Funga Arctica & Alpina
volume 1

Setting the Scene

H. Knudsen

H. Knudsen, T. Borgen & S. A. Elborne (eds.)

Preliminary version

The final version will be issued with the last volume

Photos: H. Knudsen, unless otherwise noted. Maps: Steen A. Elborne.

This volume should be cited as:

Knudsen, H. 2025. Settting the Scene. In: Knudsen, H., Borgen, T. & Elborne, S.A. (eds.), Funga Arctica & Alpina, vol. 1. Published by the author, Copenhagen. 332 pp. ISBN: 978-87-976550-0-9.

The volume is freely available online at: https://funga-arctica-alpina.dk.

Kindly supported by:

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Preface

It is with pride and pleasure that we present Funga Arctica & Alpina to our fellow mycologists and to all others interested in the cold regions of the Northern Hemisphere.

In 1978 Torbjørn Borgen moved to Greenland to become a schoolteacher and to study fungi. In 1980 the first Symposium on Arcto-Alpine Mycology (ISAM I) took place in Alaska with Henning Knudsen and Borgen as participants. In 1983, on an expedition to a subarctic valley in southernmost Greenland, we were overwhelmed by the richness of the funga and we started to investigate the Greenlandic basidiomycetes. In 1987 the former General Secretary of the Soviet Union, M. Gorbachev, gave a speech, the Murmansk Initiative. He encouraged the seven Arctic nations to cooperate more for their collective welfare. The National Geographic Society of Russia took the hint, and arranged an international congress in St. Petersburg in 1989 for the Arctic countries. As director of the Botanical Museum at the University of Copenhagen, Knudsen participated as the representative for botany for one of the seven countries in the Arctic Council: Alaska (USA), Canada, Greenland (Denmark), Iceland, Norway, Finland, and Russia. At the end of his lecture, Knudsen asked the audience if anyone knew a Russian mycologist working in the Arctic. He thereby came to know Dr. Victor Mukhin of Yekaterinburg, and the next year they met in Tallinn at the European Mycological Congress and decided to organize joint expeditions to Siberia. These took place every year for the next 16 years (1989–2004), and the similarity between the fungas of Siberia and Greenland encouraged us to study not only the Greenlandic fungi, but the funga of the whole Arctic circumpolar region. In 1987 Steen Elborne joined the project with a Ph.D. study of the white-spored agarics in Greenland. Our results are presented here and in the next six volumes of Funga Arctica & Alpina.

Thus, after 47 years of collection and documentation, both casual and organised, we can present some results. The first three volumes are issued together, and the last four will appear in the next two years. They will all be freely available online at www.funga-arctica-alpina.dk, where you can also follow the status of the project.

When we started, Gorbachev spoke of peace and cooperation in the Arctic. Since then, climate change has started to melt the ice in the Arctic Ocean and the permafrost in the arctic regions of Canada and Russia, in the Alps, and elsewhere. Huge areas that are currently under permafrost will melt, and the layer of organic matter from many years of deposition will be available as food for fungi when it thaws. The decay will increase atmospheric CO_2 and methane (from bacteria), with a destructive effect on the ozone layer, but at the same time new land for agriculture and forestry will be exposed in the newly ice-free areas. Russia and China will send their goods to Europe through the Arctic Ocean, which will be faster and cheaper than the long passage through the Suez Canal. The USA may attempt to claim Greenland for defence. Many transformational events will take place in the Arctic in the years to come, and the fungi will have their role. We are gratified to be able to document the fungi at the starting point of these events, before everything changes.

Henning Knudsen, Torbjørn Borgen, and Steen A. Elborne

Acknowledgements

A project like this, which unites several smaller projects conducted over many years and in many places, cannot be successful without the help and assistance of numerous people, to whom we wish to pay our respects. We have received help from people at local biological and arctic stations, at small airports, and in the field; local people have assisted us with transportation and lodging, advised us on localities, etc. This courtesy is normal in places where there are few people and everybody depends on each other. Although normal, we are nevertheless deeply grateful to all these known and unknown people. Most of them are nameless to us, but not forgotten, and we are thankful to them all for making our investigations possible.

Table 1 gives an overview of the places where, when and with whom we have collected arctic-alpine fungi. In many of these localities we were in the company of Danish or foreign colleagues, especially during the International Symposia for Arcto-Alpine Mycology, and during those Nordic Mycological Congresses that took place in cold areas. All of these colleagues from most of the cold areas in the Northern Hemisphere shared their knowledge and often their collections with us, and we are grateful to them and happy to be able to pay something back.

Torbjørn Borgen worked as a schoolteacher from 1978–2000 in Paamiut (Frederikshåb) in southwestern Greenland. The town is surrounded by arctic nature; thus, during this period he was often mushroom hunting alone or with the help of colleagues, friends and family. He is grateful for their company and help.

Henning Knudsen participated in expeditions to Siberia for 16 consecutive years (1989–2004) and on six subsequent occasions; some of these took place in arctic or alpine areas. Numerous colleagues participated and collected with him, and he is grateful to all of them for both their collections and their help, especially to the leader of these expeditions, professor Victor Mukhin of the Institute of Animal and Plant Ecology in Yekaterinburg, Russia; to Dr. Heikki Kotiranta of Helsinki; and to the mycologist and former collections manager Peer Corfixen of the Natural History Museum of Denmark (C), who accompanied him on all the expeditions.

We have received financial help from a number of sources. The Aage V. Jensen Foundation has been our most generous supporter, and their support was especially crucial for our expeditions in 2016–2018 to different parts of Greenland with the specific purpose of photographing as many species as possible for the funga. The Jakob E. Lange Foundation under the auspices of the Danish Botanical Society supported some of the early expeditions to Siberia for Knudsen. It is a pleasure for us to present the results to these and other sponsors after such a long time.

Early in the project, the Carlsberg Foundation supported a Ph.D. study for Steen A. Elborne. Before the study was completed, Elborne was headhunted by a private company. Thus, it is gratifying to now be able to demonstrate some of his unpublished results, especially in parts of volumes 5 and 6.

In 1983 and 1984, the late dendrologist Søren Ødum of the former Royal Veterinary and Agricultural College in Copenhagen (Landbohøjskolen) kindly invited Knudsen and Elborne to participate in studies of *Betula pubescens* scrubs in southern Greenland. These studies were later published in 1990 in Meddelelser om Grønland, Bioscience vol. 33.

A number of Danish colleagues have collected independently in Greenland, but allowed us to use their collections. These include Morten Lange (collected in 1946, also several years in Iceland), Peter Milan Petersen (collected 1969–1973), Henry Dissing (1972–1989), Erik Rald (1992–1993), Flemming Rune (1992–1993), David Boertmann (1967–2016), and Hans Henrik Bruun (2023–2024). Thomas Læssøe and Elborne participated in a student excursion from Århus University in 1981, and Læssøe was again in Greenland with Knudsen in 1984. Jens H. Petersen (Århus) joined Knudsen and Borgen in 1983, and Knudsen and Elborne in 1989. On the expedition in 1991, Victor Mukhin (Yekaterinburg, Russia), Nils Hallenberg (Gothenburg, Sweden) and Mikako Sasa (Novozymes; Copenhagen) participated. University of Copenhagen botanists Christian Bay and Bent Fredskild have shared their collections from remote places, as did the phytopathologist Eigil de Neergård of Landbohøjskolen (1976–1979). Colleagues from abroad, collecting in Greenland, have also shared their collections with us, e.g., Sigmund Sivertsen (Trondheim, Norway, 1998), who collected discomycetes with Henry Dissing.

A number of colleagues have kindly supplied us with photos. These include Jens H. Petersen (1983, 1989), Thomas Læssøe (1981, 1984), Pierre-Arthur Moreau (from ISAM VII in Norway, 2005), Ursula Peintner (ditto), Leo Jalink (from ISAM VI in Greenland, 2000) and Henrik F. Gøtzsche (West Greenland, 2018).

A number of colleagues have directly or indirectly supported the project by revising and publishing parts of our material (see Literature section for specific papers): Gro Gulden (Natural History Museum, University of Oslo: *Galerina*); Jan Vesterholt (associated with the Natural History Museum of Denmark: *Hebeloma*); Ursula Eberhardt and Nicole Schütz (Staatliches Museum für Naturkunde, Stuttgart, Germany), Henry Beker (Brussels, Belgium: *Hebeloma*); Machiel Noordeloos (Rijksherbarium, Leiden, Netherlands: *Entoloma* p.p.), Beatrice Senn-Irlet (Bern, Switzerland: Crepidotaceae), Mikael Jeppson (Trollhättan, Sweden: *Lycoperdon*); Morten Lange (former Institute of Thallophytes, now part of the Department of Biology, University of Copenhagen: *Calvatia*), Knud Hauerslev (Copenhagen: corticioid and resupinate tremelloid fungi, unpublished), and Jens H. Petersen (Århus, Denmark: club fungi, unpublished).

Knudsen participated in all the ISAMs from 1980 to 2016, except for 2005. Borgen participated in 1988, 1996, 2000 and 2005. Elborne participated in 1992, 2000, 2005 and 2008. During these symposia we met most of the mycologists in the Northern Hemisphere working on arctic-alpine fungi, and were thus able to draw on their expertise. This was a valuable help on our long and winding road. Especially, we wish to thank the founder of these symposia, Gary C. Laursen (University of Alaska Fairbanks), for his generous invitation to Knudsen and Borgen to participate in the first symposium in Alaska. At the first ISAM, Joe Ammirati was a dedicated helper and co-organizer. We also thank the Office of Naval Research for inviting us to stay and use their facilities at the Arctic Research Laboratory in Barrow during the symposium.

Our good colleague, the entomologist and mycologist Erik Rald of Copenhagen, passed away before he could publish his material collected in Narsarsuaq in 1992 and 1993. We are grateful to his family for allowing us to use his photos and material deposited in the fungarium of the Natural History Museum of Denmark (C).

All of our collections from cold regions were databased over the years by the former collections manager at the fungarium, Peer Corfixen. He was a pioneer in the digitisation of fungal specimens in Denmark, databasing ca. 20,000 collections of basidio- and ascomycetes. We are grateful for his accurate and painstaking work at an early point (the 1990s) in the history of digitisation. He was the main force behind the creation of the ca. 100,000 fungal records presently in the database at C.

When Corfixen retired, he was replaced by the present Head of Geology and Botany, Christian Lange. He has provided necessary assistance with the database and technical issues with microscopes and cameras. This made our work much easier, and we warmly thank him for his help in the fungarium.

Justin Wynns (C) continues with the collections work and databasing of specimens from Greenland and Siberia, and he skilfully performed the proofreading and layout of vols. 1-3. We are grateful for his efforts.

Librarian Inger Marie Refskou Poulsen kindly assembled our list of references, which were taken from many different sources.

Henrik F. Gøtzsche collected with us in 2018 in southwestern Greenland and made important photographs and collections for the project. He also helped with computer problems alon the way.

The Nordic Mycological Congress has taken place in Denmark, Sweden, Norway or Finland every other year since 1972. In a few cases, the congresses were held in cold places, which allowed us to collect for the project, e.g. in Skibotn (Norway, 1992), Kuusamo (Finland, 1978), Rovaniemi (Finland, 2013) and in Iceland in 1993.

Joint Russian-Nordic mycological expeditions to several regions in Siberia enabled us to collect many arctic and alpine fungi. These expeditions were all arranged by Victor Mukhin from the Institute of Plant and Animal Ecology in Yekaterinburg. The expeditions took place in Salekhard during ISAM V (1996), Tiksi (V. Mukhin, 1999), Altai (V. Mukhin, 2001), Taimyr (V. Mukhin, 1993), Kamchatka (V. Mukhin, 1998), and Altai/Ukok (A. Shiryaev, 2019, 2020). We are grateful to our Russian colleagues for arranging and guiding these expeditions to remote localities.

Anna Bogacheva (Institute of Geography, Vladivostok) kindly gave us information and photos about the occurrence of *Puccinia urbanii* in the Russian Far East.

We thank the curator of fungi of the Natural History Museum, University of Oslo for the loan of *Puccinia svendsenii* and the curator of the Tromsø Museum (Norway) for lending us the type of *Puccinia allii-sibirici.*

We thank Karen Hansen, curator of fungi at the Swedish Museum of Natural History (S), for kindly sending us photos of *Puccinia fischeri.*

In 1987 the director of Pinngortitaleriffik (Grønlands Naturinstitut), Klaus H. Nygaard, kindly allowed us to use the station while searching for fungi in the Nuuk area. In 2018 we likewise used the field station Nuuk-Basic in Kobbefjord near Nuuk while botanising, which was facilitated by Katrine Raundrup of Pinngortitaleriffik.

Last but not least, we thank our respective partners, Mikako Sasa, Anne-Mette Larsen and Lilian Andersson, for their support and patience. This project would not have been possible without their long-standing, kind, and patient support.

The Editors

The editors in 2017 in front of the airstrip at Constable Pynt, central East Greenland, at the border between the Low Arctic and High Arctic. From left: Borgen, Elborne, Knudsen.

Henning Knudsen, born in 1948, cand. scient. in mycology from the University of Copenhagen in 1973, curator of fungi at the Copenhagen Botanical Museum (now a part of the Natural History Museum of Denmark) from 1974–2015, director of the Botanical Museum from 1986–1989 and 2000–2003, member of the board during various periods, and member of Artdatabanken's committees for Swedish biodiversity (Stockholm, Sweden).

His main interests are the biodiversity, taxonomy, ecology and geography of basidiomycetes. His main works include serving as co-editor and co-author with Lise Hansen (Copenhagen) of Nordic Macromycetes vols. 1-3 (1992–2000), co-editor and co-author with Jan Vesterholt (Copenhagen) of Funga Nordica (2008) and Funga Nordica, ed. 2, vols. 1-2 (2012), along with a number of popular books. With Victor Mukhin (Yekaterinburg), Heikki Kotiranta (Helsinki) and Peer Corfixen (Copenhagen), and several others on an irregular basis, he arranged collecting expeditions to Russia (Siberia) more than 20 times. With Shiang-Hua Wang (Yunnan, China) he made expeditions to northern and southern China five times; with Mikako Sasa (Copenhagen) to Japan five times; and to numerous North American (Alaska, Montana) and European arctic-alpine localities, often in connection with the ISAMs or Nordic Mycological Congresses; see map (Fig. 2) and list (Table 1) below.

Torbjørn Lindhardt Borgen, born in 1945, was a primary school teacher in Denmark from 1975–1977 and in Paamiut (Frederikshåb), Greenland from 1978–2000. His main interests are the taxonomy of Hygrocybeae and *Cortinarius*, and the ecology and mycogeography of basidiomycetes. His major work "Taxonomy, ecology and distribution of *Hygrocybe* (Fr.) P. Kumm. and *Camarophyllopsis* Herink (Fungi, Basidiomycota, Hygrocybeae) in Greenland" with Eef Arnolds (The Netherlands) was published in 2004, followed by further papers on Hygrocybeae and *Cortinarius*, as well as collaborative work with Henry Beker (Eberhardt et al. 2021) on *Hebeloma* in Greenland. His book on the most common Greenlandic fungi with photos by J. H. Petersen (Pupiit Kalaallit Nunaanni) was the first mushroom book to be translated to the Greenlandic language. He works for the Danish Mycological Society evaluating incoming records for their website. He has performed field work in various parts of Greenland including Zackenberg (NE Greenland), and in the alpine zones of the Faroe Islands, Iceland, Switzerland, Norway, Finland and Russia (see Fig. 2 and Table 1), in addition to participation in mycological congresses.

Steen Andrew Elborne, born in 1957, cand. scient. in mycology from the University of Copenhagen in 1987, with Knudsen as supervisor. He worked at Hussvamp Laboratoriet (The Dry Rot Laboratory, Copenhagen) from 1991–2024, and has been a member of the board of the Danish Mycological Society since 1991. His main interests are the biodiversity, taxonomy, ecology, geography, and distribution of basidiomycetes, especially white-spored agarics. His main publications include the treatment of mycenoid genera in Nordic Macromycetes vol. 2 (1992), and of the mycenoid genera and *Hohenbuehelia* in Funga Nordica (2008). He has performed field work in various parts of Greenland, and in the alpine zones of Iceland, Norway, Scotland, France, Bulgaria, Austria, Germany, Russia and the USA, partly through participation in ISAMs and Nordic Mycological Congresses (see Fig. 2 and Table 1).

As the editors' expertise is in the fleshy basidiomycetes, we were lucky enough to persuade **Drs. Aad J. Termorshuizen** and **Charlotte Swertz** (The Netherlands) to write the treatment of rust fungi (vol. 2). They had already published a rust funga for the Netherlands (Dutch Rust Fungi) in 2011, but still agreed to treat the arctic and alpine rusts for this project.

Similarly, **Drs**. **Teodor Denchev** and **Cvetomir Denchev** (Sofia, Bulgaria) wrote the treatments for the smut fungi (vol. 3). They had already written a precursor, The Smut Fungi of Greenland (2020), but have considerably enlarged the number of arctic and alpine smut fungi in volume 3.

We are grateful for their contributions, which have made the funga more complete, and given us a better basis for comparing and understanding the interactions between all basidiomycete groups across cold areas.

1. Methods, principles, definitions, map, localities

Definitions

Funga is a term equivalent to "flora" or "fauna": a synopsis of the fungi of a defined area. It is a word coined from the Greek "fungi", but it is not a Greek word. Some authors use the term "mycota" instead, but that word is also used in the naming of formal ranks like Basidiomycota and Ascomycota. "Mycobiota" is a synonym, but the parallel terms "Zoobiota" and "Plantbiota" are rarely used.

