly small fructifications, the corticolous species perform best (0.09), followed by myxomycetes preferring wood (0.0046) and litter (0.0043), with the nivicolous species having the lowest index (0.0006).

Discussion

As shown in chapter 2, a large number of myxomycetes is known either from the type locality alone or from less than 20 collections world-wide. In spite of the increasing interest in myxomycete research in the last decade (as reflected by the sharply increasing number of newly described species), the taxonomy of myxomycetes is far from being consolidated, and only 439 (43%) of the 1008 taxa described on the subgeneric level can be regarded as better-known. Myxomycetes are one of the most challenging subjects for taxonomic research. In contrast to other micro-organisms, they already possess a considerable number of morphological traits to distinguish taxa, yet are still small enough to show a mixed mode of reproduction (sexual and apomictic), with the consequences (a large number of

clones with minor morphological differences) discussed in chapter 1. It is this reason that most of the data presented above were calculated for the better-known species only.

Among the five orders of myxomycetes (excluding Ceratiomyxales), the Physarales are the most specious, whereas the Echinosteliales are poorest in species. These facts, and the different microhabitat preferences of the members of each order, are well known by every student of the group (although no numbers have been presented so far).

Morphology of fruiting bodies.—The most constant feature of the myxomycete fructification seems to be the spore, in contrast to the shape and the dimensions of the fructification (variation in sporotheca volume extends over six orders of magnitude). Spore diameters are relatively constant: 623 (67%) of the 933 species investigated have spores between 7 and 12 µm in diameter (Fig.1a). This translates into spore volumes between 150 and 900 μm^3, a variation within one order of magnitude. Only the nivicolous species with their large spores extend into the next order of magnitude. Obviously, spore size underlies heavy evolutionary constraints: if spores are too large, they will not float in the air, if they are too small, they cannot carry enough resources to ensure the development of a viable myxamoeba or myxoflagellate. Since these two constraints act directly against each other, the resulting range in spore volume is relatively narrow. The terminal fall velocity is the crucial parameter for the potential travel distances of propagules like spores (Okubo & Levin 1989) and depends strongly on the spore radius (Fig. 2a). This results in non-linear graphs of possible travel distances in relation to spore diameter and horizontal wind speed, with every µm loss in spore diameter as a substantial gain of potential dispersal radius. This radius probably attains only 1 to 10 m under the conditions of the low wind speeds on a forest floor (0.1–2 km/h, Fig. 2b) where most myxomycetes fruit. However, a strong winter storm, or a tropical thunderstorm with its connected air turbulences and thermals could well carry spores to higher atmospheric layers. As shown by calculations for the jetstreams, stratospheric air currents with speeds of 200 km/h that span the globe, spores could be carried for kilometres in these currents, but hardly travel around the globe (if no additional thermals moved them upwards again). Still not considered is the lower air pressure in these altitudes (which should cause spores to fall faster). Furthermore, the question remains, to which extent spores can withstand the intense UV radiation and low temperatures. These considerations make the long-term dispersal of myxomycete spores less probable than it is often assumed and coincide with observations that series of collections of one species differ slightly over longer distances but are very homogenous within a given locality. As it is the case for higher fungi, the existence of different biospecies (within a given morphospecies) in different continents seems possible. The dispersal potential of myxomycetes is furthermore lowered by the small dimensions of the fruit bodies, often elevating the

sporotheca not more than one or a few millimetres over the substratum. However, thermals with upwardly moving air currents seem to occur quite often in forested areas, as one can see on the fruit bodies of *Ganoderma applanatum*, a common wood-destroying polypore, where the large brackets are often covered by spores on their upper surfaces. Especially in the Tropics, myxomycetes often inhabit aerial substrata (chapter 10), where the initial fall height in the metre-range increases the probability for spores to be caught by thermals.

The consideration made herein can be confirmed by a comparison with mosses. Since most of the species are of macroscopic size and present during most of the year, their distribution patterns are already fairly well known. Similar to myxomycetes, spores of mosses are often between 10 and 15 µm in diameter (Mogensen 1983). Also the number of spores per capsule is within the same range as for myxomycetes (most commonly 50 000 – 500 000, but much smaller numbers occur for large-spored species, Longton & Schuster 1983). In contrast to myxomycetes, some species have very large spores (up to 200 µm diam.). In these cases (e.g. *Riccia*, a genus inhabiting temporarily flooded bare ground), other dispersal mechanisms (such as floatation by water) seem to prevail. However, also for mosses with spore diameters in the range of those common for myxomycetes, the conditions for long-distance dispersal of mosses in nature seem to be rarely realized (van Zanten & Pocs 1981). This agrees well with the fact that numerous species and even whole genera of mosses are endemic to certain regions, e.g. Japan, the North American Pacific coast, or the Appalachians (Schuster 1983). However, even more species show highly disjunct ranges, sometimes with gaps over whole continents which must have been bridged by spores. Other studies show that geologically very recent, isolated islands possess a considerable number of moss species (Longton & Holdgate 1977). Van Zanten (1978) found a correlation between the extent of ranges and the ability of spores to survive desiccation and frost in studies on New Zealand mosses. These observations allow successful long-distance dispersal in mosses to appear possible in principal but much more rarely in reality.

For sporocarp-developing myxomycetes, the related sporotheca volumes and numbers of spores per fructification vary widely from a single spore to almost a billion (Fig. 1b). Obviously, these numbers are much higher in species with aethalia. These of a species such as *Lycogala flavofuscum* (spores ca. 5.5 µm, fructification often exceeding 5 cm in diameter) can contain about 10^{12} spores. Very probably, species forming large aethalia and pseudoaethalia realize another dispersal strategy than those with simple sporocarps. This is indicated by the fact that genera such as *Fuligo* and *Lycogala* (where all species form aethalia) show positive geotropism, whereas many other myxomycetes with sporocarps can from their fructifications upside down, e.g. perpendicular to the surface on the sheltered lower side of a log.

Two methods of dispersal are most common for such species. *Lycogala* has aethalia with a solid outer peridium which are so superficially similar to puffballs that the genus was described as an *Lycoperdon* by Linne (Lado & Henandez 2000). *Enteridium* and *Tubifera* are two other genera with these features; and all three have rather small (5–7 µm) spores covered with a reticulum of elevated ridges. These structures make the spores very hydrophobic – water droplets falling into the spore-mass assume a spherical shape, and can be moved between the tips of a forceps in this condition (pers. obs.). These genera all show positive geotropism, forming their fructifications at the highest place that the migrating plasmodia can reach. Like in puffballs, impact of rain drops causes a spore burst, and the rather small spores become airborne. As shown in Fig. 2b, the rather small spores of these genera should achieve longer potential travel distances than most other myxomycete species. Genera such as *Fuligo*, *Amaurochaete* or *Symphytocarpus*, which form decorticate aethalia and pseudoaethalia, seem to rely more on insect dispersal (compare chapter 1). In these cases, spores are with 9–12 µm diam. larger, relatively thick-walled and ornamented with spines. The spores seem to be less hydrophobic, and insects can be seen quite often feeding on the fructifications. Beetles specialized upon slime mould fructifications (chapter 1) often have a preference for Stemonitales fructifications. Relying on other organisms instead of air as a vector, spore size is no longer that limiting, and consequently the spore sizes in these genera move towards the upper end of the range commonly found in myxomycetes.

However, most species of myxomycetes develop sporocarps, and most of these are stalked. Interestingly, the species with phanero- and aphano-plasmodia usually form many dozens to several thousands of sporocarps from a single plasmodium, which are often arranged at more or less regular distances on the substratum. Since a plasmodium diverts its resources in that way (in contrast to the always sessile, aethalium-forming species), sporocarp size must be limited by a certain factor, i.e., larger sporocarps must face some kind of disadvantage. Indeed, at least stalked sporocarps seem not to exceed a certain upper size between 0.08 and 0.8 mm^3 sporotheca volume, where a large proportion (43%, compare Figs. 3a, b) of species with stalked sporocarps can be found.

Obviously, the development of a stalk is a resource allocation problem: a stalk increases the probability that the spores dry out and become airborne, but uses up resources which could be allocated to the production of more spores. As indicated by Fig. 3b, stalk length correlates with the sporotheca size over a wide range of magnitude, but from a certain sporotheca size its length seems to decrease again.

A resource allocation model was developed to look for a possible theoretical limit of the size for a stalked fructification. The simplifying assumptions explained under “Methods” are very probably not exactly fulfilled in Nature. First, in terms of energy, the DNA-containing spores should represent a

higher effort per volume unit than it is necessary to form the same volume of stalk material. This should lead to an overestimation of the resources that are necessary for stalk development. Second, the specific weight of a volume with spores may be higher than that of the same volume of stalk material. If the cross-sectional area of the stalk is assumed to increase with sporotheca volume (as an approximation for weight), this should in contrast lead to an underestimation of resources that have to be invested for stalk development. The relationship between sporotheca diameter and the necessary diameter of the stalk tip used for the model is in the range observed for myxomycete fructifications (Fig. 4a, e.g. a sporotheca diameter of 50 µm versus a stalk diameter of 4.1 µm; 100 µm versus 10 µm; 250 µm versus 50 µm; 500 µm versus 130 µm, or 1 mm versus 0.37 mm). The results of the calculations are shown in Fig. 4b. For small sporotheca volumes the amount of resources needed for stalk development increases sharply with stalk length. Thus, it should be expected from the model that small fructifications (as occurring in Protosteliales, Dictyosteliales and Myxomycetes possessing protoplasmodia) have a clear upper limit for stalk length. If this limit is assumed to be at 20% (not more than one fifth of all resources should be used for stalk development), the dimensions shown in Fig. 3b correlate well with those predicted by the model. For larger volumes, limits for stalk length are not defined as narrow as for small ones. However, the curves for large volumes are much closer to each other than it is the case for small volumes. In other words, up to a volume of ca. 0.8 mm^3 more volume means that a longer stalk can be formed using the same proportion of resources. For larger volumes, this is not the case. Under the assumption that about 80% of the resources have to be allocated for the sporotheca, a maximum stalk length of about 1–1.2 mm should be possible with a sporocarp volume of ca. 0.5–0.8 mm^3, which is close to the limits observed in reality (Fig. 3b).

As a second result the model explains why myxomycetes with large plasmodia do better when diverting their resources into many small stalked fructifications. If they would combine all resources into one big fructification, no significant gain in stalk length can be achieved. But, this “all eggs in one basket” strategy would mean that the single fructification faces a high probability of being destroyed by rain, animals, or fungi. In contrast, numerous small fructifications have a high chance that at least one survives. Moreover, for most substrata it is necessary only to elevate the sporotheca above a water film which may cover the substratum surface. Exceptions are the aethalium-forming species with sessile fructifications. Species with the “puffball strategy” have a robust, thick cortex to keep the highly hydrophobic spores dry, whereas animal-dispersed species may “want” to have their fructifications destroyed by the animals.

