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

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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 approxi-

mately 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.

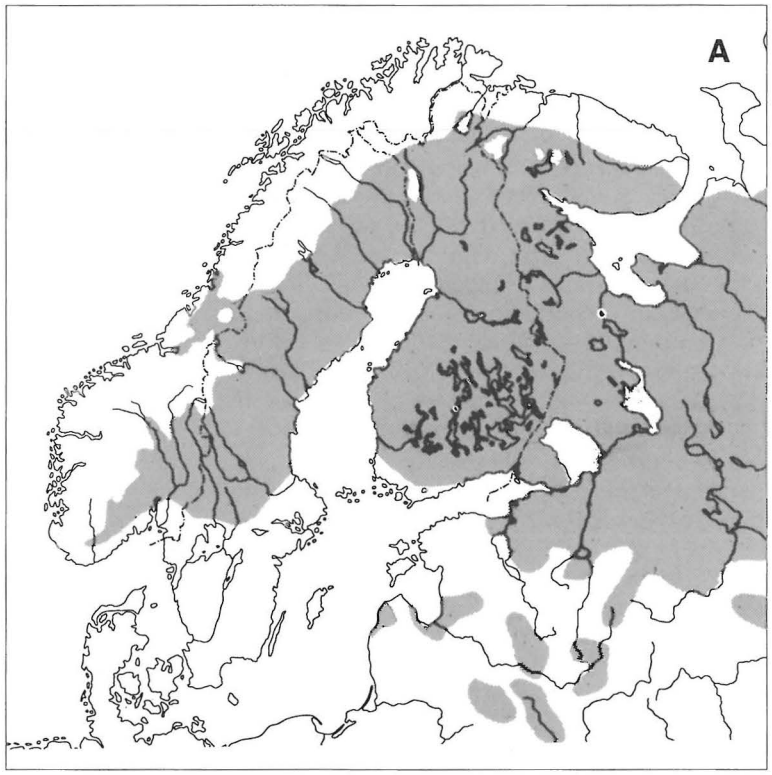
Materials and methods

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 only those aspects that are of interest for the habitat description of myxomycetes. No-