Basidiomycetes are fungi belonging to phylum Basidiomycota. All species of Basidiomycota known to occur in arctic-alpine areas (as we define them) are included, with a few exceptions (basidioparasites on lichens and basidioyeasts).

The Arctic is a climatic zone in the northern part of the Northern Hemisphere where the average temperature for July is below 10 °C. It is equivalent to the Polar zone as defined by Rivas-Martínez et al. (2004). "The Arctic" is thus a geographic area around the North Pole (see section on Climate below), but "arctic region" is used in general for cold places. It has not always been possible for us to distinguish between the two. Likewise, it has not always been possible to separate between the geographic "Arctic", the climatic "Arctic", and the general term "arctic", as in arctic conditions. We ask for the reader's forbearance.

Alpine regions included in this work are defined as areas of the Northern Hemisphere that are part of a mountaintop above the treeline. The alpine zone occurs at different altitudes depending on the latitude. In the context of this work, we only consider alpine areas in the Temperate and Boreal zones as defined by Rivas-Martínez et al. (2004). These areas include the Cryoboreal and Oroboreal subzones of the Boreal zone. From the Temperate zone, we include a part of the Orotemperate subzone.

Which of these areas we include depends on the vegetation present. We demand the presence of at least one species from at least two of the three genera *Salix* (willow), *Betula* (birch), and *Dryas* (mountain avens). *Bistorta vivipara* (bistort) may be present, but is in itself not a sufficient criterion for including a region among our target areas. Thus, even though there are alpine areas in the Mediterranean and Tropical bioclimatic zones of the Northern Hemisphere (e.g., Mt. Kilimanjaro, Mt. Fuji, Tibet), they do not include the plants and associated fungi that fit our definition of the alpine zone.

This definition of the alpine zone, based on the presence of two characteristic woody species, is empiric, and is based on our experience collecting fungi in many different cold places. We chose this definition in order to exclude some borderline areas and to make delimitation more precise. The transition from High Arctic or alpine to temperate lowland is gradual, and even in temperate lowland dunes along the Atlantic a few species of fungi associated with *Salix repens* occur that have their main distribution in arctic areas, like *Russula norvegica*, *R. subrubens*, *Multiclavula vernalis*, *Inocybe* spp. and *Cortinarius* spp. In the map of the European bioclimatic zones by Rivas-Martínez et al. (2004), we compared the areas designated as "Orotemperate" with the distribution maps of Hulten (1937) for species of *Salix*, *Betula*, and *Dryas*, and were thereby able to designate areas to include in this funga. We decided to exclude areas where only one shrub was present, in order to be sure of our final selection of areas and eliminate sporadic occurrences. In this way, we ended with the map of areas (Fig. 2) for which we have included available data on the occurrence of basidiomycetes. Not surprisingly, higher mountains and places further inland (away from the milder Atlantic air) are more likely to have arctic fungi, and conversely, lower mountains and sites closer to the Atlantic are less likely. Our solution works well across Europe, except for western Ireland, where *Dryas* and *Salix herbacea* are found down to sea level, with *Dryas octopetala* in e.g. The Burren National Park. However, since this is clearly not an alpine area, we have not included it.

Areas with conifers, except for species of *Juniperus,* belong by our definition to the subalpine/subarctic zone and are consequently not included. Fungal records from arctic areas on timber of conifers are also excluded, as such wood has either been imported, or is driftwood.

Areas with creeping willow (*Salix repens*) and associated fungi are widely distributed in temperate regions, but are also sparsely found in neighbouring arctic and alpine areas. This species is however not considered by us to be arctic-alpine, and it is thus not considered.

Areas with downy birch (*Betula pubescens* s.l. and its variety *czerepanovii*, syn. *B. tortuosa*) and other tree-like birches occur mostly in the subarctic/subalpine zone, but are included when they border the arctic/alpine zone.

Areas with mountain avens (*Dryas* spp.) are common in arctic-alpine regions on calcareous soil. They are generally included, except for Ireland (see above).

Exception for Greenland: This work was originally intended as a funga of Greenlandic basidiomycetes. Therefore, it includes more detailed information for Greenland than for other arctic places. For this reason, we have chosen to include a list of all known species of vascular plants from Greenland (see "Parasitism", chapter 9a), in order to give a more detailed account of what may occur in arctic areas than it has been possible to do elsewhere with the scattered information from the literature. A consequence of this is that some species are included that must be classified as subarctic/subalpine/boreal rather than arctic-alpine (the Greenland Mountain Birch Zone). These species have a very limited occurrence in a few fjords in southernmost Greenland (Feilberg 1984).

Arctic-alpine taxon: If a species includes subspecific taxa, we include the taxon growing in arctic-alpine areas. If this is not the parent taxon, but a different subspecific taxon, the subspecific taxon is included, but the parent taxon may only be discussed in the "Notes" section at the end of the volume.

The Southern Hemisphere includes both arctic and alpine areas, but is not considered in this work.

Methods

GBIF (the Global Biodiversity Information Facility) has established itself as the most important registry of organisms in the world.

Index Fungorum (Kew) is our source for the taxonomy and spelling of fungal names, where not otherwise noted.

Plants of the World Online (Kew) is our source for the taxonomy and spelling of vascular plant names, where not otherwise noted. Common names are taken when possible from Stace (1991).

Funga Nordica (Knudsen & Vesterholt 2012) is generally followed for taxonomic concepts of species and infraspecific taxa.

The Methuen Handbook of Colours (Kornerup & Wanscher 1978) is generally used for defining colours.

Munsell Soil Color Charts (Munsell 1975) are used for some brown colours, for example in *Cortinarius*.

Spores were generally measured and photographed at 1000×, except for rusts (vol. 2), smuts, and tremelloids (vol.3), where they are generally shown at 400×. The terms used for describing spores are generally three dimensional terms (e.g., “ovoid” or “ellipsoid”, not “ovate” or “elliptic”).

The size of cystidia and basidia of various kinds are given to the nearest full micron.

Reagents were used to reveal some characters not otherwise visible.

- Melzer’s solution: to demonstrate an amyloid reaction (blue) or dextrinoid reaction (brown).
- Cotton blue solution: to demonstrate a cyanophilic reaction (blue).
- iron sulphate ($FeSO_4$), solid or hydrated: to show a colour reaction from white to pink or turquoise in *Russula* sect. *Xerampelinae*.
- congo red: used to dye a microscopic section red.
- 10% potassium hydroxide: used for a macroscopic spot test in *Cortinarius*, sometimes in *Russula* (context) and *Hygrocybe* (pileipellis).

Terms in descriptions

Terms used in the descriptions of the fungi come from Flora Agaricina Neerlandica, vol. 1 (Bas et al. 1988). For groups not included in that work, they are taken from Eriksson et al. 1972-1988 (Corticiaceae of North Europe), Ryvarden & Melo 2014 (polypores), Vánky 1994 (smuts), and Termorshuizen & Swertz 2011 (rusts). Descriptions are made to be simple and consistent for species in a genus. General terms are taken from mycology, not from zoology (flesh, gills) or botany (fruitbody, sporocarp).

Distribution

Fungi treated in this work are distributed in three main categories: arctic-alpine, arctic, or alpine. Other terms like cosmopolitan, boreal, or temperate are used more casually. The distribution of the fungi is further classified as circumpolar, North American, and/or Eurasian. Southern Hemisphere occurrences are not discussed. Finally, the countries where the fungi have been recorded are listed. More specific locality information is noted in parentheses, e.g., "USA (MT, CO)", or "Russia (Altai)".

Notes

Additional information not directly relevant to species descriptions may be included in the Notes section at the end of each subsequent volume. Such cases are marked with an asterisk (*) and arranged alphabetically in the Notes.

Materials, map and table of collection sites

Materials

Material: Most of the specimens we studied are deposited in fungarium C, the herbarium acronym for the former Botanical Museum of the University of Copenhagen, now part of the Natural History Museum of Denmark. In a few cases where material was not available in C, it was necessary to borrow specimens from other fungaria. We are grateful to the curators of the Swedish Museum of Natural History in Stockholm (S), Lund University (LD), Uppsala University (UPS), the Natural History Museum in Oslo (O), and the Arctic University of Norway in Tromsø (TROM), University of Oulu (OULU) and Univerity of Turku (TUR) for loans.

Species descriptions were made from fungarium specimens. If insufficient material was available for study, we supplemented the descriptions with information gleaned from the literature.

We have to date collected and reviewed ca. 15,500 collections of basidiomycetes from Greenland, ca. 1500 from Iceland, ca. 4000 from Russia north of 60°N, and ca. 1600 from other alpine and arctic areas (Austria, Germany, France, Switzerland, Poland, Romania, Norway, Svalbard, Finland, and the USA).

Microscopes: Knudsen used an Olympus AX70 microscope at 400 and 1000× with a connected DigiRetina 16 high resolution camera.

Borgen used an Olympus CH2 microscope with a trinocular tube at 10, 40, 60 and 100× with a periplane CWHK 10X/18L eyepiece and a connected Nikon Coolpix 4500 camera.

Elborne used a Euromex BioBlue 4253 Trinocular NeoLED microscope at 400 and 1000× with a connected CMEX 6.3 megapixel camera.

Photos: The work for this funga has been ongoing for over 45 years. During this period, cameras and photography have changed considerably. In the beginning, our photos were taken with traditional cameras using film like Kodachrome, Agfachrome and Fujichrome. As photography became digital, we used a Canon G7X camera or similar; and finally we started to use mobile phones, first with one lens and now with three lenses. The many years of different techniques, cameras, people, and field conditions have resulted in a heterogeneous mass of pictures. We obtained many good pictures in the field, but there were times when arctic conditions, mosquitoes, rain, storms, angry musk oxen, etc. resulted in suboptimal photos. For the same reasons, many of Borgen's photos were taken at his home in Paamiut after the daily excursion. Unless otherwise noted the photos were taken by the authors. Jens H. Petersen took photographs for the project in Greenland in 1983 and 1989, as did Thomas Læssøe in 1984. Erik Rald took photos in Narsarsuaq in 1992–1993, and Henrik Gøtzsche helped on our trip in 2017. Recently it has been possible to find good photos on the internet that are freely available. We have used these in some cases, crediting the photographer, noting the locality, and using "CC" as an abbreviation for creativecommons.org.

Field notes: For many collections we made notes on the fresh material in the field, especially on smell and taste, ecology, colour changes and similar ephemeral characters. Due to the constant travel to new localities, staying in tents, etc., it was rarely practical to make spore deposits, except when Borgen made them in Paamiut.

Drying of material: It was often impossible to dry the collections in the normal way, i.e. on sieves with an electrical heat source below, or on a warm radiator. Most collections were made in the field far away from electricity, so another system had to be invented, as follows: The collections were dried outside the tent in aluminium sieves over a kerosene lamp. Three sieves were laid on top of each other, and three aluminium curtain rods were fastened to the bottom sieve, forming a tripod. To keep the heat in, the system was surrounded by an oilcloth, and a plastic bag was attached to the top with clothes pegs. In case of rain, the plastic bag could be stretched out vertically by standing a small stick on top of the sieves, so the rain would run off. In case of wind, the system was stabilized by strings connecting the curtain rods to a stake pressed firmly into the ground.The lamp was filled with kerosene every night just before bedtime and the wick was lowered as much as possible. In this way, the kerosene lasted for almost eight hours (until the next morning), when new kerosene was added. When dry, the specimens were stowed away in newspaper packets. The packets were numbered according to our field books, and labelled with the genus or a form name, e.g. "corticioid". This facilitated sorting in the fungarium back home.

If we were not constrained by weight limits on the expedition, alcohol could be used instead of kerosene, but it burns much faster and will not last eight hours. An easier model for use on a smaller scale is a steel box, e.g. a biscuit box, with 8-hour candle lights on the bottom, 1-2 sieves fastened to the sides of the box away from the heat, and small holes in the lid so the heat can escape.

Maps: Distribution maps for each species were made using SimpleMappr (Shorthouse 2010). Coordinates were entered to one decimal place. A mm-sized dot on the map corresponds with ca. 67 km in nature, so in areas with many collections the dots merge. Each map was made automatically from coordinates taken from three main sources:

a) 1200 rusts from fungarium C, and 2000 smuts from C and the Denchevs' herbarium. These appear on the maps as green stars.

b) 12,300 records gathered from public databases. These appear on the maps as red circles. They were harvested from March 2024–June 2025, many from GBIF, and also from the databases at S, O, and the Finnish Museum of Natural History (Luomus) in Helsinki (H). Data from other sources were indirectly included by having been added to GBIF.

c) Published records from the literature (listed at the end of the volume). These appear on the maps as yellow squares. We expected to add many records from the literature, but most of them corresponded with museum specimens.

The number of records in GBIF is rapidly increasing and can be difficult to evaluate precisely. When a species has many thousands of records in GBIF, it indicates an area of distribution. It is not possible to check these data points individually, but we trust that the overall patterns are correct.

In recent years, other problems are surfacing. For example, environmental DNA studies of soil yield inventories of all the organisms present in a sample, without knowing the source of the DNA. Was a certain species actually growing in the soil, or could the DNA have come from vectors like wind, birds, man, or other animals? The results of such studies are less dependable, and we have therefore not used them.

It should be kept in mind that for older records, localities are rarely as precise as they are today. Places like “Finmark”, “Kamchatka”, or “Yukon” can denote a range of some hundreds of kilometres in diameter. Some databases account for this by indicating the range of uncertainty for the record in question. We have only used such imprecise localities in cases where no other records were nearby, or for rare species of limited distribution.

Records from areas outside arctic and alpine zones are not included on the maps, but may be briefly mentioned in the text in the “Distribution” section for each species, e.g., “temperate” or “boreal”.

Fig. 1. A view from the south side of Hassells Fjeld overlooking the airport at Kangerlussuaq. This is one of the driest places in Greenland and was therefore appropriate for building the long landing strip needed for international flights. The fjord receives meltwater from the Inland Ice.

Map of arctic and alpine localities visited by the editors from 1980–2023.

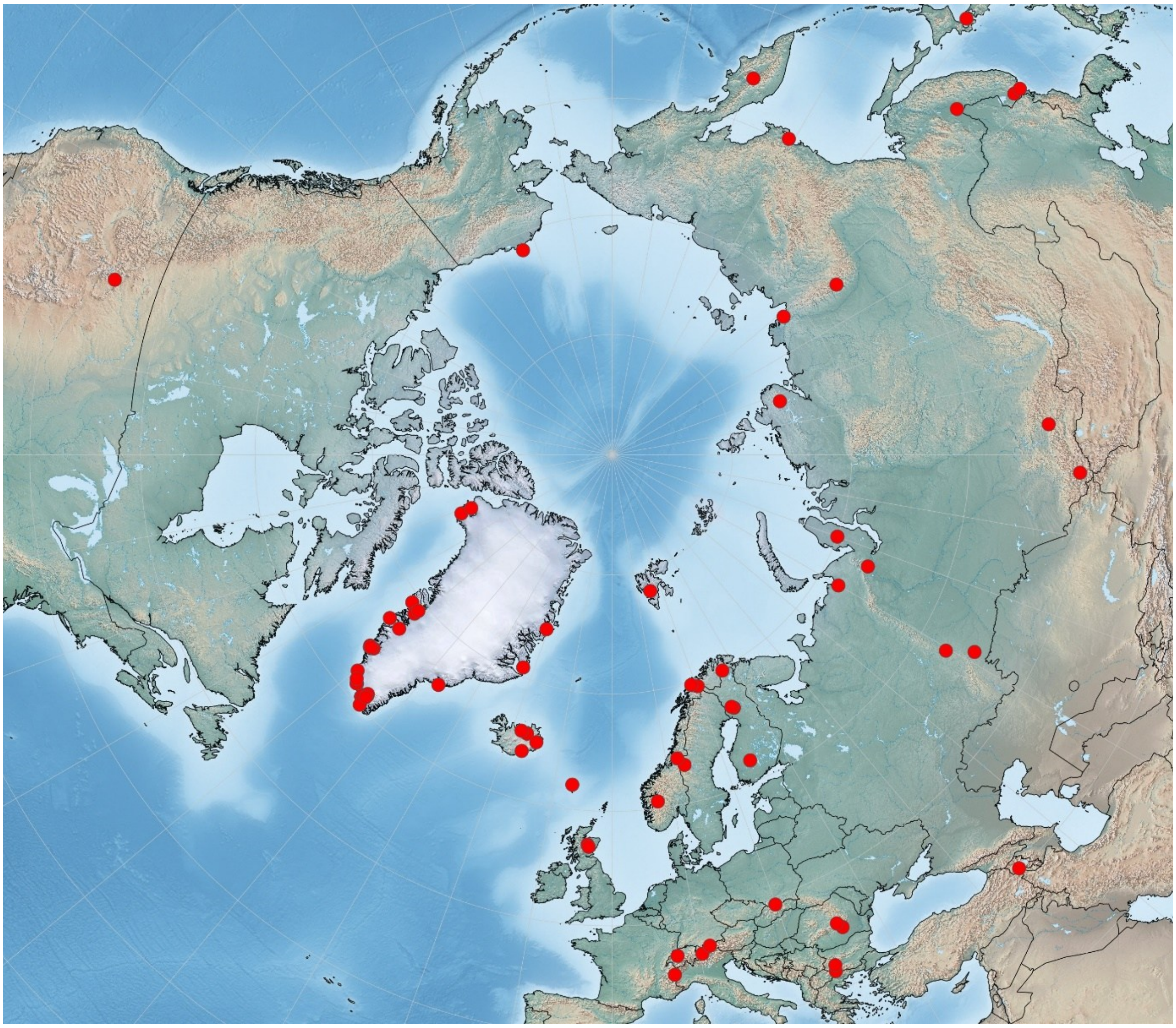


Fig. 2. Map of localities where one or more of the three editors have collected basidiomycetes during the last 45 years. Some localities were visited more than once, and Borgen was living in Paamiut (Frederikshåb) in southern Greenland from 1978 to 2000. Some of the localities were visited during the quadrennial symposia on Arcto-Alpine Mycology (ISAMs, see pp. 22-32). The first symposium was held in Alaska in 1980, and subsequent meetings were held in arctic and alpine regions in 1984, 1988, 1992, 1996, 2000, 2005, 2008, 2012 and 2016. The Nordic Mycological Congresses were initiated in Denmark in 1972 to focus on Scandinavia (Denmark, Norway, Sweden, Finland, and Iceland); these have been held every second year since, also including two visits to Scotland. Whenever these congresses took place in cold environments we used the opportunity to collect for this project. From his base in Paamiut, Borgen also had opportunities to visit other parts of Greenland. In 1989 Knudsen started a series of collecting trips to Siberia, to obtain material for comparison with other arctic areas, especially Greenland. Finally, each of us made separate journeys to other cold areas to give us a more complete knowledge of the arctic and alpine fungi.