Another exception are a few species where clustered sporocarps that form a common long stalk. Usually, they occur on very wet, often white-rotten wood soaked with water, e.g., *Tubifera bombarda*, *T. microsperma*, *Metatricha vesparium*, or *Arcyria cinerea* var. *digitata*. Here, stalk lengths of almost

1 cm can be achieved by a new principle: a number of sporocarps cluster to form a single, bundled stalk. Perhaps, this bundle of individual stalks is much more stable than a solid stalk of the same dimensions would be. Furthermore, mechanical structures of the stalks vary between myxomycetes and other stalk-forming micro-organisms. As it is easy to observe by breaking apart dry sporocarps, Stemonitales with an epihypothallic type of development have stalks with better mechanical features

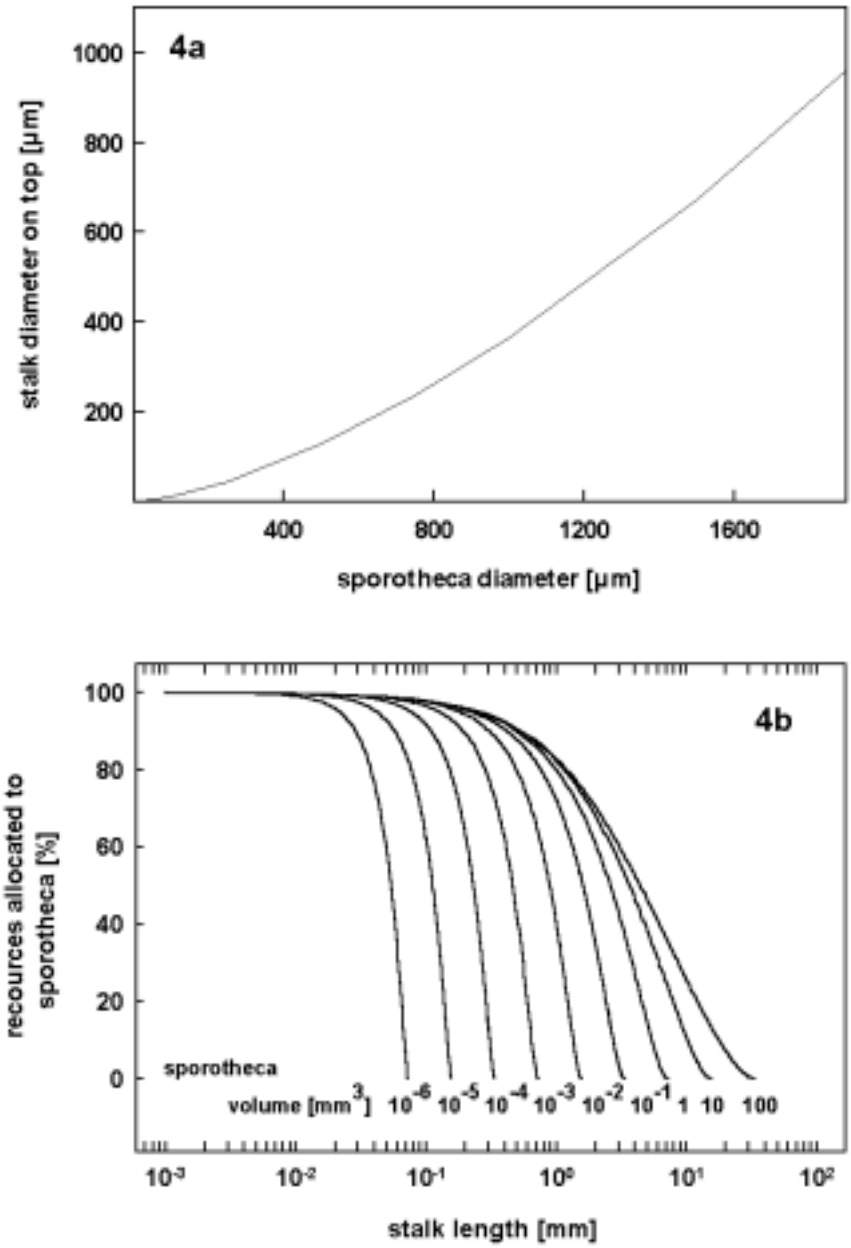

Fig. 4a. Theoretical relationship between sporotheca diameter and stalk diameter (above) for a proportionality factor of 0.2 between sporotheca volume and the cross-section area of the stalk. Fig. 4b. Amount of resources necessary for formation of a stalk and sporotheca for various combinations of sporocarp volumes and stalk length. The given numbers for volumes refer to sessile sporocarps.

than Trichales with a subhypothallic development. Not surprisingly, Stemonitales form the largest stalked solitary sporocarps among myxomycetes, and the stalks can reach a few mm in length. Another exception seem to be some Dictyosteliales. Here, the stalk is unusual long and slender (compare Fig. 3b), but not as stable as in myxomycetes, since the fructifications soon collapse.

The crucial point applying to all these considerations is the assumption that a stalk considerably increases the probability that spores dry out and become airborne, at least on continuously wet substrata. Several lines of evidence support this: (i) wood-inhabiting species (a compact substratum with a high water retention) have the highest percentage of stalked species, (ii) stalks tend to be longer for wood-inhabiting myxomycetes (Table 3), and (iii) tropical collections of wood-inhabiting species were found to form a longer stalk than temperate ones (compare chapter 9), since logs stay longer wet in tropical forests.

Ecological species groups.—The assumption that a stalk is the main structure to increase the chance of spores drying out, correlates well with observations that wood-inhabiting myxomycetes have the highest proportion of stalked species. In contrast, although often of comparable sporotheca sizes, litter-inhabiting myxomycetes have a higher percentage of sessile species and tend to develop shorter stalks among stalked species (Table 3). Especially in arid regions, litter dries out much faster and more frequently than wood.

Nivicolous species form the largest spores and sporocarps among all ecological groups, which tend to be either short-stalked or plasmodiocarpous. In this microhabitat, the substratum regularly dries out within a couple of weeks, when the snowfields retreat in spring and expose the previous year´s remnants of herbaceous plants to the sun (compare chapter 6). For a short time, the substratum warms up due to the intense radiation, but stays wet by melt water provided by the retreating snow. A few days later it can dry out completely after the snow has melted away. For a short time prior to the development of the herbaceous vegetation in the alpine meadows, the substratum is fully wind-exposed. These peculiarities of the substratum can explain the morphological features. Stalks are of minor importance, since the substratum dries within a short period of time. Coincidentally, nivicolous species of *Lamproderma* (e.g., *L. atrosporum, L. carestiae*) have much shorter stalks than wood-inhabiting representatives of this genus (*L. arcyrionema, L. columbinum*). Due to the stronger winds in mountains and the totally exposed substrata, spores can be larger (and, probably have to, to provide enough resources for a quick start to utilize the rather short time window for development in spring). To decrease the terminal fall velocity of the rather big spores, they are strongly ornamented. Indeed, the most prominent spore ornamentations can be found among nivicolous species.

As a general rule, species with rather small sporocarps tend to be more common in dry to arid regions, where substrata stay wet for a short period of time and dry out quickly. In continuously humid regions, robust species with phaneroplasmodia and larger sporocarps prevail (chapter 10). The mean sporocarp values of a few surveys which are sufficiently complete (including studies with the moist chamber method) indicate this: Kazakhstan (chapter 8, arid, 25 species): 0.056±0.015, Russian Karelia (chapter 5, boreal, moist, 79 species): 0.19±0.033, German Alps (chapter 7, montane, humid, 57 species): 0.15±0.023, south-western Virginia (Stephenson 1988, 1989, montane, humid, 114 species): 0.15±0.022, and Ecuador (chapter 9, tropical montane, wet, 73 species): 0.15±0.025 (for these comparisons, the Ceratiomyxales and all species forming aethalia or pseudoaethalia were excluded). One major reason for the small average sporocarp sizes of arid myxomycete assemblages is their high percentage of corticolous myxomycetes. In tropical forests, the diversity of corticolous myxomycetes decreases strongly with increasing elevation and annual rainfall (chapter 10). In contrast, about 30% of all species recorded within the Kazakhstan study (chapters 8, 14) are preferentially corticolous.

With their short generation times and high reproductive potential, micro-organisms are well suited to quickly utilize spatially and temporally changing habitats. However, these opportunities have to be explored. Dispersal via durable propagules is the appropriate life strategy. If no other vectors, such as animals, exist, these propagules have to become airborne, which is not easy for organisms living on wet substrata that are often saturated with water or even covered by a water film. The answer to this evolutionary challenge is the formation of usually stalked fruit bodies. Besides the myxomycetes, evolutionary lines leading to fruit bodies occur in several groups of micro-organisms and were evolved in parallel at least for some of these groups.

Among prokaryotes, several groups of bacteria develop spores, but only the myxobacteria possess fruiting bodies. These structures range from slimy agglomerations of cells (*Myxococcus*) or simple, stalked fruit bodies (e.g., *Melittangium*) to elaborate, branched and up to 1 mm tall forms (*Chondromyces*, *Stigmatella*). The morphology of the fruiting bodies is rather important for species differentiation (Reichenbach 1993). Spores are usually formed within sporangioles, sac-like structures with a durable peridium. When released, the spherical to ellipsoid, 1.2–2.5 µm (and up to 5 µm) long spores should easily be able to travel over long distances (compare Fig. 2b). Spore diameters can be significantly smaller due to the smaller genome sizes in prokaryotes. Currently, about 40 species of myxobacteria are recognized .

The Acrasiales, a species-poor group of eucaryotes, develop fructifications consisting of a chain of stalk cells and spores arranged in a row or in spherical masses. The most common species, *Pocheina*

rosea (Cienk.) A.R. Loebl. & Tappan, possesses a stalk of 150–250 µm height and a spore case of 40–110 µm diam.; the spores are 7–12 µm diam., falling within the same range as for most myxomycetes.

The best proof for the evolutionary advantage of the fruit body are the Dictyosteliales, where thousands of cells aggregate to form these structures in a cooperative effort, using cAMP as messenger substance. In relation to the size of the sporotheca (called sorus in this group), the dictyostelids form the longest, but least stable, stalk (Fig. 3b), which correlates with their occurrence in the wet soil-litter interface in (most often tropical) forests. With average sizes of 2–8 µm, the smooth, often ellipsoid spores are on the lower end of the typical range for myxomycetes.

As in the previous group, the Protosteliales also have always stalked fructifications which typically contain only a single spore. Stalk lengths vary widely, and spores range from 7–20(–30) µm, with sizes often exceeding those of myxomycetes. On the other hand, some species evolved active mechanisms for spore discharge, and members of the group are quite common in aerial habitats (Moore and Spiegel 2000).

Besides the formation of fruiting bodies, another common feature of these groups of "myxomycete-like micro-organisms" is the fact that they are predatory on other micro-organisms, most often bacteria. Differing in many features, but also often possessing a stalked fructification, conidiophores of a plethora of hyphomycetes can also be mentioned. Fruitings develop on single hyphae or on groups of hyphae. Here, due to the higher stability of the hyphal structures, the stalk / conidiophore quotient is probably most often higher than in the groups mentioned above.

From these considerations, the following evolutionary trends seem to prevail in myxomycetes, and probably in all groups of myxomycete-like micro-organisms: (i) Spores are the primary type of propagules able to reach new habitats. Their dimensions stay within narrow limits, with the upper boundary probably determined by the amount of DNA carried, and the lower boundary determined by the non-linear negative correlation between spore diameter and potential travel distances. (ii) It can be expected from the estimations of potential travel distances, that long-distance dispersal is rather rare in myxomycetes, which is in accordance with the finding that local populations of one and the same species often show minor differences. (iii) A common feature of myxomycete-like micro-organisms is the development of fruit bodies. In wind-dispersed forms, these are usually stalked. (iv) The development of the stalk can be seen as a resource-allocation problem, and the tendency to allocate resources for stalk development increases in wet climates and with the water retention of the substratum. This indicates that the primary function of the stalk is to allow the spores to dry out and become airborne. (v) As shown by the distribution of observed measures, the size of stalked

fructifications seems to be limited. This assumption is supported by a resource allocation model. (vi) The optimum for stalked fructifications lies between a stalk length of 0.5–1.5 mm and a sporotheca volume between 0.05 and 0.5 mm^3, which is realized for most species of myxomycetes. The species-poor groups of Protostelids and numerous myxomycetes with protoplasmodia fall beyond this optimum. (vii) Additionally, the model explains why myxomycetes with large phaneroplasmodia divert their resources to develop many small stalk fructifications. (viii) These considerations about fruit body morphology do not hold true for myxomycetes with other dispersal strategies. Two of these, the "puffball strategy" and insect dispersal, occur in species with aethalia or pseudoaethalia. (ix) The distribution of fruit body features among the ecological groups in myxomycetes (as defined by microhabitat preferences) indicates evolutionary pressure for certain features associated with certain microhabitats which, in turn, influences the distribution of the species of a myxomycete order within microhabitats.

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Chapter 16. World-wide distribution patterns in myxomycetes

In spite of the increasing number of papers published on local surveys of myxomycetes, information available on the distribution of these organisms is far from being complete. The greatest obstacle to reveal the true patterns of myxomycete biodiversity on Earth is the incompleteness of most of the published species lists. So far, except for the investigations shown in this thesis work, no attempts were undertaken to estimate the completeness of a local species inventory. Since most (>95%) of all published surveys do not include abundance values for the species recorded, statistical methods can not be employed to judge their completeness. However, an experienced collector can do this fairly accurate from reviewing such lists.

To overcome these deficiencies, three approaches were undertaken to obtain an idea about the patterns of world-wide myxomycete diversity: (1) for about 440 better-known species of myxomycetes, the distribution among the major vegetation zones was assessed according to the experience of the author, (2) checklists were data-based for the more intensively studied regions of the world, and (3) the most complete local species inventories on myxomycetes were compared with each other. Within these approaches, the amount of data available decreases from (1) towards (3), whereas data quality increases. For the purposes of this chapter, surveys, floras and inventories that used the moist chamber method (recovering an additional 20–60% of all potentially occurring species, depending on myxomycete habitats) together with field observations were considered.