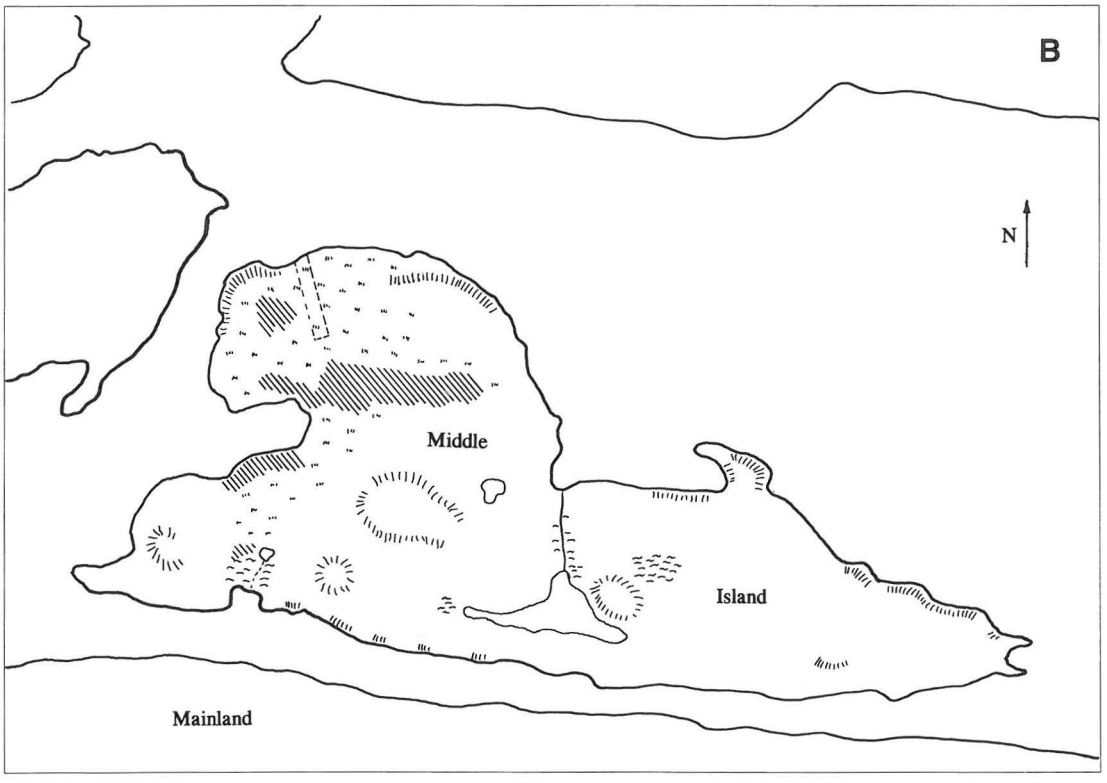


Fig. 1. Study area.
A) Geographical location. The distributional range of boreal woodland (according to Bohn 1993) is dotted.
B) Schematic map of Sredniy Island showing the distribution of settled area (hatched) with meadows, the rock outcrops and the three lakes. With the exception of the peatbogs and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

menclature 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.

Damp, 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 myxo-mycetes.

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 micro-habitat 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.

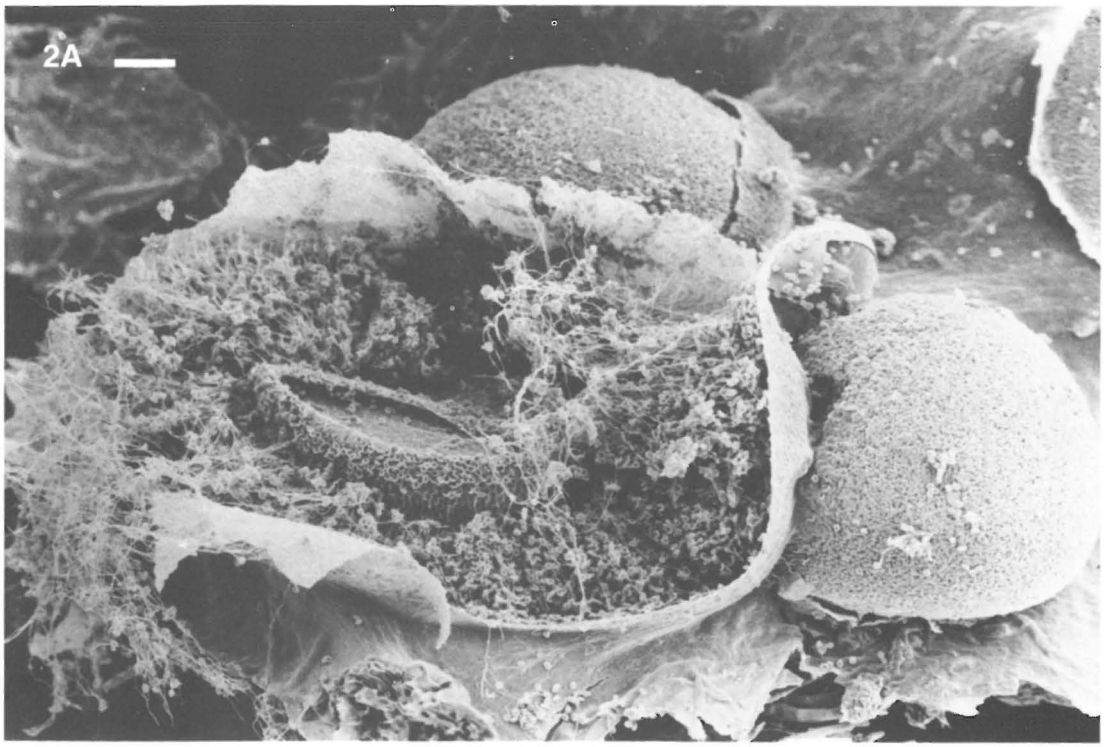
R *Clastoderma debaryanum* A.Blytt: 47341, 47381 = 6768