Table 1. Collection sites where one or more of the authors have collected arctic-alpine fungi. We also visited a number of localities to establish criteria for including montane regions in our definition of "alpine". These included the Caucasus (Armenia), Sierra de Guaderrama (Spain), and eastern Tibet (China); places where no alpine fungi were collected.

Year	Country	Region	TB	SAE	HK
1978	Greenland	Paamiut	x		
1979	Greenland	Paamiut	x		
1980a	Greenland	Paamiut	x		
1980b	Alaska	Point Barrow, ISAM I			x
1981a	Greenland	Paamiut, Qaqortoq, Kangilinnguit, Narsarsuaq	x		
1981b	Greenland	Narsarsuaq, Narsaq, Johan Dahl Land		x	
1982a	Greenland	Paamiut, Kangilinnguit, Narsarsuaq	x		
1982b	Sweden	Jämtland, Välliste		x	x
1983a	Greenland	Narsarsuaq, Nanortalik, Paamiut	x		x
1983b	Scotland	Cairngorms, extra NMC		x	x
1984a	Greenland	Narsarsuaq, Nanortalik			x
1984b	Switzerland	Graubünden, Ftan, ISAM II			x
1984c	Greenland	Paamiut, Narsarsuaq, Kangilinnguit	x		
1984d	Iceland	Reykjavik, Skaftafel, Myvatn, Akureyri		x	
1985	Greenland	Paamiut, Narsarsuaq, Kangilinnguit	x		
1986	Greenland	Paamiut, Kangerlussuaq, Godhavn	x	x	
1987a	Greenland	Nuuk, Qooquut, Ugpik	x	x	x
1987b	Greenland	Paamiut	x		
1988a	Svalbard	Longyearbyen, Barentsburg, ISAM III	x		x
1988b	Greenland	Paamiut	x		
1988c	Greenland	Qaanaaq, Dundas		x	
1989	Greenland	Jamesonland		x	x
1990a	Russia	Siberia, Labytnangi, Yamal			x
1990b	Greenland	Paamiut	x		
1991a	Greenland	Narsarsuaq, Kangilinnguit, Ivigtuut, Paamiut	x		x
1991b	Scotland	Cairnwell, NMC extra		x	x
1992a	France	Alps, Lanslebourg, ISAM IV		x	x
1992b	Norway	Tromsø, Skibotn, NMC XI			x
1992c	Greenland	Paamiut, Igaliko, Narsarsuaq	x		
1992d	Russia	Yamal, More-ju			x
1993a	Greenland	Paamiut	x		
1993b	Iceland	Reykjavik, Hallormsstadir, extra NMC		x	x
1993c	Russia	Taimyr Peninsula			x
1993d	Faroe Islands	Streymoy [excluded]	x		
1994a	Russia	northern Ural Mts.			x
1994b	Greenland	Paamiut	x		
1995a	Greenland	Paamiut, Kangerlussuaq	x		
1995b	Russia	Magadan			x
1996	Russia	Siberia, Yamal Peninsula, ISAM V	x		x
1997a	Greenland	Paamiut, Sermiliarsuk	x		
1997b	Russia	Kamchatka			x
1998a	Greenland	Paamiut	x		
1998b	Russia	Khabarovsk			x
1999a	Russia	Yakutia, Tiksi			x
1999b	Greenland	Zackenberg	x		
1999c	Greenland	Paamiut	x		

Table 1, continued.

Year	**Country**	**Region**	**TB**	**SAE**	**HK**
2000a	Greenland	Kangerlussuaq, Sisimiut, ISAM VI	x	x	x
2000b	Russia	Irkutsk			x
2001	Russia	Altai			x
2002a	Poland	Tatra Mts.			x
2002b	Greenland	Paamiut, Narsarsuaq	x		
2002c	Greenland	Kangerlussuaq, Illulissat, Qasigiannguit		x	
2002d	Svalbard	Longyearbyen, IMC Oslo		x	
2002e	Russia	Chelyabinsk			x
2003a	Russia	Primorsk			x
2004a	Russia	Siberia, western Sayan Mts.			x
2005a	Russia	northern Ural Mts.			x
2005b	Norway	Finse, ISAM VII	x	x	
2005c	Finland	Hyytiälä, NMC XVII			x
2006a	Romania	Transsylvania, Brasov, Prahova			x
2006b	Greenland	Zackenberg, Daneborg	x		
2007					
2008a	USA	Montana, Rocky Mts., ISAM VIII		x	x
2008b	Greenland	Paamiut, Kuummiut, Nuuk	x		
2009a	Greenland	Kobbefjord, Nuuk	x		
2009b	Norway	Steinkjer, Mokk, NMC XIX		x	
2010					
2011					
2012	Finland	Kevo, Utsjoki, ISAM IX			x
2013	Finland	Pohtimolampi, Rovaniemi, NMC XXI			x
2014					
2015	Greenland	Narsarsuaq			x
2016a	Greenland	Kangerlussuaq, Sisimiut	x	x	x
2016b	Japan	Nagano, Mt. Hakudate, ISAM X			x
2017a	Greenland	Jameson Land	x	x	x
2017b	Iceland	Akureyri	x	x	x
2018	Greenland	Narsarsuaq, Kangilinnguit, Nuuk, Kangerlussuaq	x	x	x
2019a	Russia	Altai, Ukok		x	x
2019b	Greenland	Paamiut, Narsarsuaq	x		
2020	Bulgaria	Rila Mts., Pirin Mts.		x	x
2021	Germany-Austria	Alps		x	x
2022					
2023	Sweden	Åre, Jämtland			x

2. Exploration of arctic and alpine fungi before 1980

Arctic regions

At the end of the 19th century, many exploring expeditions were sent to the Polar Regions. The international rush to be the first to reach the North Pole also included exploration of the polar habitat: its land, geology, plants, animals, etc. The fungi were not a specific focus, but were traditionally included as a part of the plants. The well-known difficulty of preserving large fleshy fungi far away from a permanent heat source resulted in a meagre yield from the early expeditions. If they were collected at all, fleshy mushrooms were put in alcohol, thereby preserving their morphology but dissolving their colours. Among the larger fungi, only puffballs and polypores were collected with good results. The majority of the collections were thus what are known as "black dots", microscopic fungi occurring on dead stems of herbs, and on living plants attacked by rusts and smuts.

Early Arctic explorers had detailed instructions on how and what to collect. For example, professor Eugen Warming of the Botanical Garden in Copenhagen wrote in his instructions to Christian Kruuse on the Amdrup Expedition to the East Coast of Greenland from 1898–1899 regarding the collection of fungi (Kruuse 1904): "Gathering of fungi. All dry, black spotted portions of plants; all leaves lying loose on the ground; and the dung of reindeer, hares and other animals, may be expected to have fungi growing on or in them. All living plants the colour of which is not natural must be gathered."

These instructions would result in many fungus specimens, and were no doubt inspired by the success of the Danish mycologist Emil Rostrup in describing Greenlandic fungi through the study of vascular plant specimens in the Copenhagen Botanical Museum. Rostrup placed each sheet under a binocular microscope, excised small dark dots, rusts, and smuts, and studied them under the light microscope. In this way, without ever having been to Greenland, he managed to register 629 species of fungi (Rostrup 1888, 1891, 1894, 1904). Naturally, most of the harvest was pyrenomycetes and other microfungi; only 148 were basidiomycetes. Warming's mention of dung colonized by fungi was in clear reference to the work of Emil Christian Hansen of the Carlsberg Laboratory, who was granted a Gold Medal from the University of Copenhagen based on his study of Danish dung fungi (Hansen 1876) before he started working on the purification of yeast in beer.

The first reported Arctic fungi may have been those recorded from Lapland by the Norwegian botanist Søren Christian Sommerfelt (1826). Lindblom (1841) later reported a few species from Svalbard. Læstadius (1860) described the beautiful wax-cap *Hygrocybe lilacina* and other species from Torne Lappmark, Sweden. Petter Adolf Karsten treated the fungi of eastern Lappmark in 1866 (Karsten 1882) and those of Svalbard in 1872. The Englishman Robert Brown collected fungi on the large Greenlandic island Disko and published them in "Florula Discoana" (Brown 1868). Leopold Fuckel participated in "The second German expedition to the North Pole", where he collected various specimens including fungi (Fuckel 1874, Bonorden 1874). Berkeley (1880) studied the fungi from the British Arctic expedition of 1875–1876.

Rostrup (1883) started his interest in cold region fungi with a trip to northern Sweden in 1882. This was followed by the Swede Carl Johan Johanson (1885), who studied the fungi of Iceland (at that time a Danish colony), and those of Finmarken (Johanson 1886). Gustaf Lagerheim (1884) explored Luleå Lappmark (Sweden). Lars Romell visited the famous scientific station in Abisko in 1911 and 1912, describing several new species, especially of polypores (Romell 1912). Torne Lappmark was also visited by Tore Fries (1914).

Allescher & Hennings (1897) treated the fungi from Drygalski's expedition to Umanak in northwestern Greenland, but still the number of fungi known from Arctic regions was very low at the turn of the century. Ferdinandsen & Winge (1908) reported eight species from northeast Greenland. The Norwegian botanist and mycologist Axel Blytt thoroughly explored many regions of Norway, and he was evidently the first to separate the funga into four climatic groups: 1) species occurring in the conifer belt, 2) species reaching the birch zone, 3) species reaching the willow zone and 4) species living in the lichen (alpine) zone. He did not record many species, but he had a good understanding of the different zones (Blytt & Rostrup 1905).

Fewer expeditions were made after the first rush to explore unknown places and their possibly unknown fungi, perhaps due to discouraging results from the pioneers. In the New World, Saccardo et al. (1904) investigated the fungi from Harriman's Alaskan expedition, and Arthur (1929) investigated the rusts of Alaska and Yukon. Dearness (1923) reported the results of the Canadian Arctic Expedition of 1913–1918, and Cash (1953) made a checklist of Alaskan fungi.

After the first Arctic explorations, before ISAM

In the Old World, Ivar Jørstad made fine studies of the Norwegian rusts, first in Trøndelagen, southern Norway (1921) and Novaya Zemlja (1923), and later in Kamchatka (1934). Dobbs (1942) continued with Novaya Zemlja; Tranzschel (1891) covered northern Russia (Archangelsk, Valogda); Lavrov (1926) searched Central Siberia along the lower course of the Yenisei; and Murashkinskiy & Ziling (1928) visited Altai and the Sayan Mountains. Kawai and Otani (1931) searched for fungi on Sakhalin, and Sydow & Sydow (1913) continued in northern Japan.

The efforts by Rostrup in Greenland were continued by the Danish pharmacist J. Lind with a number of papers from arctic areas (Lind 1917, 1924, 1927a, b, 1929, 1933), finishing his studies with the first paper with comparative studies of microfungi from different Arctic areas (Lind 1934). He gathered the literature, compared all the species, and made an overview of the microfungi in Arctic regions. He found 422 species, of which only 45 or ca. 10% were basidiomycetes (rusts and smuts).

Larsen (1932) reviewed the historical literature on Icelandic fungi from O. F. Müller (1770) to Rostrup (1903), then added his own studies so that 543 species were included. Later, Christiansen (1941) added more fleshy fungi, and after World War II Lange (1949) added more species for comparison with his Greenlandic studies. Jørstad worked with rusts from northern regions, including Iceland (Jørstad 1952a, 1963). In 1962 the Icelandic mycologist Helgi Hallgrimsson published for the first time, with several subsequent papers up to 2006, when he published a checklist of Icelandic basidiomycetes (Hallgrimsson & Eyjólfsdóttir 2006). Special groups were treated by Hallgrimsson & Hauerslev (1985, lignicolous fungi) and Gøtzsche (1984, myxomycetes).

In Finland the dominant mycologist was Petter Adolf Karsten, who wrote many books and described ca. 2000 new species, including records from Svalbard (Karsten 1872), Finnish Lapland, St. Petersburg, the Kola Peninsula, Transbaikal, and other cold places. More recently, Paavo Kallio worked on Arctic boletes (unfinished), and on papers with Esteri Kankainen (Kallio & Kankainen 1964, 1966). Esteri Ohenoja made lists of Svalbard fungi (Ohenoja 1971), of fungi from the vicinity of Kuusamo in northern Finland (Ohenoja 1979), and of larger fungi from Finnish Lapland (Ohenoja 1996). She was active in organising congresses in cold Finnish places like Kevo (in 1965, 1970 and 1995), Utsjoki (in 2012) and Rovaniemi (in 2013). She also made a list of fungi from the surroundings of Hudson Bay, Canada (Ohenoja & Ohenoja 2010) including Rankin Inlet (Ohenoja 1972).

After the interruption of World War II, expeditions slowly began again. In the summer of 1946 the Danish mycologist Morten Lange joined a Danish expedition to Kangerlussuaq (Søndre Strømfjord), an air base constructed by the Americans and situated in the deepest fjord in western Greenland. The dry continental climate in the area limits its snowfall, making it easier to keep the airstrips clear (Fig. 1). Lange collected ca. 230 species of basidiomycetes in the valley and surrounding localities like Ivigttuut (Lange 1948b, 1955, 1957).

In 1948 two papers both pointed toward the future study of arctic-alpine fungi: the Swiss mycologist Jules Favre (1948) issued his work on the fungal societies of raised bogs in the Jura Mountains, and simultaneously Lange (1948b) issued the first of three parts of his study of the macromycetes of Greenland. Coincidentally, Favre (1955) continued with the higher fungi from the Swiss National Park at the same time that Lange (1955) published the second part of his work on Greenlandic Agaricales. The near-simultaneous publication of these two works meant that neither had the opportunity to consider the conclusions of the other. Together, they constitute the modern beginning of arctic-alpine mycology. Lange (1957) subsequently finished his Greenlandic treatment, including the remaining larger fungi, along with comments on ecology and plant geography. Favre (1960) also continued his studies with his impressive and beautiful catalogue of the subalpine higher fungi, which was issued after his death. Lange and Favre once met in Geneva, and although the two men must have had a lot to discuss, Lange regrettably did not speak French, whereas Favre only spoke French! (Lange 1996).

In 1954 the Czech mycologist Albert Pilát and the Swedish mycologist John Axel Nannfeldt went to Abisko in northern Sweden (Pilát & Nannfeldt 1955), also concurrent with the early studies of Lange and Favre, and of Doug Savile in Canada (Savile 1954). The Norwegian mycologist Asbjørn Hagen (1941, 1950) made studies of rusts and smuts from Svalbard, followed by the Polish mycologist Alina Skirgiello, who visited Svalbard in 1958 (Skirgiello 1961, 1968). Morten Lange and the Norwegian mycologist Gro Gulden studied the fungi of Jotunheimen in Norway (Gulden & Lange 1971). Gulden continued with studies of *Lepista* (Gulden 1983) and *Mycena* (Gulden & Jenssen 1982), with monographs of different alpine groups from Norway (Gulden et al. 1985b, 1988), with monographs of *Galerina* from various arctic-alpine places (Gulden 1987, 1988, Gulden & Vesterholt 1999, Gulden & Hallgrimsson 2000), including DNA studies (Gulden et al. 2001, 2005), with a broader treatment of the basidiomycete funga of Svalbard (Gulden & Torkelsen 1996), and a contribution to an agaric flora of Svalbard (Gulden 1996b). In the second ISAM report (Laursen et al. 1987a), more studies from Svalbard were published, e.g. Huhtinen (1987a). Jalink & Nauta (1989) added agarics from Edgeøya, as did Ohenoja (1971). Väre et al. (1992) looked for mycorrhiza in this very northern locality. Elvebakk and Prestrud (1996) included two chapters on Svalbard fungi in their Catalogue, i.e. Gulden and Torkelsen (1996) on macrofungi, and Elvebakk et al. (1996) on microfungi, including rusts and smuts.

Milan Petersen was inspired by Lange, and was especially interested in the ecology of Arctic fungi. He stayed at the Arctic Station in Godhavn (Disko, Greenland) for three years to study the fungi growing in burned places in the Arctic (Petersen 1975), and the general ecology and phenology of basidiomycetes (Petersen 1977).

The Japanese mycologist Yoshio Kobayasi was fascinated by the small fungi found in cold areas and recorded the results of his expedition to the Alaskan Arctic (Kobayasi et al. 1967). He and his colleagues later continued to Greenland (Ammassalik) and focused mostly on ascomycetes and lower fungi (Kobayasi et al. 1971). Kobayasi participated in the first ISAM meeting in 1980 in Barrow, Alaska, which formed the basis for international cooperation between arctic-alpine mycologists (see below).