Methods

For the first approach, a database was compiled for all better-known species (category 3 in chapter 2, known from more than 20 localities world-wide) . For these 439 species, distribution within the world's major vegetation zones was assessed. Five zones were differentiated: arctic regions – tundra beyond the timberline, boreal regions – boreal coniferous forest, temperate – deciduous and mixed forests, meridional – warm-temperate deciduous forests with hot summers but still cold winters, including Mediterranean areas, tropical – tropical dry to wet deciduous forests, scrublands and deserts free of frost around the year. Two additional factors were considered. The first is the humidity of the habitat were a species is usually found: wet – almost continuously wet environments with no dry season, moist – regions with regular rainfalls but dry periods in-between, dry – areas with a pronounced dry season lasting for more than two months (e.g., Mediterranean regions, tropical dry forests), arid – desert-like areas with only occasional rainfalls. As a second factor, the altitudinal distribution of the species was estimated within four categories: lowland – regions with the climate and vegetation typically for the respective zone, foothills – elevated regions with a slightly cooler climate and a vegetation poorer in species than the respective vegetation zone, montane – montane, usually coniferous forests close to the timberline, alpine – regions above the timberline, usually with a meadow-like vegetation or a sparse cover mostly of herbs.

Due to the temporal character of the myxomycete fructifications and the short development time of many species, numerous species are occasionally recorded (e.g., within periods of exceptional weather) for a certain vegetation zone but are much more common elsewhere. A typical example is the checklist of myxomycetes for Germany, where about 50% of the ca. 320 recorded species are represented by less than three specimens. In such cases, only the vegetation zone was considered where a species regularly occurs. In a similar manner, the occasional records of temperate species from mountains of the Tropics where disregarded, to get a clearer picture of their climatic preferences.

For the second approach, a comparison of species lists for the more intensively studied regions of the world, a set of criteria was established to judge if a regional inventory is suitable for this purpose. These are: (i) The study must be a checklist aimed towards a complete species inventory and has to include results from moist chamber cultures (ii) a larger region, possessing all ecosystems typical for the respective vegetation zone, must be covered, (iii) the survey intensity must be sufficient in relation to the size and the heterogeneity of the region. To illustrate this, the approximate number of specimens seen and moist chamber cultures carried out is given wherever data were available (often by questioning the authors personally).

The third approach includes the use of local surveys. Here, the criteria for selection were: (i) a more or less homogenous area with the vegetation typical for the respective vegetation zone must be covered, (ii) all microhabitats suitable for myxomycete occurrence must be investigated, (iii) at least an estimation of species abundances must be given, or all observed colonies for a species were recorded. Abundance estimations were made (or calculated when total abundances are given) as described by Stephenson et al. (1993). This estimate is based on the proportion of a particular species on the total number of records in the respective survey: R – rare (<0.5%), O – occasional (0.5–1.5%), C – common (>1.5–3%) and A – abundant (>3%).

All surveys with abundance estimations for the species were compared using a coefficient of community (CC) index (Stephenson 1993). Originally, the formula used to calculate this index is based solely upon the presence or absence of species: $CC = 2c/(a + b)$. Here, a is the total number of species in the first data set being considered, b is the total number of species in the second data set, and c is the number of species common to both data sets. The value of CC ranges from 0 (the data sets being compared have no species in common) to 1.0 (all species are present in both data sets). This range was maintained for a modification of the formula created to compare data sets by using abundance estimations. Here, values of c were defined as lower than 1 if the species in question is rare in one but more common in the other data set (Table 1).

	A	C	O	R
A	1	0.8	0.5	0.2
C	0.8	1	0.8	0.5
O	0.5	0.8	1	0.8
R	0.2	0.5	0.8	1

Table 1. Values for c (originally the number of species common to both data sets) in dependence from their abundance estimations.

As a case study, world distribution maps were compiled for two species, using the collection of the author, a data base of ca. 3000 published papers and the respective reprint collection, and personal information received from colleagues.

Results

Distribution data base.—When assessing the zonal distribution of the better-known species of myxomycetes from the experience of numerous collecting trips and literature reports, species richness seems to increase from the arctic to the meridional zone but to decrease again in the Tropics (Table 2). Judged from these "soft" data, the meridional zone, characterized by a still seasonal climate with cool to cold winters but hot summers is most suitable for the majority of species. Except for the Ceratiomyxales (here like in most papers treated as myxomycetes but taxonomically belonging to the protostelids), all orders of myxomycetes behave in a similar manner. In the Tropics, the Echinosteliales and Liceales, with all or a considerable part of the species forming tiny fructifications from protoplasmodia, are even poorer in species than the three other orders with phanero- or aphano-plasmodia.

Table 2. Distribution of the 439 better-known species of myxomycetes among the major vegetation zones. Shown are total numbers and percentages (a given species can be assigned to more than one vegetation zone).

Zone	Cer [a]		Ech		Lic		Tri		Phy		Ste		Total	
arctic	—	—	2	14.3%	—	—	2	2.6%	6	3.3%	1	1.2%	11	2.5%
boreal	1	16.7%	3	21.4%	9	12.0%	12	15.4%	34	18.9%	18	20.9%	77	17.5%
temperate	1	16.7%	12	85.7%	59	78.6%	60	71.9%	128	71.1%	69	80.2%	329	74.9%
meridional	3	50.0%	13	92.9%	63	84.0%	63	80.8%	149	82.8%	82	95.3%	373	84.9%
tropic	5	83.3%	4	28.6%	22	29.3%	33	42.3%	89	49.4%	39	45.3%	192	43.7%
total	6	100%	14	100%	75	100%	78	100%	180	100%	86	100%	439	100%

[a] Abbreviations used for the orders of myxomycetes are Cer = Ceratiomyxales, Ech = Echinosteliales, Lic = Liceales, Tri = Trichiales, Phy = Physarales, and Ste = Stemonitales.

The great majority of the species have a multizonal distribution, although many seem to be more common in one vegetation zone than in all others (Fig. 1a). Most common are species with a temperate-meridional (155, 35% of 439), temperate-tropical (75, 17%) or meridional-tropical (70, 16%) distribution. About one half (34) of the latter category are members of the Physarales, as it is the case for two thirds (14) of the species with a tropical distribution centre. A typical example of a myxomycete with a temperate distribution is *Leocarpus fragilis* (case study I, see p. 297), found but rarely in arctic regions, very common in temperate Zones and fairly common in southern temperate regions. Further southwards the species is limited to mountain ranges, e.g. the Mexican volcanoes or the Himalayas. It has a distribution gap in the Tropics but reappears in temperate regions of the southern hemisphere. Case study II (*Ceratiomyxa morchella*, p. 298) is typical for a limited number of tropical myxomycetes. The species is most abundant in moist Neotropical forests and has a few outposts in subtropical regions such as Florida or the Caribbean islands.

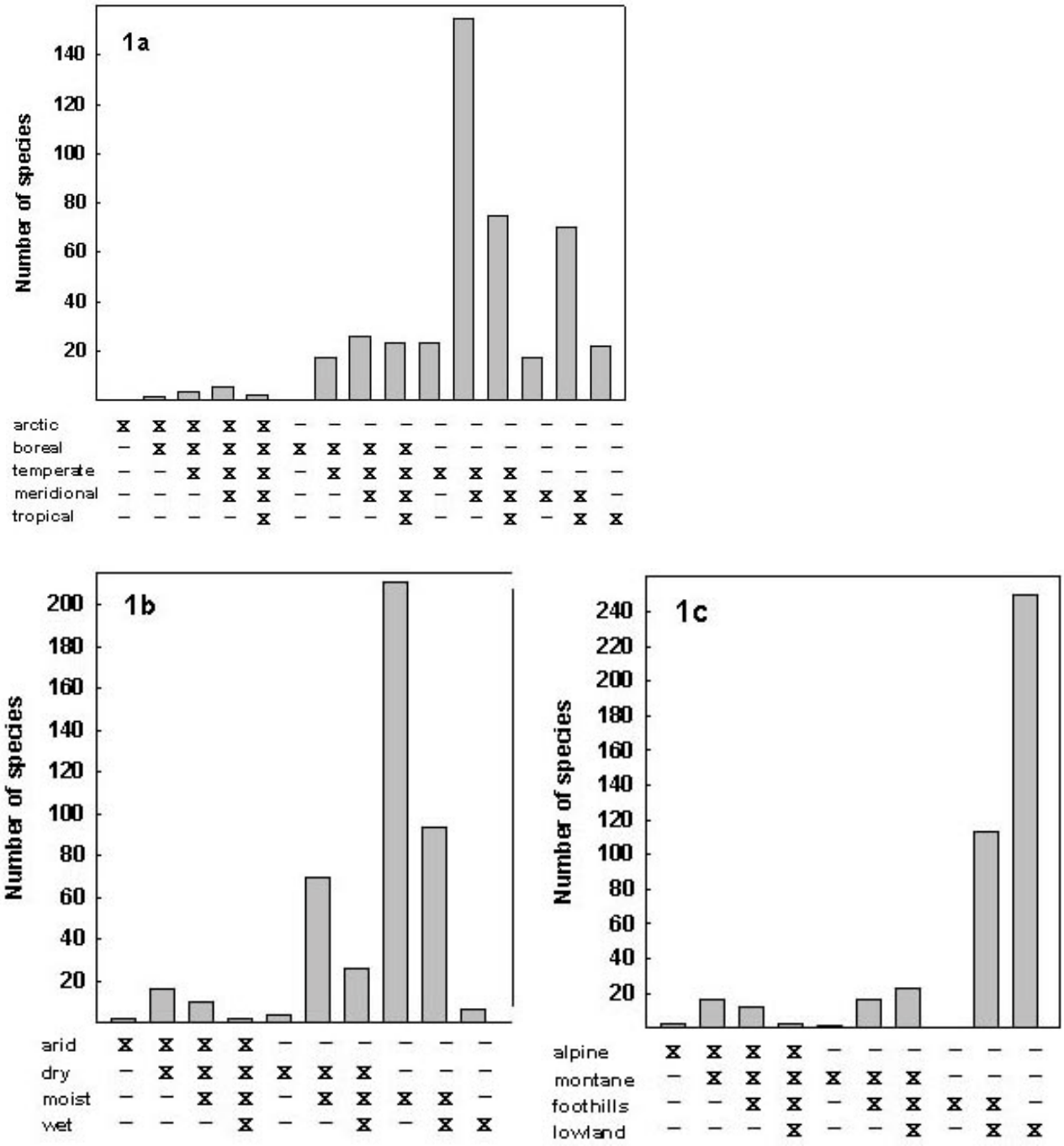

Fig. 1. Distribution of the 439 better-known species of myxomycetes among the major vegetation zones (1a), a moisture (1b) and an elevational gradient (1c). The distribution pattern as assessed for the respective parameter is shown by the combinations of crosses in the legend.

As one would expect for myxomycetes, most species prefer moist habitats (moist-wet: 93 species, or 21% of the total, moist (211, or 48%) and fewer are found towards the drier end of the gradient (dry-moist: 69 species, 16%, and dry-arid: 16, 4%, compare Fig. 1b). About half of the species seem to occur most abundantly under moist (defined as a humid climate interrupted by dry periods) but not

continuously moist conditions. An estimated 5% of the better-known species seem to prefer arid regions. Prominent examples are *Protophysarum phloiogenum* (corticolous) and *Kelleromyxa fimicola* (coprophilous), both classified as centred in arid regions. Except for the latter, all of the 18 species preferring arid or arid-dry conditions are litter-inhabiting (10) or corticolous (8). Taxonomically, most of these species are members of the Physarales (11) or Echinosteliales (4).

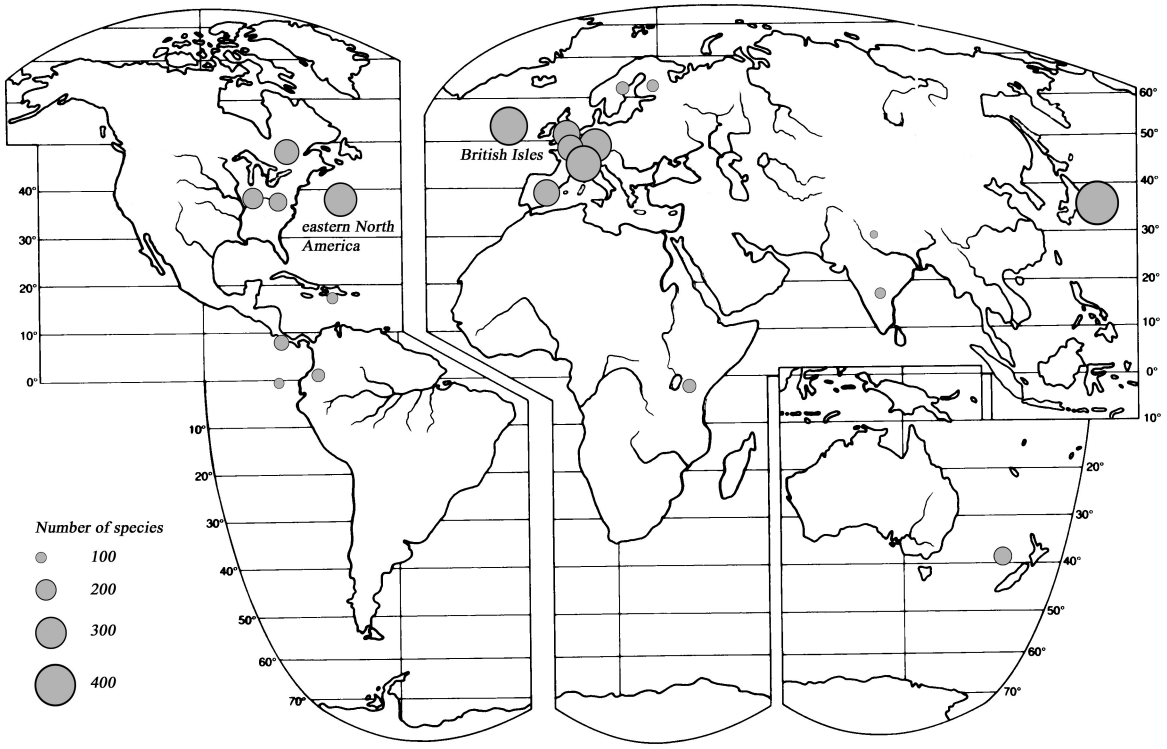

Fig. 2 World map showing the total number of species recorded for a number of well investigated, larger regions listed in Table 3.