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,

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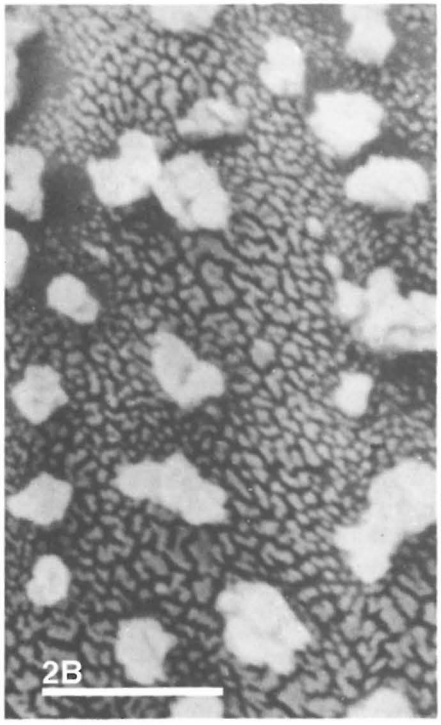
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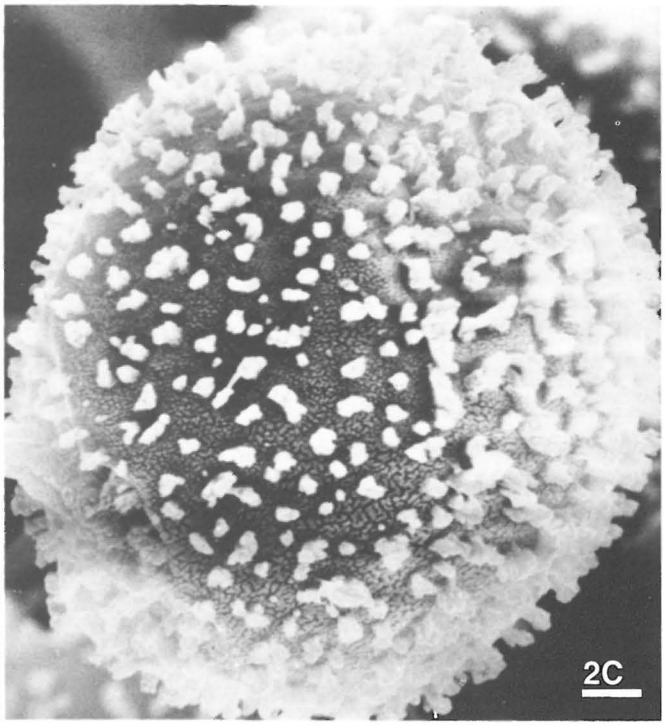

2C

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.

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 ...

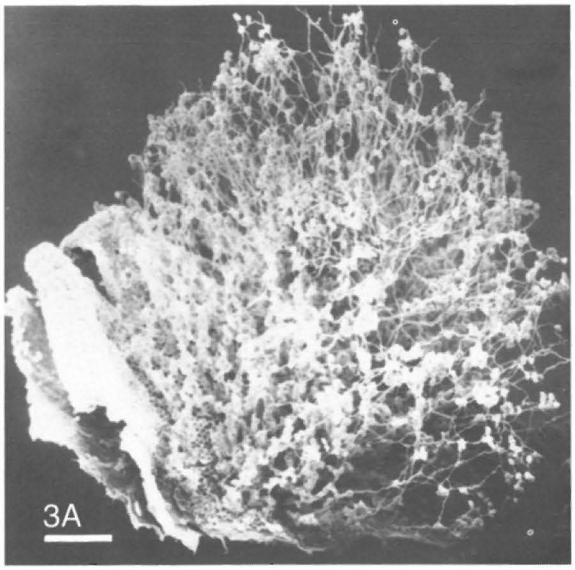
Common on the island, with a wide microhabitat spectrum from the decayed wood of several tree species to *Epilobium* litter in the pioneer community. Collected only in autumn.