In eastern North America, early papers addressed the rusts of Nova Scotia (Fraser 1913), and the broader funga of Nova Scotia (Wehmeyer 1935). Bigelow (1959) studied some tricholomataceous fungi from northern Canada, and Miller (1968, 1969) and Miller & Gilbertson (1969) published on the polypores of Alaska. Miller et al. (1973) worked on arctic and alpine agarics from Alaska and Canada, and Grund and Stuntz (1968, 1980, 1983) covered *Inocybe* for Nova Scotia. Linder (1947) covered the fungi of eastern Arctic Canada.

With huge arctic, subarctic, alpine and subalpine regions inside its borders, the cold areas of Russia have been investigated by many mycologists. A comprehensive list of literature is given in Karatygin et al. (1999). Tranzschel (1914) explored Kamchatka, Lebedjeva (1924) described new fungi from polar Siberia, and later gave an overview of fungi from arctic Siberia (Lebedjeva 1928). Katenin (1964) made a paper on mycorrhiza of Arctic plants. Vasilkov (1966, 1967, 1969, 1970a, 1970b, 1971, 1974, 1975, 1978) made numerous papers on agarics and *Leccinum* from northern Siberia. Karatygin contributed with papers on rusts and smuts (1982-1999). Stepanova and Tomilin (1975-1981) worked on the tundra of the Taimyr Peninsula. Nezdoiminogo (1982, 1993), made monographs of *Galerina* and *Cortinarius* from the Russian Far East including its Arctic parts. Viktor Mukhin worked on the structure of the wood-decaying fungi in the subarctic transition between forest steppe and tundra (Mukhin 1978, 1991, 1993), and he arranged ISAM V on the Yamal Peninsula in 2004. Nadya Matveyeva edited a large catalogue of the biodiversity of polar deserts in northernmost Canada, Greenland, Svalbard, Novaya Zemlya, October Revolution Island and Georgs Island (Matveyeva et al. 2015).

Alpine regions

The history of the exploration of fungi in the Alps is complex. Many mycologists live in the Alps or at least nearby, such that collecting trips have hardly been seen as expeditions, but rather as exploration of the immediate surroundings, without special emphasis on altitude. Exploration of the Alps thus generally included long investigations over time, hiking up and down from some suitable resting place to study the fungi.

One of the early explorers was the German mycologist Max Britzelmayr, who explored the Northern Limestone Alps (Kalkalpen) in Germany. He published his findings in 15 issues of Bericht des Naturhistorischen Vereins in Augsburg from 1879 to 1897 (390 pp.). The diagnoses were later issued again in Botanisches Centralblatt (Britzelmayr 1898a, b, 1899a, b), and the whole work was summarized in tabular form by von Höhnel (1906). Britzelmayr described many new species, although not many of these are recognized in modern mycology.

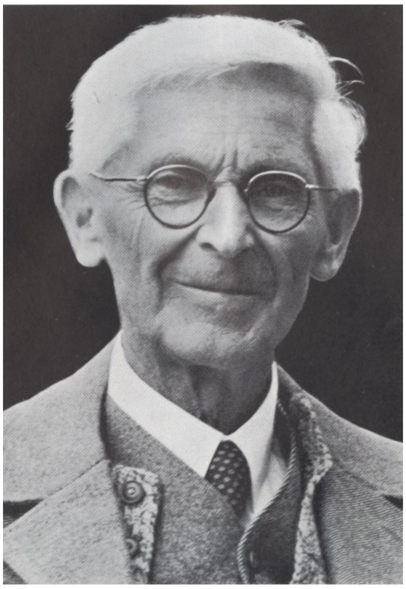
At the same time, Boudier (1895) described new fungi from Valais in the French Alps. Otto Jaap (1907) published Beiträge der Pilzflora der Schweiz. Certainly there have been numerous other small explorations of the Alps, but they have not necessarily been reported. One of the first people to make a larger study was the French mycologist Roger Heim, who published from 1922-1947. He was followed by Jules Favre, whose classic drawings and descriptions are still valuable in dealing with high mountain fungi (Favre 1948, 1955, 1960). Favre’s work was based on 66 excursions to the Alps over more than 30 years. In Germany, Schäffer (1947) made observations on the agarics from Ober-Bayern (1947), and Eisfelder (1962) described the fungi from the Pitztal in Tyrol, Austria. Finally, the French mycologist Robert Kühner started a series of very detailed descriptions of a number of genera from the Alps (Kühner 1972a, b, c, 1974, 1975a, b, 1976a, b, 1977a, b, c, 1978, 1981, 1983), also in collaboration with Denise Lamoure (Kühner & Lamoure 1965, 1970, 1971, 1972; Lamoure 1969a, 1971, 1974a, b, 1975, 1977, 1978, 1982a), and culminating with a catalogue of fungi from Vanoise (Kühner & Lamoure 1986). Lamoure was also president of ISAM IV in Lanslebourg in 1992.

The Swiss mycologist Egon Horak (1962) made another type of study focused on the interactions of mushroom societies; he was followed by Senn-Irlet (1987a). Horak was also president of ISAM II in Ftan. The same basic idea was behind the work of Schmid-Heckel (1985), who made a study of the fungi from the northern Kalkalpen in Germany with a distinct ecological angle, incorporating altitude as an ecological factor as well as temperature and rain, and including all groups of basidiomycetes. In the Italian Alps, Jamoni & Bon (1991, 1992, 1993, 1995) made four books on the fungi of the massif of Monte Rosa.

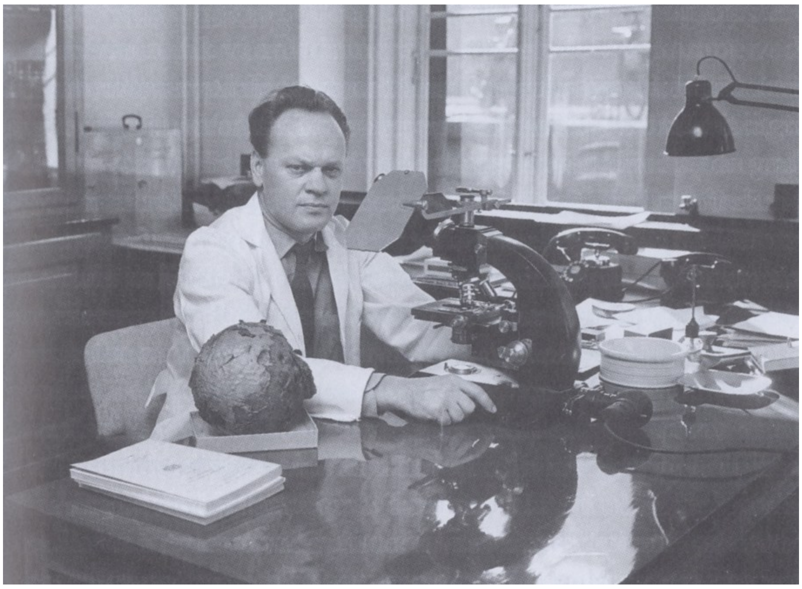
Beyond the Alps, the Tatra Mountains in Poland were investigated by Wojewoda et al. (1985), and more recently by Anna Ronikier at the alpine-subalpine level (Ronikier 2008). Bon & Ballarà (1995, 1996, 1997) made a series of papers on basidiomycetes of the Pyrenees. The Norwegian mycologists Gro Gulden, Kolbjørn Mohn Jenssen, Jens Stordal, and the Swiss mycologist Beatrice Senn-Irlet started a series of monographs on arctic and alpine fungi (Gulden et al. 1985b, 1988; Senn-Irlet et al. 1990). Hallgrimsson & Eyjólfsdóttir (2006) made a checklist of Icelandic basidiomycetes, and Sigurdsson (2015) followed with a handbook of the most common species in Iceland. Borgen (1993) made a handbook of 64 species from Greenland (in Danish and Greenlandic) and Armada et al. (2023) recently described more than 100 species from the Alps.

Apart from these books and papers on arctic and alpine regions, many works have dealt with the fungi of borderline arctic, subarctic, and boreal regions. Studies focused on these areas are outside of our scope, but they form a transition to the fungal literature for warmer regions. Some examples are Strid (1975), who studied the fungi of *Alnus incana* forests between 64°N and 66°N in North-Central Scandinavia, Dennis (1972, 1980a, b, 1986) and Watling (1983a, b), who worked in the Scottish Isles, and Ronikier (2008), who studied the fungi of the subalpine Tatra Mountains.

These works are among the most important, but many others exist (see Literature, p. 259). Along with the initiative of Gary Laursen and Joe Ammirati in creating the ISAM meetings (1980–2016), they form the basis for contemporary arctic-alpine mycology. This funga, which will cover ca. 1400 basidiomycetes in the following six volumes, would not be possible without the previous work of all these mycologists.



Jules Favre (1882–1959)



M. Lange (1919–2003), as newly appointed professor in 1957.

3. The International Symposia on Arcto-Alpine Mycology (ISAM): Exploration of arctic and alpine fungi 1980–2025

Progress in arctic and alpine mycology, combined with general concern about global warming and melting of the ice, has gradually led to more research focused on organismal life in these areas, including the fungi. As discussed below in "The World Wide Web of Willows" (chapter 9c), willows predominate in all Arctic regions, and their general preference for moist habitats drew focus to the amount of ice, drought and other climatic changes. It should be remembered that the Symposia were not limited to research on basidiomycetes but to all fungi, but this work is focused on basidiomycetes.

In 1980 Gary Laursen and Joe Ammirati received permission to invite a group of 20 mycologists working on cold-area fungi to the Office of Naval Research and its Naval Arctic Research Laboratory in Barrow, Alaska. Since that time, symposia were held every fourth year and a report/book was issued following ISAMs I, II, III/IV, V, VI, VII, VIII, and X. For a summary of ISAMs I-VII, see also Gulden & Høiland (2008).

Photos from the 10 ISAMs are shown on the next pages, followed by photos from collecting trips to Arctic and alpine localities in Siberia, Iceland, Norway, Sweden and Finland.

Fig. 3. View of Constable Pynt, Jameson Land, central East Greenland. The airstrip and station can be seen in the middle of the image on the right-hand side. Across the fjord and 30 km to the right (south) lies the small settlement of Ittoqqortoormiit (Scoresbysund), one of the few places in Greenland that issues licenses to kill polar bears, which come up the fjord on ice floes.

ISAM I – Point Barrow, Alaska, 16–23 August 1980.
Volume Editors: G. A. Laursen & J. F. Ammirati (1982).

Participants: Back row: J. Ammirati (USA), H. Knudsen (Denmark), A. Linkins (USA), H. Dissing (Denmark), P. M. Petersen (Denmark), M. Lange (Denmark), R. Korf (USA), G. Gulden (Norway), Y. Kobayasi (Japan), O. Miller (USA), S. Sivertsen (Norway), N. Fries (Sweden), M. Moser (Austria), P. Kallio (Finland), D. Savile (Canada), E. Horak (Switzerland). Front row: G. Laursen (President, USA), G. E. Hall (USA), H. Heikkilä (Finland), B. Lange (Denmark), D. Lamoure (France), E. Ohenoja (Finland), B. Rosey (USA), B. Kelley (USA).

Inspecting a permafrost boulder at ISAM I in Barrow, Alaska, 1980. Some of the participants (from left) are H. Dissing, R. P. Korf, P. M. Petersen (hidden by the yellow oilskin), P. Kallio, B. Lange (red jacket), M. Lange, and D. Lamoure.

ISAM II – Ftan, Unter Engadin, Switzerland, 26 August–2 Sept. 1984.
Volume Editors: G. A. Laursen, J. F. Ammirati and S. A. Redhead (1987).

Participants: Back row: Y. Kobayasi (Japan), L. Holm (Sweden), S. Huhtinen (Finland), M. Lange (Denmark), J. Debaud (France), O. Petrini (Switzerland), G. Laursen (USA), E. Horak (president, Switzerland), O. Miller (USA), E. Müller (Switzerland), H. Knudsen (Denmark), M. Moser (Austria), S. Redhead (Canada), H. Dissing (Denmark), R. Watling (Scotland), S. Sivertsen (Norway), P. Döbbeler (Germany). Middle row: B. Senn-Irlet (Switzerland), K. Holm (Sweden), H. Miller (USA), G. Gulden (Norway), K. Metsänheimo (Finland), D. Lamoure (France), E. Watling (Scotland), J. Magnuson (USA). Front row: A. Leuchtmann (Switzerland), T. Schumacher (Norway), I. Brunner (Switzerland).

Egon Horak, president of ISAM II, with Gro Gulden.

ISAM III – Longyearbyen, Svalbard, 10–19 August 1988.

Volume Editors: O. Petrini & G. A. Laursen (1993).

Participants in the midnight sun: O. Skifte (Norway), B. Senn-Irlet (Switzerland), K. Bendiksen (Norway), L. Holm (Sweden), E. Bendiksen (Norway), M. Moser (Austria), H. Dissing (Denmark), H. Knudsen (Denmark), A.-E. Torkelsen (Norway), M. Lange (Denmark), K. M. Jenssen (Norway), T. Borgen (Greenland/Denmark), S. Sivertsen (president, Norway), N. Lundqvist (Sweden), E. Ohenoja (Finland), C. Currah (Canada), M. Nauta (The Netherlands), S. Huhtinen (Finland), G. Gulden (Norway). Missing: K. Holm (Sweden), L. Jalink (The Netherlands), D. Lamoure (France), V. Mukhin (Russia), T. Schumacher (Norway).

Marijke Nauta, Leo Jalink and Beatrice Senn-Irlet. Nauta & Jalink collected independently on Edgeøya, the second largest island in Svalbard.

ISAM IV – Parc National de la Vanoise, Lanslebourg, France, 24 August–4 September 1992.

Volume Editors: O. Petrini & G. A. Laursen (1993).

Participants: E. Ohenoja (Finland), D. Lamoure (president, France), G. Durrieu (France), E. Horak (Switzerland), M. K. Adhikari (Nepal), unidentified participant, M. Moser (Austria), E. Bendiksen (Norway), R. Courtecuisse (France), A. Raitviir (Estonia), K. Kalamees (Estonia), H. Dissing (Denmark), V. Mukhin (Russia), S. Huhtinen (Finland), O. Tarchevskaja (Russia), O. Miller (USA), H. Miller (USA), T. Schumacher (Norway). Seated: L. Jalink (The Netherlands), M. Nauta (The Netherlands), G. Gulden (Norway).
Missing: S. Elborne (Denmark), H. Knudsen (Denmark), B. Senn-Irlet (Switzerland).

Esteri Ohenoja and Kuulo Kalamees working with the day's harvest. On the left, Ain Raiitvir is studying Helotiales. They all participated in ISAM IV, but the photo is from ISAM VI.

ISAM V – Labytnangi, Russia, 15–27 August 1996.
Volume Editors: V. A. Mukhin & H. Knudsen (1998).

Participants: N. V. Kolesnikova (Russia), O. Skifte (Norway), A. Chlebicki (Poland), B. Chlebicki (Poland), E. Ohenoja (Finland), unidentified participant, A.-L. Ruotsalainen (Finland), A. Y. Ivanova (Russia), O. Nikolayeva (Russia), I. V. Karatygin (Russia), O. Y. Marfenina (Russia), M. Dyakov (Russia), S. P. Arefyev (Russia), V. Mazepa (Russia), unidentified participant, N. V. Psurtseva (Russia), Y. Fomina (Russia), O. Lazareva (Russia), Y. K. Novozhilov (Russia), U. Peintner (Austria), O. Morozova (Russia), Y. Romanova (Russia), A. Y. Kovalenko (Russia), V. M. Shishmaryov (Russia), H. Knudsen (Denmark), M. Lange (Denmark), T. Borgen (Greenland/Denmark), B. Lange (Denmark), S. G. Shitayov (Russia), V. G. Shtro (Russia). Seated: V. Mukhin (president, Russia), I. Goldberg (Russia).

Victor Mukhin (Yekaterinburg, Russia), president of ISAM V, has led many expeditions to arctic and alpine Russia.

I.V. Karatygin et al. made a catalogue of species and literature from the Russian Arctic.

ISAM VI – Kangerlussuaq & Sisimiut, Greenland, 12–21 August 2000.
Volume Editors: D. Boertmann & H. Knudsen (2006).

Participants: Back row: A. Raitviir (Estonia), E. Ohenoja (Finland), T. Borgen (president, Denmark), P.-A. Moreau (France), A. Jumpponen (USA), R. Petersen (USA), G. Gulden (Norway), E. Horak (Switzerland), M. Sasa (Denmark), V. Mukhin (Russia), T. Hoshino (Japan), M. Moser (Austria), K. Kalamees (Estonia), C. Cripps (USA), R. Senn-Irlet (Switzerland).
Seated: S. Elborne (Denmark), K. Hughes (USA), A.-M. Larsen (Greenland/Denmark), J. Trappe (USA), L. Jalink (The Netherlands), M. Nauta (The Netherlands), B. Senn-Irlet (Switzerland).

Torbjørn Borgen, president of ISAM VI.

P.-A. Moreau and T. Borgen discussing a waxcap.

ISAM VII – Finse, Norway, 9–15 August 2005.

Volume Editors: K. Høiland & R. H. Økland (2008).