Also the other end of the gradient (species found most often in moist to wet or wet habitats) is dominated by the Physarales (41 of 99, or 41%). However, only eight species display a clear preference for continuously wet conditions, and four of these belong to the genus *Ceratiomyxa*. Most of the moisture-enduring or -preferring species are wood-inhabiting (55 of 99, or 52%), and another 31 (31%) are litter-inhabiting.

Species richness in myxomycetes reaches a maximum in lowlands and declines towards mountainous regions. As to be expected, all of the 18 montane-alpine or alpine species are nivicolous, whereas most (15 of 17) of the species preferring montane regions or foothills are wood-inhabiting. Members of the genus *Cribraria* (8 species, all occurring on coniferous wood) account for this.

Regional checklists.—A comparison of the absolute richness in species for the well investigated regions of the world (Table 3, Fig. 2) verifies the distribution pattern obtained by the first approach: increasing species diversity from arctic to temperate regions, which decreases again in the Tropics. A high number of species, usually between 30 and 40%, are very rare in a region, and this number seems to increase with recording intensity. In comparison with the ca. 1000 subgeneric myxomycete taxa described world-wide, no region seems to house more than one half of this total number.

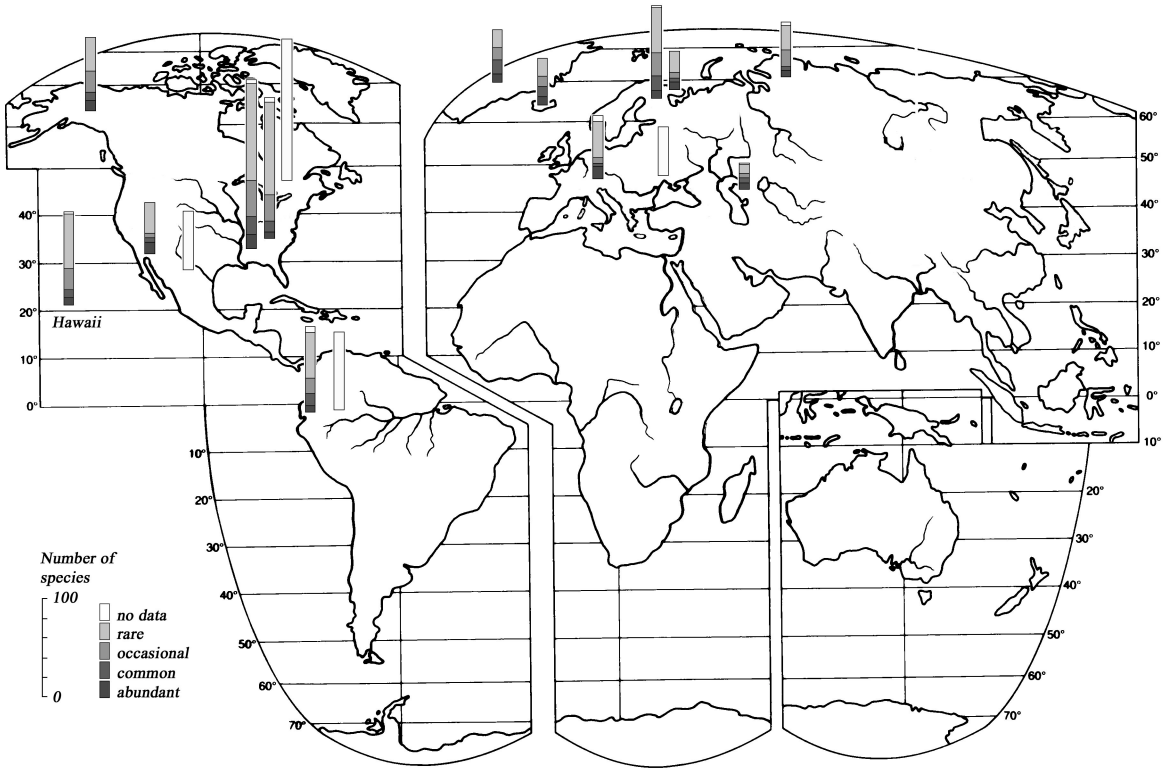

Fig. 3 World map, showing total species numbers and proportions of abundance classes for the local surveys listed in Table 4.

Local surveys.—The most exact figures provide surveys were abundance values or estimations are given for all recorded species. Consistently, only a few species are really abundant in a given region, and 30–60% are very rare (their records contributing less than 0.5% to the total number of records). This proportion seems to increase with the total number of records made. The absolute numbers of species recorded are remarkably constant for all surveys from one vegetation zone: 50–60 for arctic regions, 60–100 for the boreal zone, 30–60 for deserts (with a higher number for warmer deserts having succulent plants), 120–180 for the eastern temperate North America, and 80–100 for the Neotropics.

Table 3. Species richness in myxomycetes for the well-investigated regions of the world. Surveying intensity is indicated by the number of records and moist chamber cultures upon which the respective checklist is based. Species numbers in parentheses refer to the species regularly occurring in the region.

Region	Number of species *	records	cultures	Reference
boreal parts of Finland	116 (75)	>2000	>600	Hinitkka 1919, Härkönen 1977a, b, 1979a, b, 1981, 1989, Härkönen et al. 1999
boreal parts of Sweden	128 (86)	>1500	n.d.	Eliasson 1975, 1977, 1981, Eliasson & Lundqvist 1979, Eliasson & Strid 1976, Eliasson & Sunhede 1972, Fries 1899, 1906, 1910, 1912, Harling 1952, Santesson 1948, 1964, Schinner 1983
Germany	318 (151)	>20000	>1000	Schnittler et al. 1996
Netherlands	245 (149)	>20000	>1000	Nannenga-Bremekamp 1991
SE England	261 (91)	>2668	>1000	Mitchell 1999
United Kingdom	366	>100000	>4000	Ing 2000
Switzerland	340	>20000	n.d.	Ing, pers. comm..
Japan	418	>20000	n.d.	Yamamoto 1998
Canada, Ontario [a]	238 (192)	4646	>200	Schnittler, unpubl.
USA, West Virginia	179	>5000	>1500	Stephenson & Roody 1997
USA, Ohio	202	n.d.	>2000	Keller & Braun 1999
temperate North America [b]	318	>30000	>4000	Martin & Alexopoulos 1969, Stephenson & Roody 1997, Stephenson et al. 2000
Spain (with Balearic Isl.)	258	>10000	>1000	Lado 1994
Puerto Rico	106 (75)	>2000	>800	Stephenson, Schnittler, unpubl., Novozhilov et al. 2000
India, northeastern part (Himalayan foothills)	77	>1000	—	Stephenson et al. 1993
India, southern part around Madras	101	>1000	—	Stephenson et al. 1993
Ecuador: Galapagos Islands	96	>1000	no data	see chapter 9
Ecuador: mainland [c]	125	>2000	>1000	see chapter 9, Estrada-Torres, Lado, Schnittler, unpubl.
Costa Rica [d]	145	>1600	>1000	Alexopoulos & Saenz 1975, Schnittler, Stephenson, unpubl.
Tanzania	131 (49)	861	>200	Ukkola 1998
New Zealand [e]	175 (40)	>1500	650	Stephenson, pers. comm.

[a] Data combined from an one-year field study conducted in various parts of central and southern Ontario and the collection of the Royal Ontario Museum, Toronto.

[b] For temperate eastern North America, all states including and east of the line Wisconsin – Illinois – Kentucky – Tennessee – North Carolina were considered.

[c] Preliminary number, a new survey from the Amazonian region of the country added ca. 15 more species to the 111 hitherto known.

[d] Results of a checklist, compiled during more than 15 field trips.

[e] First results of an ongoing study, so far including field trips to all major regions of the country and a database of the available herbarium collections.

[*] Regularly occurring species are defined as recorded more than three times. For south-eastern England species known by more than 17 records are given as regularly occurring.

As for the other approaches, the pattern is that of an increasing species richness from the Arctic to southern temperate zones, which decreases again in the humid Tropics (Fig. 3). The most recent study, carried out in a lowland tropical forest of the Amazonian part of Ecuador, a habitat exceedingly rich in vascular plants, seems to yield clearly less than 100 species.

Within all 13 surveys were abundance classes are available, 332 species of myxomycetes (including 11 apparently undescribed taxa) were recorded. Of these, only 73 (22%) were abundant in at least one region, whereas 151 (45%) were rare throughout all study sites. Eight species were abundant at more than two sites: *Arcyria cinerea* (8 regions), *A. incarnata* (3), *Ceratiomyxa fruticulosa* (3), *Comatricha nigra* (4) *Echinostelium minutum* (8), *Lycogala epidendrum* (8), *Perichaena vermicularis* (4) and *Trichia varia* (3).

Table 5 shows the results of a comparison of these local species inventories. Already the first calculation, using only presence or absence of the species, shows desert areas as having the lowest average values for the coefficient of communities *cc* (indicating the most distinctive myxomycete assemblages). As to expect, all *cc*-values are smaller for calculations using abundance classes. With this method, average values for the assemblages from the Khibine mountains (the only survey including a number of nivicolous species) and the German survey (featuring a late-autumn aspect only) are also quite low. As with the first method, desert assemblages stand out as being very distinctive. Additionally, the two tropical study sites (Ecuador and Hawaii) seem to have a higher proportion of species that are rare or absent in other regions of the world.

Table 4. Species richness for local surveys with high recording intensity. Figures for abundant (A), common (C), occasional (O), rare (R) and doubtfully recorded (?) species are given. According to the entry in the column “Method” these were estimated (scale) or calculated (count). In the latter case, all observed fructifications were recorded. Surveying intensity is indicated by numbers of moist chamber experiments carried out (cultures) and records obtained from the field (fc) or in moist chambers (mc). If the respective area exceeds 50 km in diameter the number of collecting sites is given. Abbreviations refer to Table 5.