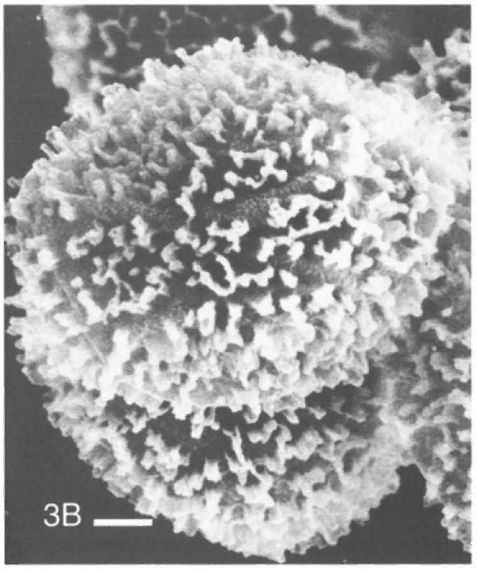
O *Diderma radiatum* (L.) Morgan: 5770 = 47499, 5771 = 47509, 5772 = 47510, 5773 = 47398, 5774 = 47415, 47471

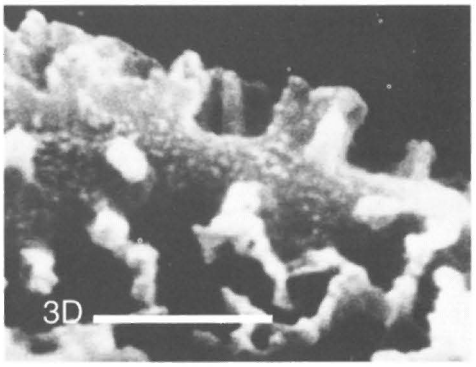
In contrast to the preceding species only collected on litter, also in autumn.

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.


3A


3B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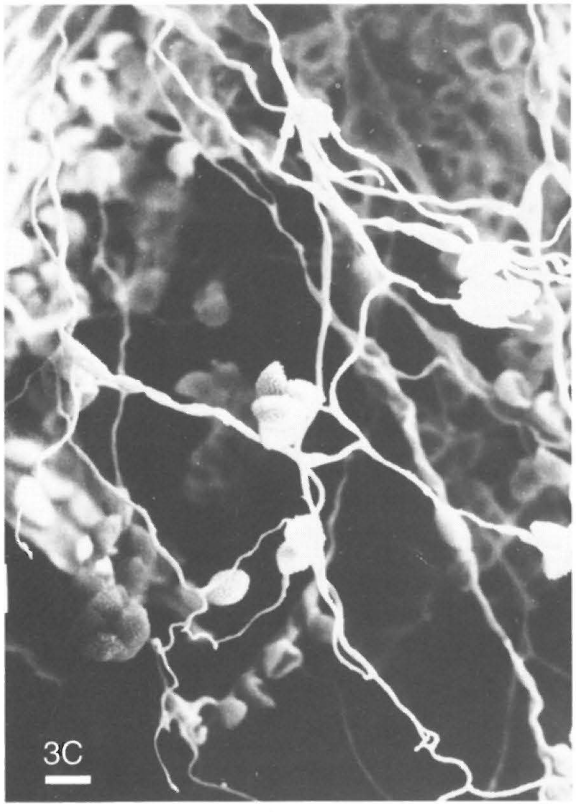
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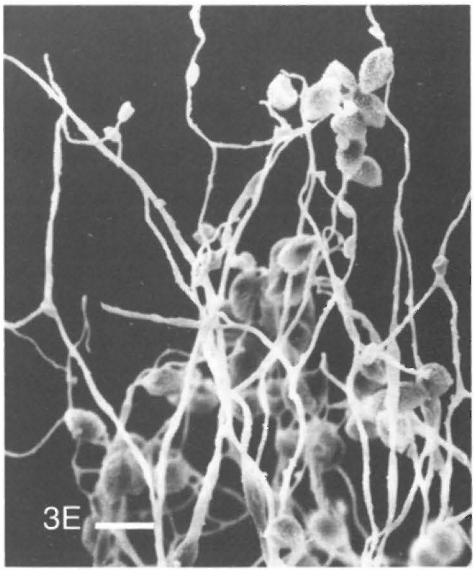
3E

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.