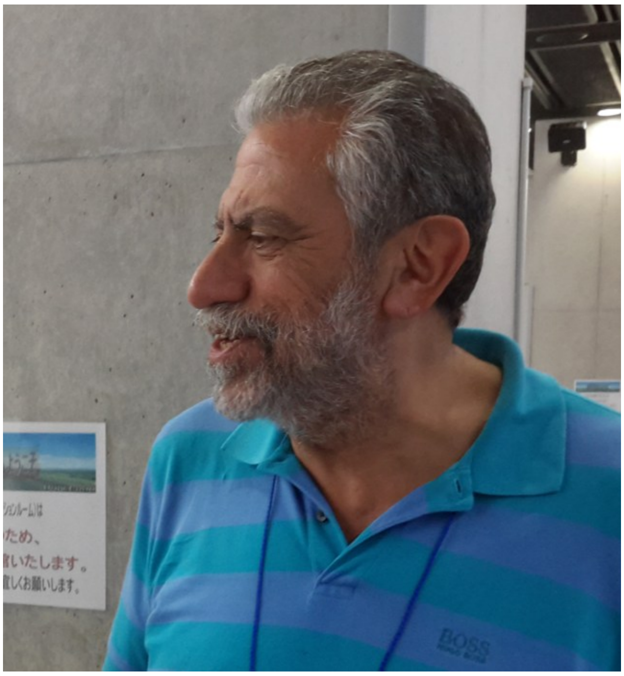
Participants: Back row: G. Corriol (France), K. Kalamees (Estonia), G. Gulden (president, Norway), G. Flatabø (Norway), K. Bendiksen (Norway), K. Høiland (Norway), Ø. Stensrud (Norway), A.-E. Torkelsen (Norway), A. Raitviir (Estonia), M. Nauta (The Netherlands), E. Ohenoja (Finland), T. Hoshino (Japan). Front row: P.-A. Moreau (France), S. Elborne (Denmark), A. Ronikier (Poland), E. Larsson (Sweden), U. Peintner (Austria), C. Cripps (USA), T. Borgen (Denmark), L. Jalink (The Netherlands).

Finse Center

ISAM VIII – Beartooth Plateau, Rocky Mts., USA, 3–10 August 2008.
Volume Editors: C. L. Cripps & J. F. Ammirati

Participants: Back row: R. Antibus (USA), A. Horak (Switzerland), E. Horak (Switzerland), H. Beker (Belgium), H. Knudsen (Denmark), C. Cripps (president, USA), T. Kasuya (Japan), M. Sasa (Denmark), M. Ronikier (Poland). Kneeling: A. Ruotsalainen (Finland), E. Larsson (Sweden); M. Nauta (The Netherlands); E. Ohenoja (Finland), A. Ronikier (Poland), P.-A. Moreau (France). Reclining: L. Jalink (The Netherlands), S. Elborne (Denmark). Photo: D. Bachman.

Cathy Cripps, president of ISAM VIII.



Henry Beker monographed *Hebeloma* for Europe (see Literature).

ISAM IX – Kevo, Utsjoki, Finland, 26 August–1 September 2012.

Conveners: E. Ohenoja & A. L. Ruotsalainen.

Participants: Back row: J. Vauras (Finland), unknown participant, C. Cripps (USA), H. Knudsen (Denmark), T. Borgen (Denmark). Middle row: D. Cripps (USA), M. Ronikier (Poland), E. Larsson (Sweden), E. Ohenoja (president, Finland), M. Sasa (Denmark), Y. Yajima (Japan), unknown participant. Front row: A. Ronikier and child (Poland), A.-L. Ruotsalainen (Finland), T. Hoshino (Japan).

Esteri Ohenoja, president of ISAM VIII.

Anna Ronikier formerly worked on subalpine fungi, and now studies myxomycetes.

ISAM X –Mt. Hakusan and Sugadaira, Kanazawa, Japan, 29 August–4 September 2016.

Convener: T. Hoshino; Volume Editor: T. Hattori (2018).

Unfortunately, a typhoon was expected on the day of the excursion to Mt. Hakusan, so the area was closed and collecting took place in subalpine areas near Mt. Hakusan in Ishikawa Prefecture.

Participants: Y. Degawa (Japan), H. Masumoto (Japan), M. Yamada (Japan), T. Sato (Japan), V. Mukhin (Russia), T. Hoshino (president, Japan), E. Ohenoja (Finland), A. Nikolaevich (Russia), T. Borgen (Denmark).
Missing: H. Knudsen (Denmark), U. Peintner (Switzerland), H. Beker (Belgium), T. Hosoya (Japan), Y. Shimono (Japan), T. Kasuya (Japan). ISAM X had 32 participants from six countries.

Tamotsu Hoshino, president, ISAM X.

Taiga Kasuya and Tamotsu Hoshino in Kanazawa.

Gilles Corriol (France) at ISAM VII. He works in the Pyrenees and made a list of the fungi in 2008.

Jukka Vauras and Ellen Larsson working on *Inocybe* sensu lato at ISAM IX.

Mycologists from five countries studying *Cuphophyllus cinerella* (vol. 5) at ISAM VII in Finse.

Jim Trappe (USA) and Henning Knudsen (Denmark) discussing truffles in front of the Greenland Inland Ice. Four species of truffles are presently known from Greenland and Svalbard: *Alpova*, *Hymenogaster*, *Rhizopogon*, and *Elaphomyces*.

Pierre-Arthur Moreau (France) at ISAM VII. His book on alpine fungi (Armada et al. 2023) includes more than 100 species.

Phlegmacium-master Meinhard Moser (Austria) seeing *P. alnobetula* for the first time. This fungus is restricted to *Alnus alnobetula* (here subsp. *fruticosa*). We have recorded it from Altai, the Alps, and Bulgaria.

N. Ushakova (Russia), V. Mukhin (Russia), the boat captain, H. Knudsen (Denmark), and M. Moser (Austria) resting at Lake Teletskoye in Altai, Russia.

Ursula Peintner (Austria) and Viktor Mukhin (president, Russia) in front of the station in Labytnangi (northern Ural Mountains) during ISAM V.

H. Knudsen (Denmark), K. Hughes (USA), and R. Peterson (USA) looking for *Collybia cirrata.*

More-ju (northern Siberia) during the Nordic-Russian joint mycological expedition across Siberia in 1992. The helicopter had just dropped us off in the middle of nowhere, and the crew in the center are waiting for a cup of tea before they return to their base in Labytnangi. We are prepared for three days' collecting at the subarctic border between the taiga and the tundra. Before the tea was ready, the heat from the fire melted the top 10-15 cm of permafrost, and we started to sway on the ground.

H. Gøtzsche (Denmark, myxomycetes), H. Kotiranta (Finland, polypores), H. Knudsen (Denmark, arctic basidiomycetes), and V. Mukhin (expedition leader, Russia, polypores) studying the map at More-ju in 1992. Several others are missing from the photo, out searching for mushrooms.

Torbjørn Borgen (Denmark) and Ursula Peintner (Austria) on a mountaintop in the northern Urals at ISAM V, protected by *Alnus alnobetula* subsp. *fruticosa*.

R. Peterson (USA), K. Kalamees (Estonia), M. Sasa (Denmark), K. Hughes (USA), M. Nauta (The Netherlands), T. Hoshino (Japan, pointing), hidden participant, C. Cripps (USA, red shoulder), G. Gulden (Norway), L. Jalink (The Netherlands), J. Trappe (USA), V. Mukhin (Russia), H. Knudsen (Denmark), B. Senn-Irlet (Switzerland), hidden participant, and R. Senn-Irlet (Switzerland) in front of the Inland Ice at the bottom of Kangerlussuaq Fjord, central West Greenland.

Nuuk-Basic or Kobbefjord Research Station (64°07'N, 51°21'W) is a field station for Arctic studies built by the Aage V. Jensen Foundation and run by the Greenland Institute of Natural Resources at the bottom of Kobbefjord near the capital, Nuuk (Godthåb). We collected here for three days.

Yosio Kobayasi (1907–1993), an arctic pioneer.

P. Milan Petersen worked on the ecology of arctic mushroom societies.

Gro Gulden, president of ISAM VII in Finse.

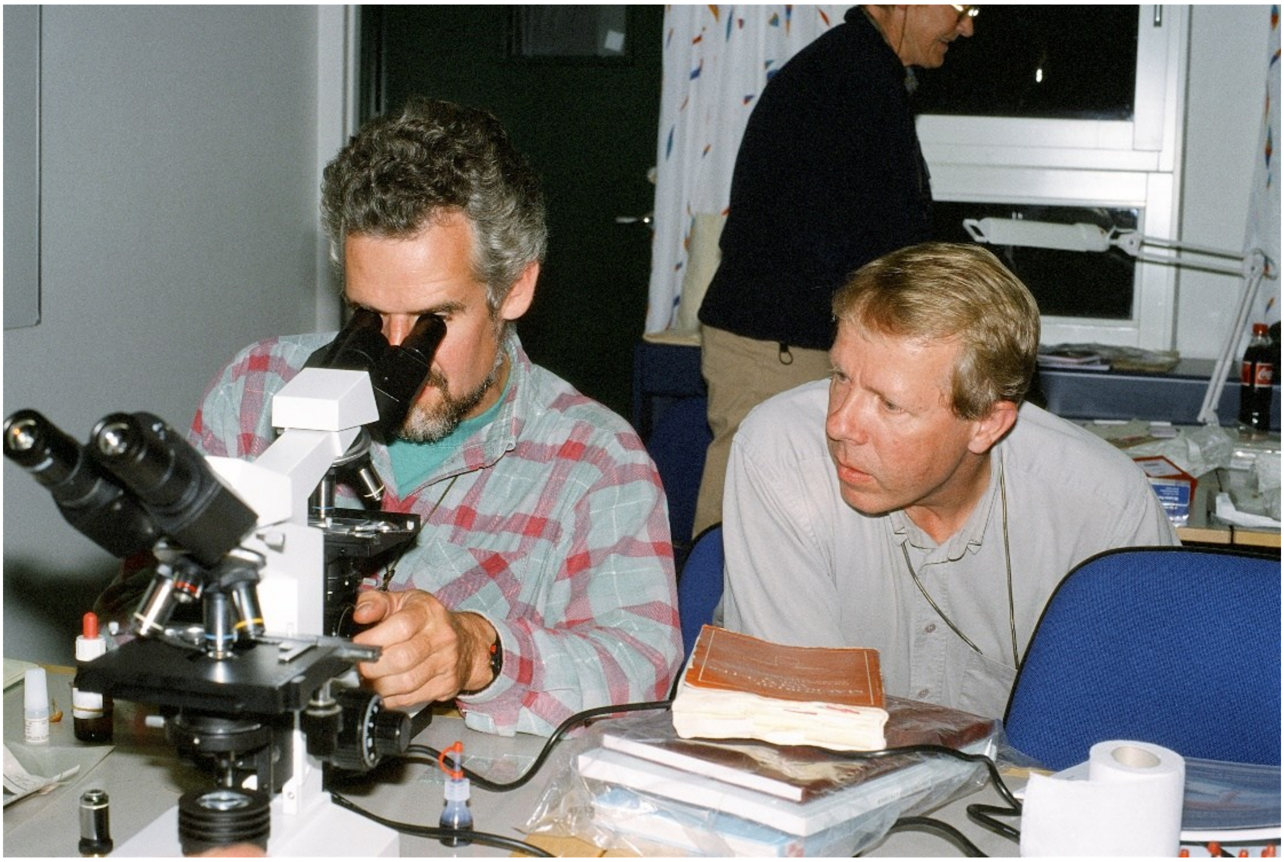
Ursula Peintner (Austria) works on *Cortinarius* sensu lato (see Fig. 47).

Ari Jumpponen with his truffle gear.

In the Ural Mountains, this vehicle helped us reach the summit.

Transition between tundra and fell-field in northern Finland, with reindeer.

M. Sasa, M. Ronikier, A. Ronikier, and A. Chlebitski in the Tatra Mountains in Poland.



Steen A. Elborne and H. Knudsen studying in Sisimiut, Greenland at ISAM VI.

Kati Bendiksen (and *Gentiana purpurea*) in Finse, Norway during ISAM VII.

Ellen Larsson, Ola Skifte, Anna Liisa Ruotsalainen, Ursula Peintner, Torbjørn Borgen, Morten Lange, Bodil Lange. Lange was celebrating his 50th season in the Arctic (1946–1996).

Alpine peak with young Japanese mycologists and the veteran Arctic mycologist Esteri Ohenoja (Finland) during ISAM X in Kanazawa, Japan.

Henry Dissing and Esteri Ohenoja departing the world's northernmost hotel in Longyearbyen, Svalbard, at ISAM III. Blinds were necessary because of the midnight sun.

4. Climate and geography of arctic and alpine regions

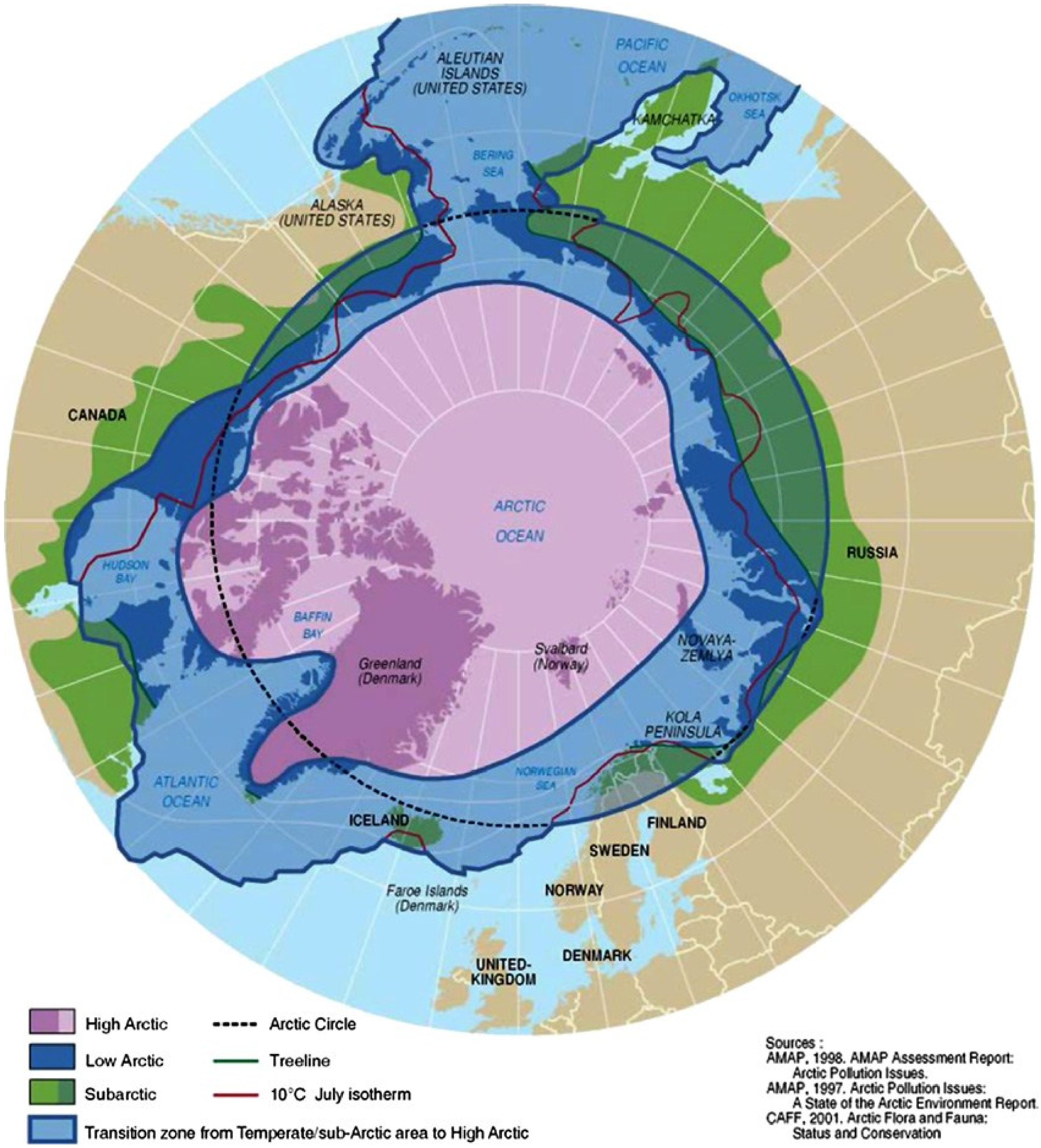


Fig. 4. Map of Arctic areas.

The Arctic zone

The Arctic is climatically divided into the Low Arctic and High Arctic, and geographically into the Nearctic and Palearctic.

Good (1964: 24) estimated the approximate land area covered by arctic and alpine vegetation. By far the largest proportion is in the Northern Hemisphere: 23.6 million km², compared to less than 1.3 million km² in the Southern Hemisphere. In the Northern Hemisphere about 60% of arctic-alpine vegetation occurs north of 60°N and is mostly in the Arctic or subarctic zones. Alpine vegetation in the Northern Hemisphere also covers much more land than its counterpart in the Southern Hemisphere. The alpine areas of North America and Eurasia are relatively small and isolated, yet they are floristically rich compared to the great circumboreal belt of arctic tundra. In the Arctic, the land is adjacent to the Arctic Ocean, which creates summer thawing and temperatures high enough for plant growth (Billings 1974: 406).

The Arctic zone as we define it includes areas where the average temperature of the warmest month is below 10 °C (Fig. 10). This isotherm is practically equivalent to the treeline. In contrast, the alpine zone cannot be delineated by a similar isotherm. The Arctic zone includes most of Alaska, northern Canada, almost all of Greenland, northern Iceland, northern Norway, northern Finland and northern Russia including Chukotka (Braque 1988). The arctic areas of Iceland, Norway, and Finland considered here are small. The northernmost part of Sweden is not truly arctic, although it may seem to be.

Fig. 5. A view of the treeless Arctic zone, showing heathland or tundra with dwarf shrubs, and towards the southern horizon the northernmost forest-tundra with scattered conifers. When the subalpine and subarctic zones are compared, it is evident that they have much in common in terms of vegetation and structure, but are very different in their dimensions. On a mountain, the transition from alpine to subalpine to the *Alnus* belt is short, spanning only a hundred to a few hundred metres, whereas in the Arctic the width of each zone may be many kilometres.