Region	Abbr.	Method	Number of species total: A-C-O-R (?)	cultures	records fc/mc	Reference
Iceland (tundra, northern boreal forest), 17 localities	Ic	scale	48: 9-10-11-18	n. d.	207/125	Götzsche 1984, 1990
Greenland (tundra, northern boreal forest), 35 loc.	Gr	scale	54: 9-14-13-18	n. d.	245/83	Götzsche 1989
Siberia, Taimyr Peninsula (tundra, northern boreal forest), 10 loc.	Tai	count	56: 7-4-17-25 (3)	270	60/331	chapter 3
Russia, northern Karelia, Khibine Mts. (montane boreal forest, tundra)	KM	scale	40: 8-4-6-22	123	>100/>20	chapter 6
Central and northern Alaska, Seward Peninsula (northern boreal forest to tundra), 3 loc.	Al	scale	75: 11-8-22-32	>300	422 in total	chapter 4
Russia, northern Karelia, Sredni Island (boreal forest)	Kar	scale	95: 8-15-24-46 (2)	82	660/113	chapter 5
Germany, Northern Ammergauer Alps (montane coniferous forest)	Ge	scale	65: 13-3-6-37 (6)	46	>350/>150	chapter 7
Kazakhstan, Mangyschlak Peninsula (winter-cold desert)	Kaz	count	27: 7-5-5-9 (1)	146	10/328	chapter 8
USA, Arizona, Sonora desert near Tucson (winter-mild desert, Chaparral)	Ari	scale	53: 12-5-4-32	n. d.	154 in total	Evenson 1962, Black-well & Gilbertson 1980
USA, Texas, Big Bend NP (winter-mild desert and arid grassland) [a]	—	count	>60	225	>100/>500	Schnittler unpubl.
Russia, Astrakhan-Volgograd (winter-cold desert and steppe), 20 loc. [b]	—	count	>50	475	>50/>1500	Novozhilov, Schnittler unpubl.
Canada, Ontario, Algonquin Prov. Park (deciduous forests, mixed hardwoods) [c]	Ont	count	121 + ca. 25	—	627/—	Schnittler unpubl.
USA, southwestern Virginia (deciduous to mixed forests)	Va	count	144: 7-11-27-95 (4)	1139	2190/1494	Stephenson 1988, 1989
USA, Great Smoky Mountains NP (meridional deciduous to montane coniferous forests)	GSM	scale	177:15-18-37-99 (4)	>150	>950/>250	Stephenson et al. 2000, 2001 (unpubl.)
Ecuador, western Andes, Macquipucuna Reserve (tropical moist to lower montane rain forest)	Ec	count	82: 7-12-17-46 (6)	475	590/443	chapter 9
Ecuador, Amazonian basin (tropical moist forest)	—	count	>80	215	>500/>450	Estrada-Torres, Lado, Schnittler unpubl.
Hawaii (tropical forest)	Ha	scale	98: 8-8-22-56 (4)	n. d.	n. d.	Eliasson 1991

[a, b] First results of ongoing studies, number of taxa estimated from both field records and moist chamber experiments.
[c] Within one year of repeated visits, 121 species were recorded. It can be estimated from moist chamber studies in other parts of Ontario, that this component will add at least another 25 species to the total number.

Table 5. Coefficients of community computed from presence-absence values (upper part) and weighted abundance estimations (lower part) for 13 local surveys of myxomycetes (compare Table 4 for abbreviations and descriptions of study sites). The last column lists the number of species for the respective survey, whereas the last row indicates the mean coefficient of community for a study site.

	Ic	Gr	Tai	KM	Al	Kar	Ge	Kaz	Ari	Va	GSM	Ec	Ha	species
Ic	****	0.55	0.46	0.34	0.42	0.40	0.32	0.08	0.21	0.26	0.21	0.17	0.21	48
Gr		****	0.51	0.34	0.51	0.45	0.40	0.17	0.26	0.27	0.27	0.25	0.31	54
Tai			****	0.42	0.49	0.51	0.41	0.21	0.19	0.34	0.31	0.32	0.35	56
KM				****	0.38	0.42	0.29	0.12	0.13	0.30	0.23	0.18	0.22	40
Al					****	0.51	0.41	0.16	0.28	0.41	0.38	0.36	0.31	75
Kar						****	0.52	0.15	0.18	0.57	0.46	0.29	0.39	92
GAP							****	0.15	0.19	0.40	0.41	0.34	0.40	65
Kaz								****	0.33	0.13	0.15	0.15	0.18	28
Ari									****	0.22	0.20	0.21	0.26	39
Va										****	0.62	0.40	0.47	142
GSM											****	0.43	0.47	176
Ec												****	0.50	82
Ha													****	82
mean	0.30	0.36	0.38	0.28	0.38	0.41	0.35	0.16	0.22	0.36	0.34	0.30	0.34	

	Ic	Gr	Tai	KM	Al	Kar	Ge	Kaz	Ari	Va	GSM	Ec	Ha	species
Ic	****	0.47	0.37	0.24	0.33	0.32	0.14	0.05	0.18	0.21	0.15	0.12	0.14	48
Gr		****	0.38	0.23	0.38	0.36	0.18	0.11	0.18	0.20	0.21	0.16	0.23	54
Tai			****	0.33	0.36	0.38	0.18	0.13	0.13	0.27	0.23	0.24	0.27	56
KM				****	0.30	0.31	0.11	0.06	0.07	0.23	0.18	0.14	0.15	40
Al					****	0.41	0.18	0.10	0.20	0.33	0.31	0.23	0.24	75
Kar						****	0.27	0.11	0.13	0.47	0.36	0.19	0.30	92
GAP							****	0.04	0.07	0.18	0.21	0.13	0.18	65
Kaz								****	0.27	0.09	0.10	0.10	0.13	28
Ari									****	0.17	0.14	0.14	0.17	39
Va										****	0.52	0.31	0.41	142
GSM											****	0.31	0.36	176
Ec												****	0.38	82
Ha													****	82
mean	0.23	0.26	0.26	0.19	0.28	0.31	0.15	0.11	0.15	0.28	0.26	0.20	0.25	

Discussion

Distribution data base.—Based on personal collecting experience and the revision of several thousands of herbarium specimens, an assessment of the zonal distribution of myxomycete species provides the "softest" but most complete data set among all three approaches. It is obvious to every collector, that only a few myxomycete species occur equally commonly in all vegetation zones. Prominent examples for such cosmopolitan species are *Arcyria cinerea*, *Ceratiomyxa fruticulosa* and *Lycogala epidendrum*. However, strong evidence exists that such species represent a complex of closely related microspecies. In temperate zones *Arcyria cinerea* occurs on wood with solitary, short sporocarps. In tropical regions, var. *digitata* Schwein., a form with much longer sporocarps and several sporothecae sharing a common stalk seems to be most common. A minute, still undescribed form with very long stalks in relation to sporotheca size and almost purely white sporothecae is common on aerial litter in the Tropics (compare chapters 9, 11). It intergrades to *A. afroalpina*, described from montane tropical Africa. Basic plant litter, e.g. banana leaves, seem to be the habitat of another undescribed form with yellow sporocarps (Stephenson, Schnittler, unpubl. results). Furthermore, surveys in Costa Rica and Ecuador yielded five times a form unknown to science that displays the typical habit of *A. cinerea* but possesses an unbranched capillitium with spiral ornamentation (Lado, Schnittler unpubl. results). As indicated by the long list of synonymous names and described varieties, *Ceratiomyxa fruticulosa* is also highly variable, and again the existence of microspecies is very likely. The var. *poroides* (Alb. & Schwein.) G. Lister seems to be limited to temperate zones, whereas the var. *arbuscula* (Berk. & Broome) Nann.-Bremek. can be found most often in the Tropics. A similar complex of microspecies is found in *Lycogala epidendrum* and the closely related *L. exiguum*. Recently, with *L. terrestre* Fries. and *L. confusum* Nann.-Bremek. ex Ing, two of these infraspecific forms were recognized at species level (Ing 2000). It is likely that future studies including molecular methods will result in a better understanding of the taxonomy of these species complexes. For the present study it can be stated, that the exclusion of very rare species (known from less than 20 records world-wide) and the lumping of microspecies within a number of common species will enlarge rather than narrow down the zonal distribution ranges as assessed for the database.

Regional checklists.—The study by Mitchell (1999) can serve as a good example for a regional checklist. This investigation covers a very long time period, and is one of the most intense in relation to the size and vegetational heterogeneity of the region covering ca. 13 000 km^2 in Sussex, southeast England. But, even after more than 35 years of investigation, 170 of the 261 reported species are relatively rare (known from less than 17 records). Similarly, all other checklists have a relatively high

proportion (one half to two thirds) known from less than four records. This proportion of very rare species seems to be remarkably constant.

Arctic regions seem to be poorest in species. This may be due to the low numbers of records from which the figures were derived. But, as demonstrated in chapter 4, also all arctic regions together (the number of about 2000 records is much better in comparison with those used to compile checklists of temperate regions) have only 150 species, significantly less than in temperate regions. Three countries dominated by temperate deciduous forests as naturally occurring vegetation are very well studied: the United Kingdom (366 species), Germany with 318 species (151 of these are more common), and the Netherlands with 245 (149 commoner species). The Netherlands not only lack myxomycetes that are typical for montane coniferous woodlands (compare chapter 7), but also nivicolous forms that have been recorded from Germany (Neubert et al. 1995, Schnittler 1998, Krieglsteiner 1993) and Scotland (Ing 1999). Compared to Europe, the recording intensity in the eastern temperate regions of North America is lower, but species numbers are comparable or even higher. A study in the province of Ontario (Schnittler unpubl.), combining ca. 3000 mainly older herbarium collections with 1500 recent field observations, resulted in a high fraction of regularly occurring species in comparison to the total number. This indicates that future records of new species are much more likely for eastern North America than for the European regions listed in Table 3. In agreement with the results from the first approach (zonal distribution preferences of myxomycetes) is the low species diversity of Tropical countries. This holds also true for countries which are studied more thoroughly, e.g., Ecuador and Puerto Rico.

Local surveys.—This approach was based on a limited number of studies only, but should give the most exact numbers. Nevertheless, the pattern of increasing diversity from arctic to southern temperate zones but decreasing again in tropical forests was confirmed a third time. Eastern North America yielded the highest species numbers of all surveys, whereas numbers are comparable for the tropical and temperate European study sites. The smallest species number is represented by the survey from western Kazakhstan (winter-cold desert).

Using this approach, abundance values were estimated or calculated for all species. The resulting distribution is similar to that found in other groups of organisms - a few very abundant species and a larger number of rare ones. As presented in chapter 9, the respective rank-abundance-plots can be described by a lognormal model. This is typical for assemblages of organisms with population sizes limited by a variety of factors. The low number of eight species which were equally common in three or more of the surveys indicate, that distribution ranges of myxomycetes would be narrower than presented herein when a biological species concept would be used. As discussed above, most of these species are highly variable, perhaps combining several biological species under one name. All but one prefer decaying wood as a substratum. Probably, microclimatic conditions are fairly stable within larger logs, which limits range restrictions set by macroclimate.

For the comparison of such local surveys, calculations using abundance classes reveal more differences between surveys than those based on presence or absence only. The coefficient of community calculations show desert and tropical myxomycete assemblages to be most distinctive. For the first habitat the reason is probably the low number of species and the high abundance of species that are absent or rare in other vegetation zones. As already mentioned, *Protophysarum phloiogenum* can serve as an example of a species limited to arid zones. It is known from California (Whitney, in Castillo et al. 1998), Colorado (Blackwell & Alexopoulos 1975), Arizona (Blackwell & Gilbertson 1984), the Gobi desert (Novozhilov & Golubeva 1986), western Kazakhstan (chapter 8), the lower Volga basin near Astrachan (Schnittler unpubl.), Tunesia (H. Neubert, pers. comm.), and southern Spain (Castillo et al. 1998). The habitat of the minute species is the bark of living desert shrubs. Lado (1998) coined the term "succulenticolous" for a number of specialized desert myxomycetes inhabiting decaying succulents, with yeasts as the most likely food organisms. Tropical myxomycete assemblages have a small number of species limited to the tropics (e.g. *Physarella oblonga*), but numerous species that are more common in the tropics than anywhere else, e.g. members of the genus *Physarum*. On the other hand, many common species of temperate regions, e.g., members of the genus *Trichia,* are absent in lowland tropical forests.

Two tendencies of myxomycete distribution found herein are surprising: most species seem to prefer temperate zones (i.e. moderate temperatures) and regions with moderate to low rainfalls (where moisture conditions fluctuate more than in very wet areas). These tendencies were confirmed by a study from India (Venkataramani & Kalyanasundaram 1986) that includes over 600 collections, mainly from the southern part of the country. Here, specimen data from localities scattered over a wide range of altitude and rainfall were correlated with climate parameters taken from the month of collection. From 658 collections evaluated, 2 (both Trichales), were made in areas with a mean monthly temperature below 10°C, 344 in areas between 10 and 20°C, 270 in areas between 20 and 30°C, and only 44 in areas with temperatures above 30°C. A comparison with total monthly rainfall showed that most of 638 collections were made in drier areas (263: >250 mm monthly rainfall, 228: 250–500 mm, 147: >500 mm). Undoubtedly, myxomycete fructifications weather faster under wet conditions, since they will be soon washed off the substratum or colonized by fungi. This decreases the potential number of colonies a collector will find within a given period of time. However, the differences in myxomycete abundance registered for gradients in rainfall in Neotropical countries (chapters 9, 10) are too large to be explained by this factor alone.

Why do most myxomycetes seem to prefer moderate temperatures for development? One explanation could be competition with fungi, especially parasitic ones, which will grow faster under high temperatures. Therefore, speciation should be more successful in temperate regions, especially for groups inhabiting moist substrata such as wood. The question why an excess of rainfall does not

favour myxomycetes is discussed in chapters 9 and 15. Only under fluctuating moisture conditions the myxomycete fructification can dry out and become effective in dispersing spores.

With these considerations, the lower species diversity of myxomycetes in the Tropics can be explained. The first negative factor is the continuous high moisture in wet tropical forests. Seemingly, species with protoplasmodia and minute fruit bodies have difficulties to survive in moist tropical climates. A good indicator for this the rarity of corticolous myxomycetes in most tropical forests. However, as indicated by their higher abundance in tropical dry forests, future investigations of the canopy region in tropical wet forests, where moisture conditions underlie more fluctuations, may reveal a higher diversity of this ecological group.