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.

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

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.

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.

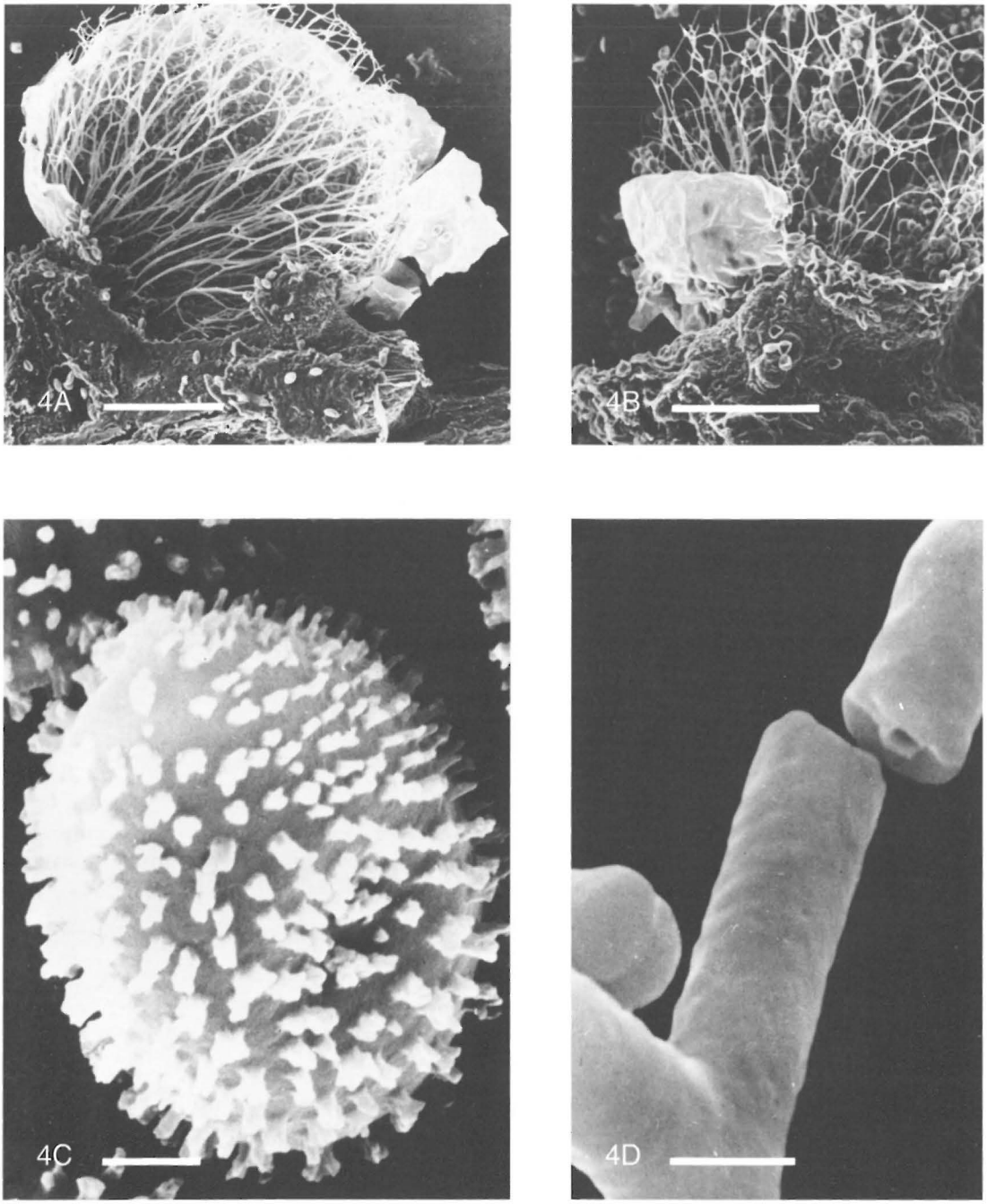

Fig. 4. SEM-photos of *Colloderma* cf. *oculatum* (2810). A, B) Two opened sporocarps with capillitium and remains of the peridium. Bar = 100 mm. C) Spore. Bar = 1 mm. D) A broken thread of the capillitium showing the tubular structure. Bar = 1 mm. Photos Y. Novozhilov.