Fig. 6. Map of mountainous (violet) and planar (green) areas of the Arctic. The four capital cities north of 60°N are also shown.

The Nearctic region

In North America, the important alpine area is in the Rocky Mountains, stretching from Canada (British Columbia and Alberta) through the western USA (Washington, Idaho, Utah, Montana, Wyoming, Colorado, and New Mexico). The highest peak in the Brooks Range in Alaska (Mount Isto at 2736 m) is considered to be a part of the Rockies by the Americans, but is treated as a separate chain by the Canadians. The case is the same for the Mackenzie Mountains (the highest peak is 2972 m). They consider the Liard River separating the Yukon from British Columbia to be the dividing line between the Rockies and the northern Canadian mountains. But as practical mycologists, we treat the whole chain from the Brooks Range to New Mexico as a coherent unit.

The southern Rockies include most of the highest peaks in the chain, mostly found in Colorado, where the highest peak is Mt. Elbert at 4401 m. Further south they are lower. Even in the southernmost state, New Mexico, a number of species of alpine willows (*Salix brachycarpa* and *S. planifolia*), alpine birches (*Betula occidentalis* and *B. glandulosa*), and alpine mountain avens (*Dryas hookeriana*) are still present. However, at this latitude, there is less rainfall and it is hotter, resulting in higher evaporation and less available water for the fungi. We have therefore excluded New Mexico and most records from Colorado from our area of investigation.

In the eastern USA, the Appalachian Mountains reach up to 2000 m, but their southern position and relatively low height exclude them from our definition of alpine. The characteristic vegetation we use to define the alpine zone is also not present.

California has high peaks in the Sierra Nevada Mountains, but the rainfall is too low for alpine vegetation to develop.

The Palearctic region

The Palearctic region is divided into Western and Eastern parts by the Ural Mountains, the geographic border between Europe and Asia. The Eastern part includes temperate, boreal and arctic Asia.

The Western Palearctic Zone

The Scandinavian Mountains are mostly situated in Norway, where the highest peaks are found (e.g. Galdhøpiggen at 2469 m). In extreme northern Norway, the Palearctic zone transitions to a narrow Arctic zone (see chapter 5). This area, which is both arctic and alpine, was dubbed the oroarctic zone by Ahti et al. (1968). However, most of the Scandinavian mountain range is south of the oroarctic zone and thus is alpine.

The Scottish Mountains include the Grampian Mountains (the highest peak is Ben Nevis at 1343 m) and the Northwest Highlands. In spite of their low peaks, the high latitude creates habitat for a few arctic-alpine fungi, but as the region is borderline between boreal and subarctic, it is not included in our investigations. Watling (1987) gave an overview of the cold-adapted basidiomycetes from the area. We visited Scotland during two Nordic Mycological Congresses (in 1983 and 1991), but only a few genuinely arctic or subarctic species were found.

The Carpathians include the Western Carpathians (Tatra Mountains; the highest peak is Gerlachovsky štit at 2656 m), the Transsylvanian Alps (the highest peak is Vârful Negoiu at 2635 m), and the Eastern Carpathians (the highest peak is Gora Goverla, Ukraine, at 2061 m). We visited a part of the Polish Tatras with Anna Ronikier (who wrote her Ph.D. on their fungi), Michael Ronikier, and Andrei Chlebitski in 2002. Although we found some subalpine species, their numbers were too low to characterize the region as alpine, and we have only considered the Tatras sporadically in our studies.

The Pyrenees are alpine in their central part (the highest peak is Aneto, Spain, at 3404 m). However, many of the Pyrenees do not have alpine vegetation because of their lower elevation and higher temperatures. Corriol (2008) described the funga of the area including some alpine species, and we include the Pyrenees here. On the other hand, a similar study from the Sierra Nevada Mountains in southern Spain by Ortega et al. (1997) did not find specific alpine species, and neither those mountains nor the central Spanish massif are considered here.

The eastern border of the Western Palearctic is the Ural Mountains. Only the northern mountains, i.e. the Polar Urals north of the Arctic Circle, are alpine and therefore included here.

The southern border of the Western Palearctic is diffuse, including alpine peaks with species of *Salix*, *Betula*, and *Dryas*. Traces of subalpine vegetation occur in many places, but an alpine funga is not or hardly developed. We consider the southern limit in Europe for the occurrence of a true alpine funga to follow approximately 42°N, from the Pyrenees in the west, through southern France to the Apennines in central Italy (Gran Sasso, with a maximum height of 2912 m), to the Rila Mountains (the highest peak is Musala at 2925 m) and the Pirin Mountains (the highest peak is Vihren at 2914 m) in Bulgaria. In the Pirin Mountains, at one locality we found a hollow of ca. 100 m in diameter with four m^2 of alpine willows, but we found no trace of an alpine funga.

Thus, Albania, Croatia, Bosnia and Herzegovina, Serbia, Montenegro, Kosovo, Macedonia, Greece, Portugal, Spain, and Turkey are excluded from our study area. Although they include high mountains, the summers are generally too warm, and the alpine snow has melted and the water has disappeared before the autumn, when it is needed by the fungi. Increased melting of summer ice in the Alps is a concern, and a number of recent studies have addressed the problem.

The Caucasus Mountains form another part of the southern border, dividing Europe from the Middle East. We believe that this area shall also be excluded, having summer temperatures that melt the snow too fast to be of use for fungi in the autumn, but this is only an assumption. The highest peak in the Caucasus is Mt. Elbrus at 5642 m. In the catalogue of Georgian “spore plants” (Nakhutsprisvili 1986) some boreal-subalpine fungi are mentioned, but no true alpine fungi.

The Eastern Palearctic Zone

The northern part of the Eastern Palearctic is included in our study area. We include all alpine parts of Russia and Kazakhstan. Korbonskaja (1969) included a number of alpine fungi in her book on the rusts of central Asia and southern Kazakhstan. From Russia, we include the Verkhoyansk Range (the highest peak is 2389 m), the Chersky Range (the highest peak is Pobeda at 3147 m), the central part of the Kamchatka Peninsula (the highest peak is Klyuchevskaya at 4750 m), the Stanovoy Range (the highest peak is 2412 m), the Stanovoy Uplands (the highest peak is 2999 m), the Eastern Sayan Mountains (the highest peak is Munku-Sardyk at 3491 m), the Western Sayan Mountains (the highest peak is 2930 m), Altai (the highest peak is Belukha at 4506 m), and the Pamir Mountains and Tian Shan (the highest peak is Pobedy at 7430 m). In many of these places the fungi are poorly known, but we have included the records that we know. In the steppes along the Arctic Ocean in Sakha (Yakutia), the annual rainfall is 100–200 mm, and even in season the fungi are sparse, but we have included what we found.

Excluded areas

We have completely excluded China (Xinjiang and Tibet), Mongolia, and Korea; and from Japan only Hokkaido is included. The region where ISAM X took place (Mt. Hakusan, Kanazawa) was not really explored due to bad weather, which closed the area for visitors. In general, central Asia is a dry place.

The High Arctic zone (Polar areas)

The northernmost Arctic areas have a very dry climate and low temperatures, with a mean annual temperature below freezing and precipitation averaging 100–400 mm/year. Although this level of precipitation is low for the formation of basidiomata, the temperatures are also low, and other sources of groundwater are available, both from melting ice and snow on the surface, and from melting permafrost underground. We do not have figures to show the influence of these factors on the number of basidiomata. Low temperatures and low precipitation result in very few flowering plants and very little dead organic material for fungi to consume, so few of them are found. Zmitrovich & Yezhov (2015) reported a very few agarics from the polar deserts ("poljarnie pustini"), and Shiryaev (2015) reported a few species of *Typhula* and *Multiclavula*. These two genera are among the "fleshy" basidiomycetes with the lowest hyphal mass in their needle-like basidiomata, growing on herbs and soil.

Fig. 7. The Arctic zone is circumpolar, stretching all the way around the North Pole. It is almost evenly cold throughout, but precipitation is far from even. The closer the land is to large bodies of water like the Atlantic, Pacific, and Arctic Oceans, the higher the precipitation (whether rain or snow). Due to the very cold water, precipitation is very low around the North Pole (see Fig. 43). This photo is from Tiksi, Russia, where the Lena River joins the Arctic Ocean. It is situated thousands of kilometres from both the Pacific and Atlantic Oceans, and thus does not receive much saturated air from them; and since the Arctic Ocean is very cold, it contributes very little humidity. The annual precipitation is only 100–200 mm, with the overall result that very few basidiomycetes were found here, in spite of the vegetation resembling that of other much more fertile localities for fungi at the same latitude.

A factor of some significance in the Arctic is the amount of sunshine in the summer, when the sun is continuously above the horizon for 4–6 months. The level of solar radiation may be even higher than in the tropics, and basidiomata tend to darken in response, with a large amount of "dark hyphae" (thick-walled hyphae). Their dark colour protects the basidiomata from damaging ultraviolet radiation, and as a result different genera may become uniformly brown, such that generic characters are evident only when the basidiomata are turned upside down!

The winter is long in arctic areas, and spring comes late. The first fungi can appear in May, but what may be called "the season" is from late July through most of August, until the first frosts come between late August and the middle of September (see Phenology, p. 112). Light frosts may occur at almost any time of the year, with varying effects on the formation of basidiomata and spores.

The Low Arctic zone

In the Low Arctic the summers are relatively long, with considerable rain, fog, and haze. The winters are cold, but much warmer than in the High Arctic. In Greenland, the border between Low Arctic and High Arctic is approximately in the middle of the island, north of Jameson Land and south of Disko Island.

Fig. 8. *Entoloma* (seen here) and *Cortinarius* are two genera that become darker than normal due to continuous strong radiation from the midnight sun.

Climatic conditions

Permafrost

One of the unique features of the Arctic climate is the presence of permafrost (Fig. 9). Permafrost is land that is permanently frozen, or at least frozen for two consecutive years. Permafrost is found everywhere that the average annual air temperature is below -5 °C or the ground temperature is below 0 °C. Most arctic and alpine regions have permafrost, and it covers ca. 20% of the Earth, including ca. 40% of Russia and Canada, generally ending around 60°N. Large northern regions are permanently frozen underground to a great depth, but further south the layer thins and areas without continuous permafrost start to appear.

The upper layer of permafrost melts in summer, and supplies trees, plants, and fungi with water. Trees may be found up to 68°N in Canada at the delta of the Mackenzie River, and up to ca. 70°N at the base of the Taimyr Peninsula (the Lukunskij grove near Khatanga). The trees are sustained by melting permafrost in regions where annual rainfall is otherwise only 230 mm. In the dry areas of central Siberia around the Lena River, trees would not be able to grow if they were not supported by melting permafrost in the summer.

Temperature

Arctic regions are generally colder than other regions because the sun is below the horizon for a large part of the year. The Arctic zone (or Polar zone) is defined as the region where the average temperature of the warmest month (July) is below 10 °C. This results in a biologically active period that is sufficiently long for plants to reproduce, but too short to sustain forests. In the northernmost forest in the world, the Lukunskij grove at the base of Taimyr Peninsula in Siberia at 70°N, the trunks of the larches (*Larix*) are still covered with an ice armour from the winter snows when the buds open in spring. The treeline is very variable around the North Pole, depending not only on latitude (see Fig. 10, the white ring), but also on the surrounding sea. Trees and forest disappear around 60–61°N in Greenland, ca. 500 km south of the Arctic circle, whereas the Lukunskij grove is situated ca. 400 km north of the Arctic Circle! This difference is partly caused by the cold sea along the eastern coast of Greenland, where melting ice drifts down from the North Pole from spring through summer. At Lukunskij the climate is influenced by the huge Siberian land mass to the south, which is warmed by the sun throughout the summer. Compare the white Arctic Circle with the blue treeline in Fig. 10.

In Greenland there are positive average temperatures from two to six or seven months of the year (north to south). The average annual temperature ranges from -16.4 °C in northern Greenland to 1.8 °C in the southernmost part. The average temperature for the summer months, July and August, is between 5 and 10 °C. The actual temperature may vary to a much greater degree, depending on local factors such as exposure (south-facing or north-facing slopes), water content of the ground, and type of soil (stony-sandy, organic debris, etc.). On a north-facing slope the temperature throughout the day may be almost constant, whereas on south- and west-facing slopes the temperature is much higher and fluctuates throughout the day. Small hummocks and low hills may also be warmer than the surrounding flatlands. In certain places relatively high temperatures can therefore be achieved, and the resulting funga can be rich.

Arctic days can be much longer than alpine days. In northern Greenland there is a long period of constant sunshine, from the end of March to the beginning of September. It lasts for months in the northernmost Arctic regions and becomes less and less towards southernmost Greenland, where the shortest day at 60°N is less than 6 hours. However, since the sun in the Arctic is quite low in the sky, alpine days can be much warmer than arctic days. Anyway, it is locally possible to reach high temperatures even in these fundamentally cold areas. Sørensen (1941) recorded 50 °C at 73°N, and Corbet (1972) recorded 33 °C at 82°N. In plants, the inside of a funnel-shaped flower in direct sunshine may have a temperature that is 3-5 °C warmer than the surrounding air.

Temperature is used to delimit the High Arctic from the Low Arctic. The High Arctic has an annual average temperature of -6.4 °C to -16.4 °C in Greenland, and of -6.7 °C to -9.4 °C in Canada.

Fig. 9. Permafrost in the Northern Hemisphere.

Fig. 10. Overlap between the treeline (blue) and the 10 °C July isotherm (red), i.e., delimitation of the Arctic.

Precipitation

The annual rainfall in Arctic regions depends on geography, especially the distance from a large body of water like the sea. Regions close to the sea generally receive more rain than regions further inland. However, this is not the only factor that influences precipitation. At 31 stations along the Arctic Ocean north of Siberia, average annual rain/snowfall was 162 mm. At 18 stations along the Pacific Ocean east of Siberia and Japan (Hokkaido), average annual rain/snowfall was 852 mm, more than five times higher. Low precipitation is a well-known phenomenon in large areas of the Arctic, the so-called Arctic deserts. Low air temperatures over the sea result in little evaporation, which reduces the incidence of rain and snow. The combination of low temperature, low humidity, and strong winds creates areas with salt crusts and salt lakes. Such areas are known from Kangerlussuaq in central West Greenland and further north, and from northwestern parts of Ellesmere Island in Canada. Although some snowfall takes place, much of the snow may blow away during the winter.

Other sources of water

In the Arctic other factors influence the amount of water available for fungi. Winter snow and frost melt during the summer, and the meltwater penetrates the ground and seeps away or forms rivulets. In such places certain fungi benefit from the water, the so-called snow patch fungi, although we have so far not identified any species exclusive to snow patches. Shrubs like *Salix herbacea* are often found in these habitats along with their symbiotic fungi.

In flat areas, the upper layer of permafrost melts in the summer, and since the water cannot run away, these flat areas can remain wet for a long time.

Fig. 11. A glacier flowing from the Greenland Inland Ice into the fjord at Kangerlussuaq (central West Greenland, 68°N), accelerated by rising global temperatures and the black layer of dirt it accumulates on its way towards the sea. The black colour absorbs heat from the sun and increases melting of the ice. Participants in ISAM IV are seen collecting fungi in the foreground. The soil and debris along the glacier is the home for a number of basidiomycete yeasts like *Mrakia*. Although they are basidiomycetes, basidiomycetous yeasts are not included in this study.

Albedo

The percentage of radiation from the sun that is reflected is called the albedo. The larger the albedo, the smaller the absorption of solar radiation. On a pure white surface such as newly fallen snow, much of the solar energy is reflected. Conversely, on dark soil much energy is absorbed, warming the soil and melting the ice below (see Fig. 11). The more water that is present in the ground, the higher the absorption of energy. Thus, in the High Arctic the ground can be warmer than the surrounding air throughout the summer (Powell 1961).

In the far north, solar radiation is continuous from March to September, and snow and ice also reflect the radiation and increase ambient temperatures. This radiation has an impact on the fungi. Many agarics have dark brown to almost black colours, in order to absorb the most possible energy and at the same time protect themselves from damaging ultraviolet radiation. Their caps may become so dark and uniformly brown that it is difficult to distinguish individual species from each another when large amounts of basidiomata occur at the same time and in the same place. This is especially apparent in the *Telamonia* group of *Cortinarius*, and in groups of *Entoloma* (see e.g. Fig. 8). The constant sun may also have the opposite effect (bleaching, Fig. 12).

Fig. 12. The caps of this *Cystoderma* are completely faded due to the perpetual sun in northern parts of Greenland in the summer. The opposite effect can also occur, especially in *Cortinarius* and *Entoloma*.

Fig. 13. Polygon soil is a characteristic feature of the Arctic, forming in places where sequential melting and freezing of groundwater occurs. Large polygons from one to several metres across form, and the centres will be slightly raised during this process. This leads to the accumulation of organic matter along the margins, which is food for fungi, and species like *Lepista multiformis* can be found there in large numbers.

Fig. 14. *Lepista multiformis* sensu lato breaking out at the margin of a polygon.

The subarctic zone

The subarctic is defined as the zone between the polar tree limit (more or less following the 10 °C mean daily isotherm for the warmest month of the year) and the economic forest line to the south as defined by Hustich (1966). This zone is, at least in North America, climatically related to the summer position of the arctic frontal weather system. It constitutes a biotic transition belt (the forest-tundra ecotone) between the treeless arctic zone and the forested boreal zone (or boreal/taiga subzone of the temperate zone, Fig. 5). Its biota forms a mosaic and mixture of both arctic and boreal origin. The subarctic zone has not been geographically stable over time, but has varied with fluctuations in climate, and will of course continue to do so.