A second factor is the high temperature, which excludes numerous species preferring lower temperatures from the hot Tropics. Prominent examples are myxomycetes fruiting usually in autumn in temperate zones, e.g., species of *Diderma* or *Trichia*, *Hemitrichia clavata*, or *Tubifera ferruginosa*. Although all these examples regard species with robust plasmodia, they do not occur in tropical lowlands and can be found in the Tropics only in higher mountains with a cool climate. On the other hand, a small number of species seems to be confined to the Tropics due to a higher temperature optimum and occur only as rarities in southern temperate zones. As mentioned, examples are species of *Physarum*, *Physarella oblonga*, *Tubifera bombarda*, or the protostelid *Ceratiomyxa morchella*.

Another possible reason for the lower number of species recorded from tropical regions could be the absence of specialized ecological groups of myxomycetes. Rocks covered by mosses and algae, constituting the main microhabitat for a number of species (chapter 5, Ing 1983, Schnittler 1999) were found to be devoid of myxomycetes in tropical regions. As a second ecological group, the nivicolous myxomycetes are absent. Due to the absence of seasons in tropical mountains, the typical grow situation for these myxomycetes (quickly melting snow banks) does rarely occur even at elevations high enough to allow the accumulation of snow. Additionally, conifers (except for members of the Podocarpaceae) are absent or rare in the Tropics. A number of members of the genus *Cribaria* is specialized on coniferous wood of montane forests.

The pattern of distribution outlined here for myxomycetes does not necessarily apply to other groups of myxomycete-like organisms. For the dictyostelids, a group where a standard isolation procedure from soil is available (thus guaranteeing an equal intensity of recording), a study by Cavender (1973) indicated a pattern of steadily increasing diversity from temperate zones to the Tropics for the 29 species he investigated. These organisms seem to reach highest species numbers in tropical forests, as indicated by a diversity centre in Guatemala (Swanson et al. 1999). As an adaptation to the continuous high moisture in their microhabitats (for most species the spoil-litter interface), dictyostelids have very long stalks in relation to fructification volume (chapter 15).

In summary, the still limited number of surveys and checklists that have a sufficient degree of completeness allow the following main conclusions: (i) Except for a number of very variable complex species, most myxomycete species seem to be really common in only one vegetation zone, (ii) most species seem to prefer temperate zones, and (iii) species diversity increases from arctic to temperate regions and decreases again in the Tropics.

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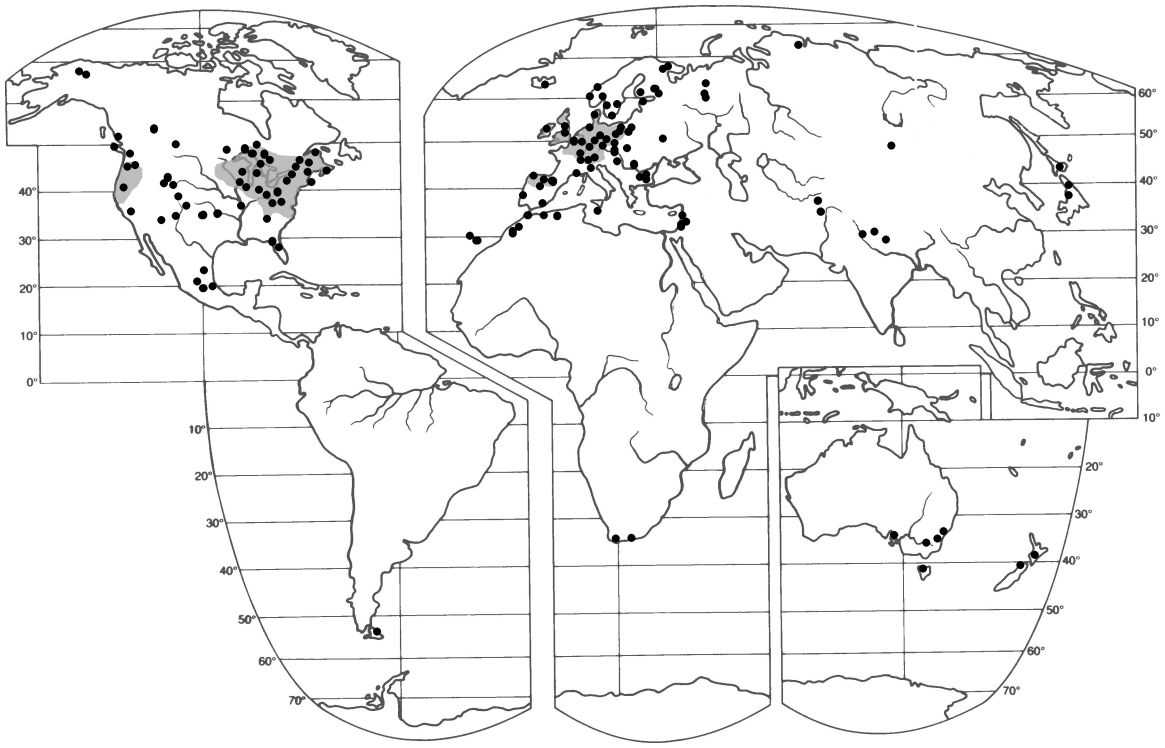
Case study I: *Leocarpus fragilis* (Dicks.) Rostaf.

With its calcareous, orange to red sporocarps resembling miniature grapes, this is one of the most distinctive myxomycetes, frequently recorded also by non-specialists of the group.

The large and robust, yellow phaneroplasmodium inhabits ground litter with an acidic pH (most often between 4 and 6). Colonies can consist of several thousand sporocarps. In dry coniferous forests, mass fructifications can develop; in 1993 one dry pine plantation in eastern Germany (Brandenburg, Eggsdorf near Berlin) had an estimated density of 200–400 colonies per hectare. With 12–14 µm, the spores are relatively large for a myxomycete, which should decrease the probability of long-distance dispersal. Local biotypes seem to exist. A form with spores in clusters of two has been described as *L. bisporus* Nann.-Bremek. & D.W. Mitch. (Proc. Kon. Net. Akad. Wet. C92: 512. 1989). Specimens from South Africa have almost globose sporocarps, whereas the typical form is egg-shaped (Schnittler, pers. obs., specimens from Kew Botanical Garden, London).

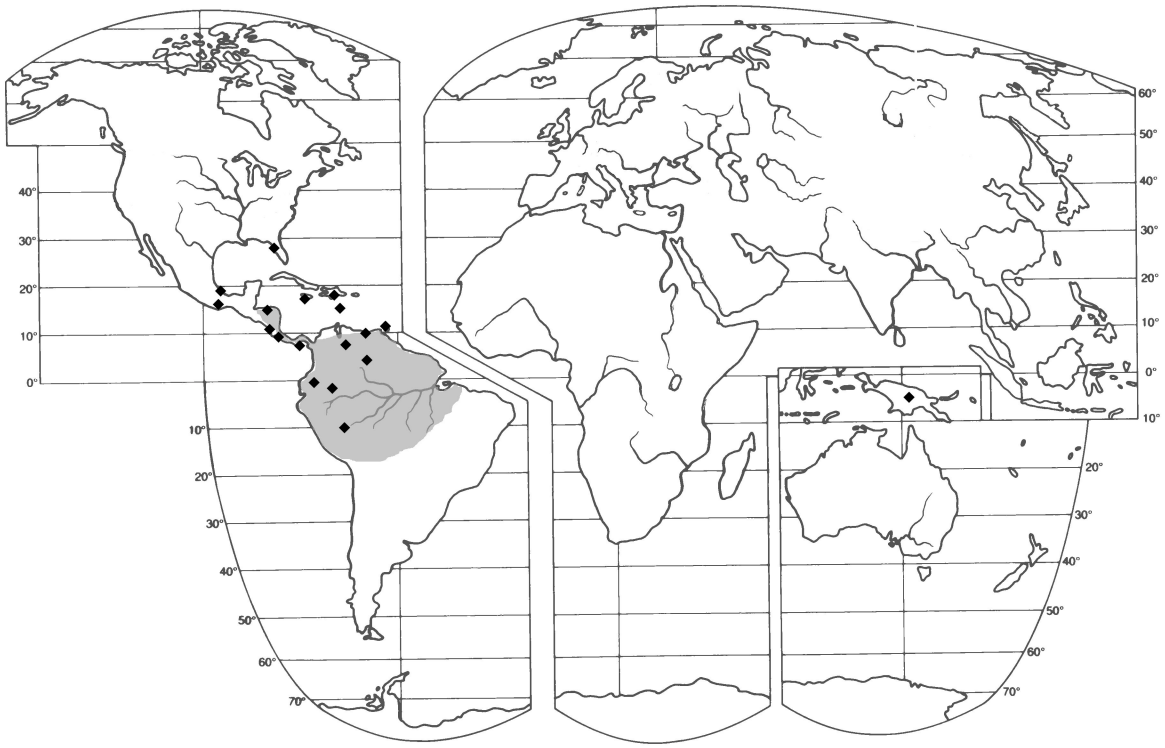


The preliminary distribution map was drawn from ca. 950 records. For regions with many records only a representative selection of specimens was data-based (grey areas on the map). As to expect for organisms having a limited number of students, beside the “true” range of a species the distribution map displays also those regions of the world where most taxonomists work. However, the two factors seem to coincide in this case. *Leocarpus fragilis* occurs but rarely in arctic regions (compare chapter 4). As a litter-inhabiting species, *L. fragilis* spreads beyond the timberline and was found in arctic tundra. Thus, its northern distribution may be limited more by climate than microhabitat availability. It is very common in the temperate zone, but seems to be less common in southern temperate zones, e.g. in the Mediterranean region or in the south-eastern United States. The species avoids highly arid regions (records from Israel and Spain come from the less arid parts of these countries) and the humid Tropics. However, outposts in montane regions occur further southward, e.g., in the Canary islands or the African Atlas. Also in fairly well studied tropical regions, e.g. Central America, Ecuador, Tanzania, or Taiwan, *L. fragilis* was not yet found. As shown by a single record from southern Argentina (Tierra del Fuego), and a few from South Africa and southern Australia, it reappears in temperate regions of the southern hemisphere. In contrast to the statement in Martin & Alexopoulos (1969: 245), *L. fragilis* seems not to be an ubiquist but has a clear preference for temperate zones.

Case study II: *Ceratiomyxa morchella* A.L. Welden

This member of the Protosteliales was unknown to science until 1954. The fructifications are very evanescent and start to decay on the day following development. However, the habit of *C. morchella* is conspicuous, since large colonies of stalked, 2.5–4 mm high fructifications cover often several square metres of large, decaying logs. The stalk is translucent colourless and crowned by a pure white, globose head that resembles a miniature morel. The ovoid spores measuring 9–11 x 6–8 µm are formed at the tip of 2–10 µm long stalks that cover the white part of the fructification like a fur.

According to studies of the author in Costa Rica and Ecuador, *C. morchella* is strongly limited to decaying wood with a very acidic pH, a rather rare habitat in tropical forests. Without exception, the habitat of the more than 100 studied records was decorticated, moderately to strongly decayed wood of thick logs with pH values between 3.0 and 4.5. This precludes any confusion with *C. sphaerosperma* Boedijn, the second tropical species of the genus that inhabits exclusively substrata



with a pH above 6.5 (up to 8), most often decaying fruit shells. Colonies with more than 10 000 fructifications are not rare, typically covering the lower side of big, fallen tree trunks which were kept above ground by their root disk or other logs. The spores are colourless and thin-walled. Lacking UV-absorbing pigments, they may not be able to survive a longer transportation in higher atmospheric layers.

The preliminary map for *Ceratiomyxa morchella* shows all localities that came to the knowledge of the author. The northernmost records are from subtropical Florida and tropical Mexico. The species is fairly common in the Caribbean region, being known from Puerto Rico, Jamaica, St. Vincent and Trinidad. Records for Costa Rica come from all parts of the country except the dry Southwest and the highest mountains. It was found twice during the study in western Ecuador (chapter 9). The real distribution centre of the species seems to be the Amazonian basin. In a study in the Yasuni National Park (eastern Ecuador) it was one of the most common species (Schnittler, unpubl. results). From these observations, a putative closed range of the species was derived (grey area). Due to the paucity of records, currently it can not be decided if the species also occurs in the Palaeotropics. It is still unknown from tropical Africa, and only a single record from eastern Asia (New Guinea) is mentioned in the literature.