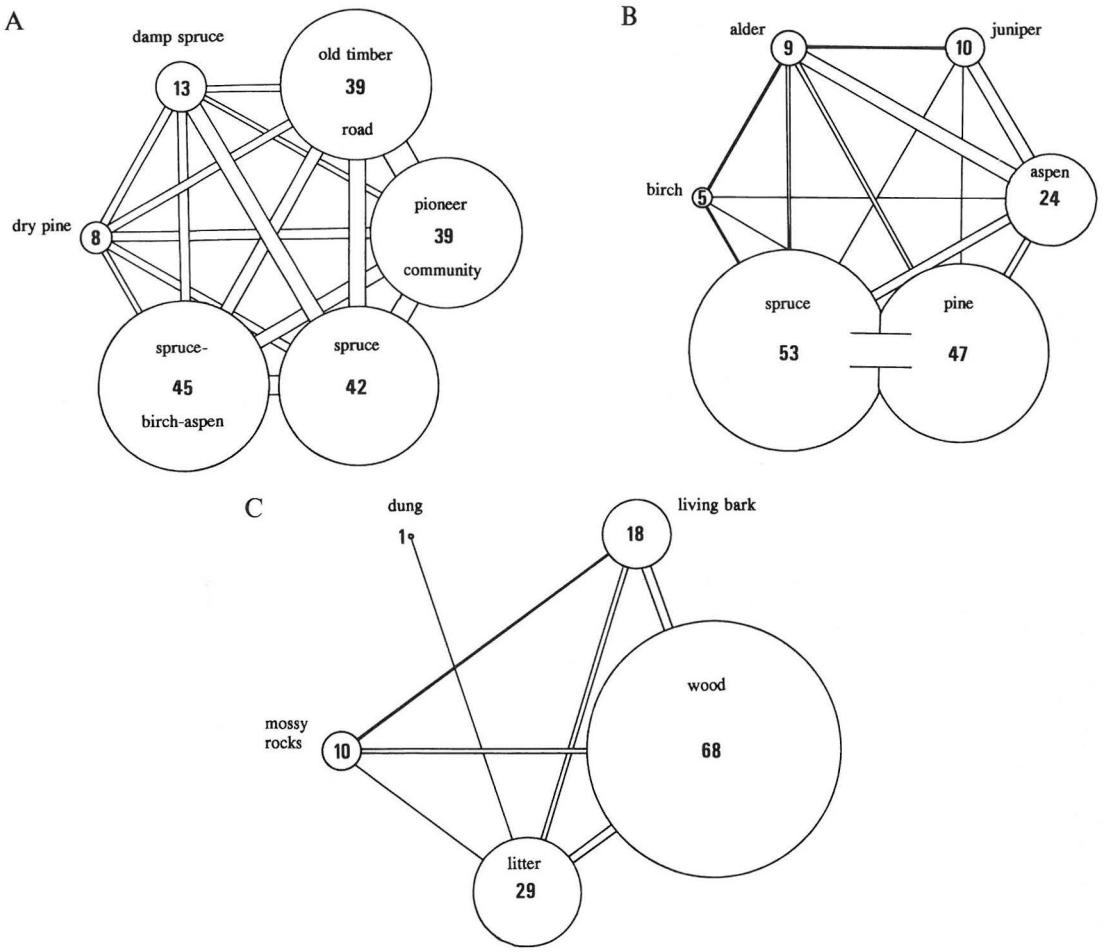

Fig. 5. Relationships of myxomycete occurrences within communities (A), on tree species (B, only for the inhabitants of bark and wood and in the various microhabitats (C). The size of the circles represents the number of species collected in the respective structure (numbers inside), the thickness of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

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).

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

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

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

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

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 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 subassociation 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*, 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.

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