The alpine zone

Precipitation in alpine regions is much higher than in the Arctic. In mountainous alpine regions precipitation is often 1000–2000 mm, or about ten times more than in normal arctic areas. Although high, this precipitation is unevenly distributed over mountains, depending on the direction of the prevailing wind. Some mountains absorb most of the moisture as wind passes over them, whereas others are "shadowed" by these mountains and only receive air that is much depleted of moisture.

Daylength in the active fungal season is shorter in alpine regions than in the Arctic, but the temperature is also higher.

Fig. 15. A southern view of Chinese mountains from the Ukok Plateau, Altai, Russia. Kazakhstan lies to the west (right) and Mongolia to the east (left).

Fig. 16. In Siberia, the alpine zone occurs on the top of mountains and is characterized by low or no vegetation. Going down a mountain, low scattered trees (here *Larix*) gradually appear, which become larger and denser, finally forming forests. A belt of *Alnus* is often present between the subalpine zone and the upper limit of the forest.

The subalpine zone

The subalpine belt is the natural zone between the treeline and the closed mountain forest of lower elevations. It is an ecotone, a mosaic of biotas. The subalpine flora, fauna, and funga vary depending on the latitude of a mountain. The width of the subalpine belt varies from extremely narrow to very wide, depending on climatic factors such as temperature, moisture, and particularly wind and strong radiation, but also slope and exposure. The exact altitudinal position of the subalpine belt is related to the geographical position of a mountain. The belt occurs at lower elevations in northern and maritime climates, and at higher elevations in dry, subtropical, continental areas. Like the subarctic belt, the position of the subalpine belt has changed over time in response to major local climatic fluctuations. We suggest that in defining the altitudinal belts of mountains, the recommendations of the International Botanical Congress in Brussels in 1910 be followed, and that those in Meusel et al. (1965) be followed in North America as they are in Europe.

Krummholz

Wind has an important role in arctic and alpine regions. At high altitudes, temperature influences the limit of tree growth and krummholz formation much more than precipitation, runoff or snow accumulation. The width of the transition zone therefore varies. In some regions it is about 100 m or more, creating an almost abrupt transition from full-grown dense forest to open alpine tundra, but in most cases there is an intervening belt of mixed meadow- and heath-like vegetation with islands of trees and krummholz or dwarf shrubs, i.e., the subalpine belt.

Between this transitional subalpine belt and the closed forest below it, there is nothing directly comparable to open boreal forest or lichen woodland. The lower limit of the subalpine belt can be defined as the place where the trees begin to form well-developed stems and crowns and cover >50% of the total ground surface, with an undergrowth of typical forest herbs and bushes.

Fig. 17. *Betula pubescens* as krummholz in northern Finland.

Thus, the mountain belts include:

- The **planar** belt, consisting of plains at the base of mountains, usually adapted for agriculture.
- The **colline** belt, a park-like area of foothills supporting some agriculture such as viticulture, rice cultivation, etc.
- The **montane** belt, the forested zone. In Europe it is used for silviculture, and is often subdivided into submontane (mainly deciduous forest), middle montane (mixed forest), and upper montane (dense coniferous forest). In North America this European subdivision seems hardly adequate, and the montane belt may need special classification, especially in the West.
- The **subalpine** belt, the forest-tundra ecotone, with dwarf trees and subalpine meadows, in some areas with mountain pastures and heaths.
- The **alpine** belt, a region of treeless alpine tundra. It is sometimes divided into low alpine, alpine, and high alpine. The high alpine zone can sometimes correspond with what is called the nival belt, which hardly supports any vegetation except lichens.

Hultén (1937) delimited the area on both sides of the Bering Strait as the Beringian zone, extending from the Lena River in Russia to the Mackenzie River in Canada, including the Chukotka Peninsula and the Alaska Peninsula. The southern border includes the Kurile Islands, the Aleutian Islands, the northern part of southeast Alaska, and northwestern British Columbia. It extends from roughly 125°E to 130°W, and south to 45°50'N.

A majority of arctic fungi (63%) are approximately circumpolar, which is also true of vascular plants and some groups of animals. Of the genera of flowering plants that are well represented in the Arctic, many sections are present and derived from temperate or alpine regions. As our understanding of fungal geography improves, we expect to see a similar pattern emerge.

Müller & Magnuson (1987) found that the original Tertiary flora of the Alps was almost destroyed during repeated glaciations over the last million years; however, during the last 10,000 years many preglacial plants have recolonized sites gradually freed from ice cover. These plants were accompanied by their plant parasitic fungi.

Rivas-Martínez et al. (2004) made a very precise bioclimatic map of Europe based on biogeographic zones and thermoclimatic belts. We have applied their system to our characterization of the European climate, with the caveat that some details may have changed between the 1990s and the present day.

Fig. 18. Camels (seen here), horses and yaks graze at an altitude of ca. 2000 m in the Ukok plateau between Russia, China, Mongolia, and Kazakhstan. It is an area where temperate-boreal grassland borders subalpine and alpine meadows and snowbeds.

5. Distribution of ecto-mycorrhizal host species in cold regions

The number of host plants (ecto-mycorrhizal symbionts) is important for the distribution of ecto-mycorrhizal fungi and for the classification of an arctic-alpine region. In the following overview of the eight large Arctic regions and their symbiont hosts, we have only included the genera *Salix*, *Betula*, *Dryas* and *Alnus*. For these genera the number of symbiont species ranges from 1 to 31 in different geographic areas. A low number of ecto-mycorrhizal hosts (1-12) is characteristic of regions that only marginally qualify for inclusion in this work. Regions with a medium number of ecto-mycorrhizal host species (13-29) are included. The highest numbers (30-32 host species) are only seen in the best developed arctic-alpine areas, i.e. in amphiberingian Chukotka (Russia) and Alaska (USA), and in the Yukon and Northwest Territories (Canada). Exceptions to the pattern occur on more or less isolated islands like Greenland and Iceland, which each have only 11 ecto-mycorrhizal host species.

We used number of host species to classify regions as alpine or not. The southernmost parts of the Rocky Mountains (New Mexico), although very high in elevation, are not considered alpine due to low precipitation. One of the few basidiomycetes from high altitudes in Colorado is *Amanita nivalis*, a species found at low altitudes in subalpine-alpine areas.

For the nomenclature of climate zones, we have followed Rivas-Martínez et al. (2004). No country is entirely within the Arctic zone, although Greenland is very close. Only eight regions include Arctic areas.

The eight Arctic regions

Alaska (USA)

Western and northern **Alaska** north of the Brooks Range has an arctic climate, changing to subarctic in central Alaska, and gradually to temperate in the south. Mean annual temperatures are below 0 °C and annual rainfall is low, from 100–400 mm. In the Aleutian Islands and Southeast Alaska the rainfall is higher. The northern part of Alaska has continuous and discontinuous permafrost.

Twenty-eight ecto-mycorrhizal host species occur in Alaska, including 21 species of *Salix* (*S. alaxensis*, *S. arbusculoides*, *S. arctica*, *S. arctophila*, *S. barclayi*, *S. barrattiana*, *S. chamissonis*, *S. commutata*, *S. fuscescens*, *S. glauca*, *S. hastata*, *S. lanata*, *S. niphoclada*, *S. nummularia*, *S. ovalifolia*, *S. phlebophylla*, *S. planifolia*, *S. polaris*, *S. reticulata*, *S. rotundifolia*, and *S. stolonifera*), two species of *Betula* (*B. glandulosa* and *B. occidentalis*), four species of *Dryas* (*D. ajanensis*, *D. alaskensis*, *D. incisa*, and *D. integrifolia*), and a single species of *Alnus* (*A. alnobetula*).

Alaska and the neighbouring regions of Chukotka in Russia and the Yukon and Northwest Territories in Canada have the highest number of ecto-mycorrhizal hosts in the Arctic, with a particularly rich *Salix* flora, and also four species of *Dryas* (not including *D. drummondii*, which is not considered to be ecto-mycorrhizal, but instead has nitrogen-fixing bacteria (*Frankia* sp.) in its roots). Kobayasi et al. (1967) made an early inventory of Arctic Alaskan fungi, resulting in 97 species of basidiomycetes.

ISAM I took place in 1980 in Point Barrow, the northernmost point in Alaska. A list of ca. 40 basidiomycetes found during the symposium is included in the report of scientific results (Laursen & Ammirati 1982: 541-542).

Canada

Huge areas of the northeastern part of **Canada** are subarctic or arctic, including Nunavut, the Northwest Territories, the Yukon, the northern part of Labrador (the Ungava Peninsula), and the western part of Hudson Bay. Precipitation is low in the north, with large areas classified as arctic desert; precipitation gradually increases in southeastern Labrador.

Yukon. The climate is arctic in its northernmost part, but only in a small area, due to the broad Mackenzie River emptying its warmer waters into the Arctic Sea (Beaufort Sea). It is one of the few places where *Populus* (*P. balsamifera*) occurs in an arctic/subarctic area. The northern part of the Yukon has continuous and discontinuous permafrost.

Twenty-eight ecto-mycorrhizal symbionts are found in the Yukon, including 21 species of *Salix* (*S. alaxensis*, *S. arbusculoides*, *S. arctica*, *S. arctophila*, *S. barclayi*, *S. barrattiana*, *S. brachycarpa*, *S. chamissonis*, *S. commutata*, *S. farriae*, *S. fuscescens*, *S. glauca*, *S. hastata*, *S. lanata*, *S. niphoclada*, *S. ovalifolia*, *S. phlebophylla*, *S. planifolia*, *S. polaris*, *S. reticulata*, and *S. rotundifolia*), two species of *Betula* (*B. glandulosa* and *B. occidentalis*), four species of *Dryas* (*D. ajanensis*, *D. alaskensis*, *D. incisa*, and *D. integrifolia*), and a single species of *Alnus* (*A. alnobetula*).

Together with Alaska, the Yukon has the second-largest number of symbiont hosts, only surpassed by the Northwest Territories. We are not aware of any large mycological reports from the Yukon.

Northwest Territories: The climate is arctic in the northern part and subarctic further south, with the subarctic part reaching further south than in the Yukon. The northern part has continuous and discontinuous permafrost.

Twenty-nine ecto-mycorrhizal symbionts are found in the Northwest Territories, including 22 species of *Salix* (*S. alaxensis*, *S. arbusculoides*, *S. arctica*, *S. arctophila*, *S. barclayi*, *S. barrattiana*, *S. brachycarpa*, *S. chamissonis*, *S. commutata*, *S. farriae*, *S. fuscescens*, *S. glauca*, *S. hastata*, *S. herbacea*, *S. lanata*, *S. niphoclada*, *S. ovalifolia*, *S. phlebophylla*, *S. planifolia*, *S. polaris*, *S. reticulata*, and *S. rotundifolia*), three species of *Betula* (*Betula glandulosa*, *B. nana*, and *B. occidentalis*), three species of *Dryas* (*D. ajanensis*, *D. incisa*, and *D. integrifolia*), and a single species of *Alnus* (*A. alnobetula*).

The Northwest Territories has the largest number of symbiotic hosts recorded from arctic-alpine areas, followed closely by the Yukon and Alaska, and far exceeding the eleven species found in the most diverse alpine area (Switzerland). We have not found any large mycological reports from the Northwest Territories.

Nunavut: The region is mostly High Arctic, including large areas of arctic desert with little or no vegetation due to the low precipitation. The number of *Salix* species is thus drastically lower than in the neighbouring Northwest Territories. The climate is very similar to the climate of northwestern Greenland. Most of the area has continuous permafrost.

Sixteen ecto-mycorrhizal symbionts are recorded from Nunavut, including 15 species of *Salix* (*S. alaxensis*, *S. arbusculoides*, *S. arctica*, *S. arctophila*, *S. brachycarpa*, *S. fuscescens*, *S. glauca*, *S. herbacea*, *S. lanata*, *S. niphoclada*, *S. planifolia*, *S. polaris*, *S. reticulata*, *S. uva-ursi*, and *S. vestita*), and a single species of *Dryas* (*D. integrifolia*).

Kohn & Stasovski (1994) investigated the mycorrhiza of plants in Alexandra Fiord, Ellesmere Island, but they did not give specific names to the fungi.

British Columbia: The provincial climate is quite variable, from temperate rainforest at the coast, to typical alpine meadows at high altitudes on the western slopes of the Rocky Mountains. The highest peak is Mount Dawson at 3377 m, but there are several other alpine peaks.

Twenty-three ecto-mycorrhizal symbionts are known from British Columbia, including 19 species of *Salix* (*S. alaxensis*, *S. arbusculoides*, *S. arctica*, *S. barclayi*, *S. barrattiana*, *S. brachycarpa*, *S. cascadensis*, *S. commutata*, *S. farriae*, *S. glauca*, *S. lanata*, *S. niphoclada*, *S. nivalis*, *S. planifolia*, *S. polaris*, *S. reticulata*, *S. stolonifera*, *S. tweedyi*, and *S. vestita*), two species of *Betula* (*B. glandulosa* and *B. occidentalis*), a single species of *Dryas* (*D. integrifolia*), and a single species of *Alnus* (*A. alnobetula*).

The Rocky Mountains seem to provide good habitat for alpine fungi, but we have not found any larger mycological reports from British Columbia.

Alberta: Mostly subarctic, but in the southwestern part of the province the Rocky Mountains bordering British Columbia are alpine. The highest peak is Mount Columbia at 3741 m, with several peaks above 3000 m.

Eighteen ecto-mycorrhizal hosts are recorded from Alberta, including 14 species of *Salix* (*S. alaxensis*, *S. arbusculoides*, *S. arctica*, *S. barclayi*, *S. barrattiana*, *S. brachycarpa*, *S. commutata*, *S. farriae*, *S. glauca*, *S. nivalis*, *S. planifolia*, *S. reticulata*, *S. stolonifera*, and *S. vestita*), two species of *Betula* (*B. glandulosa* and *B. occidentalis*), a single species of *Dryas* (*D. integrifolia*), and a single species of *Alnus* (*A. alnobetula*).

The smaller alpine area may account for the smaller number of symbiont hosts than in British Columbia. We have not seen any large reports of arctic-alpine fungi from Alberta.

Manitoba: The climate in the northern half is continental subarctic, with tundra vegetation.

Fourteen ecto-mycorrhizal symbionts are recorded from Manitoba, including 10 species of *Salix*, (*S. alaxensis*, *S. arbusculoides*, *S. arctophila*, *S. brachycarpa*, *S. fuscescens*, *S. glauca*, *S. herbacea*, *S. lanata*, *S. planifolia*, *S. reticulata*, and *S. vestita*), two species of *Betula* (*B. glandulosa* and *B. occidentalis*), a single species of *Dryas* (*D. integrifolia*), and a single species of *Alnus* (*A. alnobetula*).

In the northern part of Manitoba, roughly along Hudson Bay, there is continuous and discontinuous permafrost. Ohenoja & Ohenoja (2010) listed some fungi from Fort Churchill, mixed with records from the Northwest Territories (Rankin Inlet, Baker Lake, and Repulse Bay).

Ontario: The provincial climate is subarctic except in the southwestern and southern parts.

Thirteen ecto-mycorrhizal symbionts are recorded from Ontario, including 10 species of *Salix* (*S. arbusculoides*, *S. arctica*, *S. arctophila*, *S. brachycarpa*, *S. glauca*, *S. herbacea*, *S. lanata*, *S. planifolia*, *S. reticulata*, and *S. vestita*), two species of *Betula* (*B. glandulosa* and *B. occidentalis*), a single species of *Dryas* (*D. integrifolia*), and a single species of *Alnus* (*A. alnobetula*).

In the northern part of Ontario, roughly along Hudson Bay, there is continuous and discontinuous permafrost.

Quebec: The northern part of Quebec (the Ungava Peninsula) is Low Arctic. Toward the south the province is mainly subarctic, and is generally wetter than other subarctic regions.

Fifteen ecto-mycorrhizal symbionts are recorded from Quebec, including 11 species of *Salix* (*S. alaxensis*, *S. arbusculoides*, *S. arctica*, *S. arctophila*, *S. brachycarpa*, *S. glauca*, *S. herbacea*, *S. planifolia*, *S. reticulata*, *S. uva-ursi*, and *S. vestita*), two species of *Betula* (*B. glandulosa* and *B. michauxii*), a single species of *Dryas* (*D. integrifolia*), and a single species of *Alnus* (*A. alnobetula*).

In the northern part of the Ungava Peninsula there is continuous and discontinuous permafrost.

Newfoundland and Labrador: Northern Labrador is Low Arctic. Newfoundland is subarctic-boreal, and due to the maritime influence is not included here.

Fourteen ecto-mycorrhizal symbionts are recorded from Labrador, including 10 species of *Salix* (*S. arbusculoides*, *S. arctica*, *S. arctophila*, *S. brachycarpa*, *S. glauca*, *S. herbacea*, *S. planifolia*, *S. reticulata*, *S. uva-ursi*, and *S. vestita*), two species of *Betula* (*B. glandulosa* and *B. michauxii*), a single species of *Dryas* (*D. integrifolia*), and a single species of *Alnus* (*A. alnobetula*).

The northernmost tip of Labrador has a small area of continuous and discontinuous permafrost.

Greenland

Greenland is a part of the Danish Realm. It is the world's largest island (Australia is a continent), stretching from 60°N to 83°N, and with the exception of very small areas in the innermost part of the southernmost fjords (Feilberg 1984), it is all within the Arctic zone. The mean annual temperature is around 1 °C in the capital Nuuk, below the freezing point northwards, and a few degrees higher to the south. The bottom of a few fjords in the small non-Arctic part may reach 10 °C in July. Large parts of northern Greenland are dry arctic desert, with an annual precipitation of 100–400 mm, like elsewhere in the Arctic. The low temperature prevents the air from holding much moisture, so little precipitation is possible. However, in southern Greenland precipitation may reach 2000–3000 mm, especially at Christianssund on the southeastern tip of the island, where 2000 mm is normal. The area north of 64°N has continuous permafrost.