Theses

Only 43% of the ca. 1000 described myxomycete taxa are better known, i.e. recorded from more than 20 localities. As derived from a taxonomic database of all taxa hitherto described, from 1012 subgeneric taxa (Oct. 2000) 305 (31%) are known only from the type locality, and further 258 (26%) are very rare (observed from less than 20 localities world-wide). The high proportion of "singleton species" indicates the insufficient level of knowledge and raises doubts to which extent the current morphological species concept is useful for the group.

Due to a mixed mode of reproduction, including apomixis and occasional sexual reproduction, a purely morphological species concept does not appropriately reflect the biology of myxomycetes. An analysis of the limited data on the reproductive system of ca. 100 species shows, that most of them include homothallic (apomictic) as well as heterothallic (sexual) strains. A comparison with apomictic genera of vascular plants (such as *Rubus* or *Hieracium*) demonstrates possible taxonomic consequences. As inferred from collecting experience, the existence of an indeterminate number of local clones is very likely for most myxomycete species.

Recommendations are given for the description of new species. Under the morphological species concept currently used, the taxon in question should be known by several specimens from more than one locality. The whole body of scientific literature should be checked for related taxa, and the newly described taxon should differ from all others in more than only one significant character. Intraspecific variability as well as its microhabitat should be described. These requirements will minimize the risk of describing local clones represented by single specimens or aberrations during sporocarp development as new species.

Quantitative local species inventories produce abundance data and allow to estimate the total number of species to be expected. In contrast to other surveys hitherto published, all observed myxomycete fructifications were counted within studies including both field observations and substratum cultures. This allows the compilation of rank-abundance plots.

Estimations show these surveys to be complete to 70–90%. From rank-abundance plots, as well as from species-sample curves, the total number of species to be expected for a survey was estimated. For the latter, a new method that includes a saturation model is proposed. With the achieved degree of completeness, these surveys can function as "calibration tools" to judge pure species lists for the inclusion into biodiversity studies.

Arctic regions have a relatively stable but a species-poor myxomycete assemblage, with species' distributions limited more by microhabitat availability than by macroclimatic conditions. About 35 species occur regularly in the Arctic, and a considerable number of wood-inhabiting myxomycetes occur as far north as woody debris is present. However, except for two species, all seem to be commoner in boreal and/or temperate zones.

In boreal regions, species numbers are three times higher than in Arctic regions. Besides the significantly higher number of wood-inhabiting species, species of algae-covered rocks and nivicolous myxomycetes were observed in boreal zones.

Temperate zones have a diverse range of specialized myxomycete assemblages. A study of montane myxomycetes provides evidence for a group of species specialized on feeding upon algae.

Southern temperate zones with a climate characterized by a summer rainfall peak seem to provide the best conditions for corticolous myxomycetes. A preliminary checklist from the Great Smoky Mountains records 168 species, with 47 (28%) inhabiting bark.

Compared with other vegetation zones, deserts have the most distinctive myxomycete assemblages. A winter-cold desert in Kazakhstan was found to support 28 species of myxomycetes, with 18 of them more common. A few species were exceedingly abundant.

Tropical forests are dominated by litter-inhabiting, robust forms of myxomycetes. Typical features of tropical myxomycete assemblages are: that species with phaneroplasmodia prevail, most species preferring various types of non-woody plant litter as a substratum, and the proportion of stalked species is higher in comparison to temperate zones. Corticolous species are almost completely absent in wet tropical forests.

The diversity of tropical myxomycetes decreases with increasing elevation and annual rainfall. Investigations in Costa Rica, Ecuador and Puerto Rico show that both abundance and species richness decrease significantly along a gradient from tropical dry or moist to tropical wet forest.

Continuously high moisture does not favour the development of myxomycete fructifications. As derived from a comparison between Ecuador and eastern North America, the same species grow longer stalks in the Tropics, which increases the proportion of resources which could otherwise be used for spore development. High moisture hinders the drying of spores which enables them to become airborne, and promotes the development of myxomyceticolous fungi, which in turn reduces the number of viable spores.

In tropical forests, aerial microhabitats display a higher myxomycete diversity than those at the forest floor. Aerial substrata such as decaying leaves, stems, fruits and flower remnants have a higher

probability of drying out, thus providing the spores with a better chance to become airborne for long-distance dispersal.

In wet tropical forests myxomycetes occur on foliicolous liverworts that inhabit living leaves. This newly discovered microhabitat supports small populations of myxamoebae, which can develop fructifications in culture. At least three species occur regularly and with a much higher frequency than on litter from the forest floor.

Inflorescences of giant Zingiberales forbs harbour a specialized community of myxobacteria and myxomycetes. By means of sporocarp counts and multivariate statistics, this community was characterized ecologically. Three species of myxobacteria and six myxomycetes have a clear preference for this microhabitat, formed by decaying corolla parts which possess a basic pH and which remain in the still living inflorescence bracts. Evidence for birds functioning as dispersal factors of these myxomycetes is presented.

Interspecific competition seems to be rare, but may occur in myxomycetes. Based upon substratum cultures, sporocarp numbers were counted or estimated for the community from a Kazakh desert. These counts were used to compute niche breadths and niche overlap for the commoner species. Evidence of competition was found among species with large phaneroplasmodia.

Desert myxomycetes display two life strategies: fast developers that are able to react rapidly to singular rainfalls, and slow developers which utilize rare wet periods. Species showing the first strategy tend to develop rapidly, have small, usually stalked, sporocarps with a fugacious peridium and possess protoplasmodia or minute aphanoplasmodia. The alternative strategy is displayed by species with a phaneroplasmodium which develop more slowly into larger, usually sessile, fructifications with often well-developed, persistent peridia.

Myxomycetes are best adapted to fluctuating moisture in the environment. Dry conditions facilitate dispersal. Together with durable dormant stages, this enables myxomycetes to respond rapidly to temporally and spatially changing microhabitats. As a general pattern for all surveys, myxomycetes need very high moisture for their amoebal stages, high moisture for the plasmodial phase and dry conditions to ensure effective spore dispersal by fructifications. This explains the low abundance of myxomycete fructifications in tropical wet forests versus the high abundance in arid regions with fluctuating rainfall.

Spore size stays within narrow limits, caused by the need to carry enough resources on one hand and allow long-distance dispersal on the other. Two thirds of all species have spores between 7 and

12 µm diameter. Model calculations show, that this size is near the upper limit to allow flotation in air for a longer time.

Long-distance dispersal in myxomycetes should be a rather rare event. The terminal fall velocity for spores of the range given above should be between 130 and 380 metres per hour, which is not sufficient to overcome long distances without additional thermal air currents. The rare occurrence of long-distance should allow an undisturbed formation of local clones (which are best adapted to the local environment) but still provide occasional opportunities to invade distant regions during periods of suitable weather conditions.

The stalked fructification is typical for myxomycetes, and is the major evolutionary advantage compared with other groups of micro-organisms. Almost two thirds of all species with solitary fructifications develop a stalk. Its main function is to elevate the sporotheca above the substratum surface, to allow the spores to dry out and become airborne. Perhaps as a case of parallel evolution, also Myxobacteriales, Protosteliales, Dictyosteliales and Acrasiales "invented" this kind of fructification.

A resource allocation models shows that stalked fructifications face a size limit, which is the reason that large plasmodia usually divert their resources into many small sporocarps. As shown by a database of the better-known myxomycete species, stalk length increases with sporotheca volume. The limit is reached with a stalk length of about 1 mm and a volume between 0.1 and 0.5 mm^3. For larger volumes, stalk length decreases again. A resource allocation model was developed to estimate the proportion of resources allocated for stalk development for various sporocarp volumes and stalk lengths. It explains the size relations observed for myxomycetes as well as the way that large phaneroplasmodia divert their resources.

Distribution patterns of myxomycetes can be explained by a combination of both microhabitat and macroclimate requirements. This is shown by a first map for the highly disjunct range of *Barbeyella minutissima*, a minute species following the distribution of montane spruce-fir forests on Earth.

Most myxomycete species are not cosmopolitan, especially when abundance values are regarded. Three approaches were used to reveal patterns in myxomycete diversity: the zonal distribution of myxomycetes as assessed from collecting experience, published checklists, and local surveys. Most of the species are much more common in one particular vegetation zone than in all others.

Myxomycete diversity on Earth increases from the Arctic to the southern temperate zone, but decreases again in the humid Tropics. All three approaches indicate that eastern North America, and perhaps eastern Asia, are the global "hot spots" for myxomycetes. As such, patterns of species diversity differ from those known for vascular plants.

Acknowledgements

Major parts of this work were supported by grants from several funding agencies. Most of the taxonomic knowledge in myxomycetes I acquired during a stay at the Royal Ontario Museum, Toronto in 1996. It became possible by a scholarship from the German Academic Exchange Service (DAAD) and with the help of Prof. Dr. T. Dickinson, head of the Botany Department. The Kazakhstan journey was funded by a travel grant (40095/705.6.168) from the Stifterverband für die Deutsche Wissenschaft. Field work in western Ecuador, Costa Rica and Puerto Rico was accomplished by a grant (DEB-9705464) from the U. S. National Science Foundation.

This work would have been impossible without a close co-operation with many friends and colleagues. I am most grateful to Prof. Dr. S.L. Stephenson, Fairmont State College, West Virginia, for the unique opportunity to work two years on the diversity of Neotropical myxomycetes. His outstanding organizational skills smoothened the way to many field trips, and he taught me much of the art to write scientific publications. I am also indebted to a number of students working with us on myxomycete projects, namely M. Overking, A.R. Rollins, D.R. Black, A. Kerns and K. Kolozy, and R. Darrah as our research associate. During field work in arctic and boreal regions I enjoyed the gift of my friend Dr. Y.K. Novozhilov, Komarov Botanical Institute, St. Petersburg, Russia, to organize transportation or accommodation in the middle of nowhere, and to maintain dry specimens and an optimistic attitude even under hostile conditions. He also did most of the SEM-work shown herein. For organization of and interesting discussions during the survey in Kazakhstan I am indebted to Dr. I. Safronova from the same institution. For logistical help I wish to acknowledge Maria M. Chavarria Diaz from the Area Concervación de Guanacaste, Costa Rica, and M. Dilger from the Maquipucuna Reserve, Ecuador. Very enjoyable was the joint field work with Dr. A. Estrada-Torrez, Univ. Autonomia de Tlaxcala, Mexico, and Dr. C. Lado, Real Jardín Botánico, Madrid, Spain. Another incentive for this work was given by countless taxonomic hints and revisions of specimens, fruitful discussions and a good bit of British humor from D.W. Mitchell, Sussex, U.K. During my stay at Fairmont, I received a lot of help with the small everyday problems to organize life in a “new” country from my friends and neighbours C. & J. Murdock.

I am also grateful to Prof. Dr. F. Hellwig, Friedrich-Schiller-University, Jena, Germany, for supervising all efforts to have this work approved by the Faculty of Biological and Pharmaceutical Sciences. I am grateful to Dr. U. Bohn and numerous colleagues from the Federal Agency for Nature Conservation, Bonn, for their understanding of the special needs of my research work. Finally, I want to thank my parents, M. & Ch. Schnittler, for their patience with all problems of the numerous journeys and stays abroad that greatly helped to compile this work.

Jena, January 2001

Zusammenfassung (Thesen in deutscher Sprache)

Nur 43% der ca. 1000 beschriebenen Taxa von Myxomycetes sind einigermaßen bekannt, d.h. von mehr als 20 Orten der Welt nachgewiesen. Die Auswertung einer entsprechenden Datenbank ergibt, daß von 1012 beschriebenen Taxa unterhalb des Gattungsniveaus (Stand Oktober 2000) 305 (31%) nur vom *locus classicus* bekannt sind, weitere 258 (26%) wurden weltweit an weniger als 20 Stellen gefunden. Der hohe Anteil der nur vom Typusfundort bekannten Taxa dokumentiert den geringen Kenntnisstand über die Gruppe und wirft Zweifel auf, inwieweit das gegenwärtige morphologische Artkonzept für Myxomyceten anwendbar ist.

Der bei Myxomyceten vorherrschende Vermehrungsmodus ist eine Mischung aus apomiktischer und gelegentlicher sexueller Fortpflanzung. Ein rein morphologisches Artkonzept ist nicht ausreichend, dies adäquat zu beschreiben. Eine Analyse der vorhandenen Daten zum reproduktiven System bei etwa 100 Arten zeigt, daß die meisten sowohl homothallische (apomiktische) als auch heterothallische (sexuelle) Linien besitzen. Ein Vergleich mit weit besser untersuchten apomiktischen Gattungen der Blütenpflanzen zeigt mögliche taxonomische Konsequenzen. Aus der Erfahrung mit Herbarmaterial von Myxomyceten aus verschiedenen Regionen der Erde kann geschlossen werden, daß für die meisten Arten die Existenz vieler verschiedener lokaler Klone wahrscheinlich ist.

Empfehlungen für die Beschreibung neuer Arten. Im Rahmen des gegenwärtig benutzten Artkonzepts sollte eine neue Art nur beschrieben werden, wenn sie von mehrfach von verschiedenen Orten belegt ist. Die vorhandene Literatur ist weltweit auf ähnliche Arten zu überprüfen, und die neue Art sollte sich in mehr als nur einem wesentlichen Merkmal von bereits beschriebenen unterscheiden. Ihre innerartliche Variabilität und ihre Habitatansprüche sollten so genau wie möglich erfaßt werden. Dies minimiert das Risiko, nur von einer einzigen Aufsammlung bekannte lokale Klone oder in ihrer Entwicklung gestörte Fruchtkörper als neue Arten zu beschreiben.

Mit quantitativ durchgeführten lokalen Erhebungen wurden Abundanzen für einzelne Arten ermittelt. Dies erlaubt eine Abschätzung der Zahl der insgesamt in einem Gebiet zu erwartenden Arten. Im Unterschied zu bisherigen Untersuchungen wurden alle im Gelände oder in Substratkulturen aufgetretenen Fruktifikationen erfaßt. Das ermöglicht die Erstellung entsprechender Arten-Abundanz-Kurven.

Diese lokalen Arteninventare sind zu 70–90% komplett. Das zeigen Schätzungen aus Arten-Abundanz-Kurven und Arten-Proben-Kurven. Für letztere wird eine neue Methode auf der Basis eines Sättigungsmodells vorgeschlagen. Diese quantitativen Arteninventare ermöglichen die Abschätzung des

Vollständigkeitsgrades publizierter Artenlisten, um diese in Untersuchungen zur Biodiversität der Myxomyceten einzubeziehen.

Arktische Gebiete beherbergen eine relativ stabile aber artenarme Gesellschaft von Myxomyceten. Verbreitungsgrenzen scheinen mehr durch die Verfügbarkeit entsprechender Mikrohabitate durch das Makroklima limitiert zu sein. Nur etwa 35 Arten werden regelmäßig in arktischen Gebieten gefunden. Eine Reihe totholzbewohnender Arten wandert so weit nach Norden, wie verrottendes Holz vorkommt. Mit Ausnahme zweier Arten sind alle in arktischen Regionen nachgewiesenen Taxa in der borealen oder temperaten Zone häufiger.

Boreale Gebiete haben eine etwa dreifach höhere Artenzahl als arktische Gebiete. Neben der wesentlich höheren Zahl totholzbewohnender Arten wurden Bewohner von mit Moos- und Algendecken überzogenen Felsen und nivicole (am Rande des schmelzenden Schnees lebende) Myxomyceten nachgewiesen.

Die besten Bedingungen für corticole Myxomyceten bietet die südliche temperate Zone mit einem warmen, durch ergiebige Sommerregen bestimmten Klima. Eine vorläufige Artenliste für die Great Smoky Mountains ergab 168 Arten, von denen 47 (28%) bevorzugt die Rinde lebender Bäume besiedeln.

Wüsten haben im Vergleich mit anderen Vegetationszonen die eigenständigsten Myxomycetengesellschaften. Die untersuchte winterkalte Wüste Kasachstans beherbergte 28 Arten, von denen 18 häufiger und einige wenige extrem häufig waren.

In tropischen Wäldern erscheinen vorwiegend robuste, streubewohnende Myxomyceten. Typische Eigenschaften tropischer Myxomycetengesellschaften sind: Dominanz von Arten mit Phaneroplasmodien, insbesondere Physarales, die eine Vielzahl unverholzter Streusubstrate bewohnen. Im Vergleich zur temperaten Zone ist der Anteil von Arten mit gestielten Fruktifikationen höher. In dauerfeuchten Regenwäldern fehlen corticole Arten fast vollständig.

Die Diversität tropischer Myxomyceten nimmt mit steigender Höhe und jährlicher Niederschlagsmenge ab. Untersuchungen in Costa Rica, Equador und Puerto Rico zeigen, daß sowohl Abundanzen als auch Artenzahlen entlang eines Feuchtigkeitsgradienten von Trocken- zu Regenwäldern stark abnehmen.

Dauerhaft hohe Feuchtigkeit behindert die Entwicklung der Fruktifikationen. Ein Vergleich von Aufsammlungen aus Equador und aus dem östlichen Nordamerika zeigt, daß Fruktifikationen derselben Arten in den Tropen längere Stiele ausbilden. Dies erfordert mehr Ressourcen, die für die Ausbildung

von Sporen verloren gehen. Hohe Substrat- und Luftfeuchtigkeit verhindert die Austrocknung der Sporen und fördert die Besiedlung der Fruchtkörper mit parasitischen Pilzen. Dies reduziert die Menge der Sporen, die vom Wind erfaßt werden kann und damit auch das Ausbreitungspotential der Arten.

In tropischen Wäldern ist die Diversität von Myxomyceten in Mikrohabitaten oberhalb der Bodenschicht höher als in solchen am Boden. Substrate wie an den Pflanzen verrottende Blätter, Früchte, Blütenteile oder absterbende, hohe Stauden trocknen schneller aus und geben den Sporen eine höhere Chance, in den Luftraum zu gelangen.

Epiphylle Flechten- und Lebermoosgesellschaften tropischer Regenwälder beherbergen Myxomyceten. Dieses neuentdeckte Mikrohabitat erlaubt die Entwicklung kleiner Populationen von Myxamöben, die in Kulturen fruktifizieren. Wenigstens drei Arten erscheinen regelmäßig und deutlich öfter als in der Streuschicht.

Blütenstände von Riesenstauden der Ordnung Zingiberales sind der Lebensraum einer spezialisierten Gesellschaft von Myxobakterien und Myxomyceten. Diese neue Lebensgemeinschaft wurde auf der Grundlage von Sporokarpzählungen und nachfolgender statistischer Auswertung charakterisiert. Drei Arten von Myxobakterien und sechs Myxomyceten haben eine hohe Preferenz für dieses Mikrohabitat, das durch an den lebenden Blütenständen verrottende Teile der Corolla mit einem stark basischen pH gebildet wird. Vögel sind mögliche Verbreitungsvektoren.

Zwischenartliche Konkurrenz kann bei Myxomyceten vorkommen, ist jedoch selten. Für die Lebensgemeinschaft der winterkalten Wüste Kasachstans wurden Zählungen oder Schätzungen der in den Kulturen erscheinenden Sporokarpien vorgenommen, um Nischenbreite und -überlappung zwischen den Arten zu berechnen. Eine darauf basierende Auswertung ergab Hinweise für zwischenartliche Konkurrenz bei wenigen Arten mit Phaneroplasmodien.

Wüstenbewohnende Myxomyceten zeigen zwei verschiedene Lebensstrategien: schnell fruktifizierende Arten, die auf einzelne Regenfälle reagieren können, und langsamere Arten die auf längere Regenperioden angewiesen sind, aber austrocknungsresistenter sind. Arten des ersten Typs entwickeln sehr schnell kleine, gewöhnlich gestielte Sporokarpien aus Proto- oder sehr kleinen Aphanoplasmodien. Arten des zweiten Strategietyps besitzen meist Phaneroplasmodien, aus denen sich langsamer größere, meist ungestielte Fruktifiktionen mit robuster Peridie entwickeln.

Myxomyceten sind am besten an Lebensräume mit stark schwankender Feuchtigkeit angepaßt. Trockenheit fördert die Fernverbreitung. Zusammen mit lange lebensfähigen Dauerstadien ermöglicht dies die schnelle Besiedlung vieler in Zeit und Raum schnell veränderlicher Mikrohabitate. Als generelle Schlußfolgerung der durchgeführten Untersuchungen ergibt sich, daß Myxomyxceten

hohe Feuchtigkeit für ihr Amöbenstadium, mittlere für das Plasmodienstadium und Trockenheit für die Ausbreitungsfunktion der Fruktifikationen benötigen. Das erklärt die niedrigen Abundanzen von Myxomycetenfruktifikationen in dauerfeuchten tropischen Regenwäldern im Vergleich zu ariden Gebieten mit stark schwankenden Regenfällen.

Der Durchmesser der Sporen variiert lediglich in engen Grenzen, welche einerseits durch die Menge der mitzuführenden Ressourcen, andererseits durch die Anforderungen der Fernverbreitung bestimmt sind. Zwei Drittel aller Arten besitzen Sporen mit Durchmessern zwischen 7 und 12 µm. Modellrechnungen zeigen, daß dies nahe der oberen Grenze für längeres Schweben in Luft liegen sollte.

Fernverbreitung durch Sporen dürfte ein eher seltenes Ereignis bei Myxomyceten sein. Die terminale Fallgeschwindigkeit für Sporen zwischen 7 und 12 µm Durchmesser liegt wahrscheinlich zwischen 130 und 380 Metern pro Stunde. Dies genügt nicht, um große Entfernungen ohne die Mithilfe von Aufwinden zu überbrücken. Vorkommende, jedoch selten stattfindende Fernverbreitung durch Sporen ist aus biologischer Sicht sinnvoll: sie ermöglicht die nahezu ungestörte Herausbildung lokaler Klone (welche optimal an das betreffende Mikrohabitat angepaßt sind), garantiert aber andererseits die Besiedlung aller geeigneten Mikrohabitate und Regionen der Erde durch die betreffende Art.

Gestielte Fruchtkörper sind typisch für Myxomyceten und stellen einen entscheidenden evolutionären Vorteil gegenüber anderen Mikroorganismen dar. Fast zwei Drittel aller Arten mit Einzelfruchtkörpern entwickeln einen Stiel. Seine Hauptfunktion besteht darin, die Sporotheca über die Substratoberfläche zu heben, was den Sporen ermöglicht, auszutrocknen und zu verwehen. Wahrscheinlich als Resultat paralleler Evolution finden sich derartige Fruchtkörper auch bei den Myxobacteriales, Protosteliales, Dictyosteliales and Acrasiales.

Ein Modell zur Ressourcenverteilung zeigt, das für die Größe gestielter Fruktifikationen eine obere Grenze existieren muß. Dies ist der Grund, warum sich aus großen Phaneroplasmodien eine Vielzahl kleinerer Sporokarpien entwickelt. Wie die Auswertung einer Datenbank der besser bekannten Arten mit gestielten Sporokarpien und kugelförmiger Sporotheca (der häufigste Typ) zeigt, steigt die maximal erreichbare Stiellänge mit dem Volumen der Sporotheca bis zu einer oberen Grenze, die etwa bei Stiellängen von1 mm und einem Volumen der Sporotheca zwischen 0.1 und 0.5 mm^3 liegt. Für größere Volumina sinkt die maximal erreichbare Stiellänge erneut. Um die Verteilung der Ressourcen für die Entwicklung von Stiel und Sporotheca für verschiedene Volumina und Stiellängen zu zeigen, wurde ein Modell entwickelt. Es erklärt sowohl die beobachteten Größenverhältnisse gestielter Fruktifikationen als auch die Tatsache, daß große Phaneroplasmodien ihre Ressourcen aufteilen.

Die weltweiten Verbreitungsmuster bei Myxomyceten können durch eine Kombination von Mikrohabitatansprüchen und makroklimatischen Faktoren erklärt werden. Ein Beispiel dafür zeigt eine erste Karte des stark disjunkten Areals von *Barbeyella minutissima*, einer winzigen Art, deren Verbreitung der von montanen Fichten-Tannen-Wäldern auf der Erde folgt.

Die Mehrzahl der Myxomycetenarten sind nicht kosmopolitisch verbreitet, insbesondere wenn lokale Häufigkeiten der Arten berücksichtigt werden. Drei Methoden wurden benutzt, um die weltweiten Verbreitungsmuster von Myxomyceten aufzuzeigen: eine Datenbank der geschätzten zonalen Verbreitung, publizierte Checklisten und die hier vorgestellten regionalen Arteninventuren. Die Mehrzahl der Arten ist in einer Vegetationszone deutlich häufiger als in allen anderen.

Biodiversität bei Myxomyceten steigt von der arktischen hin zur südlichen temperaten Zone, fällt jedoch in den feuchten Tropen wieder ab. Alle drei oben erwähnten Methoden zeigen die höchsten Artenzahlen für das östliche Nordamerika und östliche Asien. Damit weicht die weltweite Verteilung der Biodiversität bei Myxomyceten deutlich von der bei Farn- und Blütenpflanzen ab.

Selbstständigkeitserklärung

Ich erkläre, daß ich die vorliegende Habilitationsschrift selbstständig und und nur unter Verwendung der angegebenen Hilfsmittel und Literatur angefertigt habe.

Martin Schnittler

Jena, Januar 2001