Eleven ecto-mycorrhizal symbionts are known from Greenland, including five species of *Salix* (*S. arctica*, *S. arctophila*, *S. glauca*, *S. herbacea*, and *S. uva-ursi*), three species of *Betula* (*B. glandulosa*, *B. nana*, and *B. pubescens*), two species of *Dryas* (*D. integrifolia* and *D. octopetala*), and a single species of *Alnus* (*A. alnobetula*).

ISAM VI took place in Kangerlussuaq and Sisimiut in 2000 (see Boertmann & Knudsen 2006).

Iceland

Iceland is for the most part boreal or subarctic, but small parts of some of the northernmost peninsulas belong to the Arctic zone. Other parts of the mountainous island are alpine or subalpine (see below). The southern part of Iceland has positive mean annual temperatures and considerable precipitation, from 600 to more than 2000 mm. In Grímsstaðir the mean annual temperature is close to 0 °C, and even lower temperatures can be expected on some of the volcanoes. The arctic part belongs to the thermopolar belt and includes the coldest parts of Iceland (northwesternmost part of Vestfirðir, northernmost parts of Norðurland eystra). A boreal climate is found elsewhere on the island. Most of the western and eastern coasts have an oroboreal climate, and most of central Iceland belongs to the cryoboreal area, with areas of permanent ice and cold highland.

Eight ecto-mycorrhizal symbionts are recorded from Iceland, including five species of *Salix* (*S. arctica*, *S. glauca*, *S. herbacea*, *S. lanata*, and *S. phylicifolia*), two species of *Betula* (*B. pubescens* and *B. nana*), and a single species of *Dryas* (*D. octopetala*).

Despite a paucity of host symbionts, Iceland has both true arctic areas scattered in the north, and alpine areas scattered in the mountains across the island.

During the ExtraNordic Mycological Congress in Iceland in 1993, a number of subarctic locations were visited. Hallgrimsson & Eyjólfsdóttir (2004, 2006) made a checklist of the Icelandic basidiomycetes in two parts. The first part includes species of rusts and smuts, and the second part includes typical arctic-alpine fungi such as *Amanita nivalis*, *Cortinarius polaris*, *C. raphanoides*, *C. alpinus*, *C. chamaesalicis*, *C. pauperculus*, *C. subtorvus*, *Lactarius brunneoviolaceus*, *L. dryadophilus*, *L. nanus*, *L. pseudouvidus*, *L. salicis-herbaceae*, *L. torminosulus*, *Russula nana*, *R. pascua*, *R. norvegica*, and *R. saliceticola*.

Norway

The small northernmost part of **Norway** belongs to the Arctic zone, and large parts of the rest of the country belong to the alpine zone. In southern Norway, the Finse area (site of ISAM VII, cf. Høiland & Økland 2008) is alpine, and at 1200 m the mean annual temperature is -1.6 °C and the precipitation is 800–900 mm. The Arctic part of northernmost Norway, approximately north of 70°N, is not as cold as other comparable sites, because of the warming effect of the Gulf Stream, but in nearby continental Abisko (Sweden) the mean annual temperature is -1 °C at a few hundred metres altitude, with low precipitation (200–300 mm). In these parts of Scandinavia, the transition between arctic and alpine zones is gradual. Where the separation of the two climate zones takes place is impossible to say, so the joint area referable to both types of climates were by Ahti et al. (1971) designated as the oroarctic zone.

The largest part of Norway south to approximately 60°N is within the temperate Eurosiberian climate zone. This is divided into two subzones, the boreal Euro-Asiatic subzone and the Atlantic-Central European subzone. In the mountains of eastern Norway bordering Sweden, the climate is cryoboreal, and permanent ice is found on the highest peaks. In the southern part of the mountains, the cryoboreal zone is split into “islands”, with a central cryoboreal core surrounded by an oroboreal zone.

Fifteen ecto-mycorrhizal host symbionts are recorded from Norway, including 12 species of *Salix*, (*S. arbuscula*, *S. glauca*, *S. hastata*, *S. herbacea*, *S. lanata*, *S. lapponum*, *S. myrsinifolia*, *S. myrsinites*, *S. myrtilloides*, *S. polaris*, *S. phylicifolia*, and *S. reticulata*), two species of *Betula* (*B. nana* and *B. pubescens*), and a single species of *Dryas* (*D. octopetala*). Although only a median number of ecto-mycorrhizal hosts occur, they include five of the most important hosts for fungal symbionts: *Salix glauca*, *S. reticulata*, *S. herbacea*, *Betula nana*, and *Dryas octopetala*.

Svalbard

All of Svalbard is in the High Arctic zone. Six ecto-mycorrhizal symbionts occur: four species of *Salix* (*S. arctica*, *S. herbacea*, *S. polaris*, and *S. reticulata*), a single species of *Betula* (*B. nana*), and a single species of *Dryas* (*D. octopetala*).

ISAM III took place in Longyearbyen in 1988 (Petrini & Laursen 1993).

Sweden

No part of **Sweden** is truly Arctic, but large areas belong to the subarctic and subalpine zones. Sweden is contiguous with countries that do include true Arctic areas, and it is therefore often included in arctic studies.

Sweden is a part of the temperate Eurosiberian climate zone. In the northern part of western Sweden, bordering Norway, the highest mountains belong to the cryoboreal subzone, and much of the lower peaks and foothills belong to the oroboreal subzone.

Fifteen ecto-mycorrhizal symbionts are reported from Sweden, including 12 species of *Salix* (*S. arbuscula*, *S. glauca*, *S. hastata*, *S. herbacea*, *S. lanata*, *S. lapponum*, *S. myrsinifolia*, *S. myrsinites*, *S. myrtilloides*, *S. phylicifolia*, *S. polaris*, and *S. reticulata*), two species of *Betula* (*B. nana* and *B. pubescens*), and a single species of *Dryas* (*D. octopetala*).

Like Norway, Sweden has a median number of symbiotic hosts, including the most important and generalist species.

Finland

Finland is a part of the temperate Eurosiberian climate zone. In its northernmost parts, approximately north of 67°N, there are smaller oroboreal and cryoboreal arctic-alpine areas, e.g. Kautokeino (-3 °C at 308 m, with 318 mm of annual precipitation). These parts are included in this work, but the rest of the country is not.

Fifteen ecto-mycorrhizal symbionts are recorded from Finland, including 12 species of *Salix* (*S. arbuscula*, *S. glauca*, *S. hastata*, *S. herbacea*, *S. lanata*, *S. lapponum*, *S. myrsinifolia*, *S. myrsinites*, *S. myrtilloides*, *S. phylicifolia*, *S. polaris*, and *S. reticulata*), two species of *Betula* (*B. nana* and *B. pubescens*) and a single species of *Dryas* (*D. octopetala*). Like Norway and Sweden, these include the most important symbiotic hosts.

ISAM IX took place in northern Finland at the Kevo Subarctic Research Station in 2012, hosted by Esteri Ohenoja & Anna Liisa Ruotsalainen.

Russia

Russia has the largest Arctic area of all countries, ca. 40% of its area. All the area along its northern border with the Arctic Ocean is Arctic.

The regions below are listed from west to east, and only include their northern parts.

Northwestern Russia is both arctic and subarctic, with mean annual temperatures below freezing, and a relatively high rainfall due to its proximity to the Arctic Ocean.

Twenty ecto-mycorrhizal symbionts are recorded from the area, including 16 species of *Salix* (*S. arbuscula*, *S. arctica*, *S. glauca*, *S. herbacea*, *S. jenisseensis*, *S. lanata*, *S. lapponum*, *S. myrsinifolia*, *S. myrsinites*, *S. myrtilloides*, *S. nummularia*, *S. phylicifolia*, *S. polaris*, *S. recurvigemmata*, *S. reptans*, and *S. reticulata*), two species of *Betula* (*B. nana* and *B. pubescens*), a single species of *Dryas* (*D. octopetala*), and a single species of *Alnus* (*A. alnobetula*).

Western Siberia is Arctic along the Arctic Ocean.

Eighteen ecto-mycorrhizal symbionts are known from the area, including 11 species of *Salix* (*S. arctica*, *S. glauca*, *S. jenisseensis*, *S. lanata*, *S. lapponum*, *S. myrsinifolia*, *S. myrtilloides*, *S. nummularia*, *S. polaris*, *S. reptans*, and *S. reticulata*), three species of *Betula* (*B. glandulosa*, *B. nana*, and *B. pubescens*), three species of *Dryas* (*D. integrifolia*, *D. octopetala*, and *D. oxyodonta*), and a single species of *Alnus* (*A. alnobetula*).

The northern part of West Siberia has continuous permafrost and south of that a belt of discontinuous permafrost.

The Ural Mountains belong in their northern parts to the subalpine zone.

Fifteen ecto-mycorrhizal symbionts are known from the Urals, including eight species of *Salix* (*S. arctica*, *S. glauca*, *S. jenisseensis*, *S. lanata*, *S. myrtilloides*, *S. nummularia*, *S. reptans*, and *S. reticulata*), three species of *Betula* (*B. glandulosa*, *B. nana*, and *B. pubescens*), three species of *Dryas* (*D. incisa*, *D. octopetala*, and *D. oxyodonta*), and a single species of *Alnus* (*A. alnobetula*).

ISAM V took place in Labytnangi in the Yamal District, Ural Mountains in 1996 (Mukhin & Knudsen 1998).

Krasnoyarsk Krai belongs in its northern part to the Arctic zone, and the annual precipitation is low.

Twenty ecto-mycorrhizal symbionts are known from the area, including 11 species of *Salix* (*S. arctica*, *S. fuscescens*, *S. glauca*, *S. jenisseensis*, *S. lanata*, *S. myrtilloides*, *S. nummularia*, *S. polaris*, *S. recurvigemmata*, *S. reptans*, and *S. reticulata*), three species of *Betula* (*B. glandulosa*, *B. nana*, and *B. pubescens*), five species of *Dryas* (*D. grandis*, *D. incisa*, *D. integrifolia*, *D. octopetala*, and *D. oxyodonta*), and a single species of *Alnus* (*A. alnobetula*).

The northern part of Central Siberia or Krasnoyarsk region has continuous permafrost.

Yakutia (Republic of Sakha) belongs to the Arctic zone and has some of the lowest recorded temperatures on Earth. The area is generally dry continental, with large areas with steppe.

Twenty-five ecto-mycorrhizal symbionts are recorded from the area, including 15 species of *Salix* (*S. alaxensis*, *S. arctica*, *S. fuscescens*, *S. glauca*, *S. jenisseensis*, *S. krylovii*, *S. lanata*, *S. myrtilloides*, *S. nummularia*, *S. polaris*, *S. rectijulis*, *S. reptans*, *S. reticulata*, *S. turczaninowii*, and *S. vestita*), four species of *Betula* (*B. fruticosa*, *B. glandulosa*, *B. nana*, and *B. pubescens*), five species of *Dryas* (*D. ajanensis*, *D. grandis*, *D. integrifolia*, *D. incisa*, and *D. octopetala*), and a single species of *Alnus* (*A. alnobetula*).

Most of Yakutia has continuous permafrost.

Chukotka belongs to the Arctic zone.

Twenty-nine ecto-mycorrhizal symbionts are recorded from Chukotka, including 17 species of *Salix* (*S. alaxensis*, *S. arctica*, *S. chamissonis*, *S. fuscescens*, *S. glauca*, *S. jenisseensis*, *S. krylovii*, *S. lanata*, *S. myrtilloides*, *S. nakamurana*, *S. nummularia*, *S. ovalifolia*, *S. phlebophylla*, *S. polaris*, *S. reptans*, *S. reticulata*, and *S. rotundifolia*), four species of *Betula* (*B. fruticosa*, *B. glandulosa*, *B. nana*, and *B. pubescens*), six species of *Dryas* (*D. ajanensis*, *D. alaskensis*, *D. grandis*, *D. incisa*, *D. integrifolia*, and *D. octopetala*), a single species of *Alnus* (*A. alnobetula*), and a single species of *Populus* (*P. balsamifera*).

Most of Chukotka has continuous permafrost. It is the area of Russia with highest diversity of host symbionts.

Kamchatka has an arctic-alpine to subarctic climate, with high precipitation due to the surrounding Pacific Ocean.

Nineteen ecto-mycorrhizal symbionts are recorded from the peninsula, including 11 species of *Salix* (*S. alaxensis*, *S. arctica*, *S. fuscescens*, *S. glauca*, *S. lanata*, *S. nakamurana*, *S. nummularia*, *S. phlebophylla*, *S. polaris*, *S. reptans*, and *S. reticulata*), four species of *Betula* (*B. fruticosa*, *B. glandulosa*, *B. nana*, and *B. pubescens*), three species of *Dryas* (*D. ajanensis*, *D. grandis*, and *D. octopetala*), and a single species of *Alnus* (*A. alnobetula*).

Tuva has an alpine climate.

Seventeen ecto-mycorrhizal symbionts are recorded from Tuva, including 11 species of *Salix* (*S. arctica*, *S. glauca*, *S. jenisseensis*, *S. krylovii*, *S. lanata*, *S. nummularia*, *S. rectijulis*, *S. recurvigemmata*, *S. reticulata*, *S. turczaninowii*, and *S. vestita*), four species of *Betula* (*B. fruticosa*, *B. glandulosa*, *B. nana*, *B. pubescens*), a single species of *Dryas* (*D. oxyodonta*), and a single species of *Alnus* (*A. alnobetula*).

Altai has an alpine climate.

Thirteen ecto-mycorrhizal symbionts are known from Altai, including 10 species of *Salix* (*S. arctica*, *S. glauca*, *S. jenisseensis*, *S. lanata*, *S. myrtilloides*, *S. nummularia*, *S. rectijulis*, *S. reticulata*, *S. turczaninowii*, and *S. vestita*), a single species of *Betula* (*B. pubescens*), a single species of *Dryas* (*D. oxyodonta*), and a single species of *Alnus* (*A. alnobetula*).

Buryatia east of Lake Baikal has a dry steppe landscape and a continental climate.

Twenty-four ecto-mycorrhizal symbionts are reported from Buryatia, including 14 species of *Salix* (*S. alaxensis*, *S. arctica*, *S. fuscescens*, *S. glauca*, *S. jenisseensis*, *S. krylovii*, *S. lanata*, *S. myrtilloides*, *S. nummularia*, *S. polaris*, *S. rectijulis*, *S. reticulata*, *S. turczaninowii*, and *S. vestita*), four species of *Betula* (*B. fruticosa*, *B. glandulosa*, *B. nana*, and *B. pubescens*), five species of *Dryas* (*D. grandis*, *D. incisa*, *D. integrifolia*, *D. octopetala*, and *D. oxyodonta*), and a single species of *Alnus* (*A. alnobetula*).

Alpine North America

United States (states that include the northern Rocky Mountains, e.g., Montana and Wyoming).

The USA includes large areas with an alpine climate, especially parts of the Rocky Mountains. Other parts of the country are also obvious candidates for an alpine climate, but we have so far not been convinced, and have therefore not included them. The Appalachians are not high enough. In the northwestern states of Washington and Oregon, Mount Rainier is tall enough to qualify, and we have found some relevant records from this peak, but not a comprehensive survey. We have identified regions with the alpine shrubs that fit our definition. There is certainly an alpine belt with alpine meadows and fell-fields, but scrubs of willow, birch, and mountain avens seem to be missing or very local.

Montana: Eighteen ecto-mycorrhizal symbionts are recorded from Montana, including 14 species of *Salix* (*S. arctica*, *S. barclayi*, *S. barrattiana*, *S. brachycarpa*, *S. cascadensis*, *S. commutata*, *S. eastwoodiae*, *S. farriae*, *S. glauca*, *S. nivalis*, *S. planifolia*, *S. rotundifolia*, *S. tweedyi*, *S. vestita*), two species of *Betula* (*B. glandulosa* and *B. occidentalis*), a single species of *Dryas* (*D. octopetala*), and a single species of *Alnus* (*A. alnobetula*).

ISAM VIII took place in the Beartooth Plateau in 2008 (Cripps & Ammirati 2010b).

Wyoming: Fourteen ecto-mycorrhizal symbionts are recorded from Wyoming, including 12 species of *Salix* (*S. barclayi*, *S. barrattiana*, *S. brachycarpa*, *S. cascadensis*, *S. eastwoodiae*, *S. farriae*, *S. glauca*, *S. monticola*, *S. nivalis*, *S. planifolia*, *S. rotundifolia*, and *S. tweedyi*), a single species of *Betula* (*B. glandulosa* and *B. occidentalis*), and a single species of *Alnus* (*A. alnobetula*).

We have occasionally included basidiomycetes from alpine sites in Colorado (with 10 ecto-mycorrhizal symbionts), Utah (9 symbionts), Idaho (11), and New Mexico (8). In general, the alpine regions of these states only marginally qualify as such, due to insufficient rainfall and high summer temperatures.

Alpine Eurasia

Northern Europe

For the countries below, the climate is briefly characterized and the names of their arctic-alpine symbiont hosts are listed alphabetically. The frequent occurrence of hybridization between different species of *Salix* and between different species of *Betula* has not been considered. *Bistorta vivipara* has not been included, but it occurs in practically all European countries, except for the lowlands. *Helianthemum nummularium* and other species of *Helianthemum* are also excluded. Read more about these plants in the Ecto-mycorrhiza section (p. 166).

Ireland is within the temperate Eurosiberian climate zone, but it includes two small orotemperate areas on the west coast.

Four ecto-mycorrhizal symbionts are recorded from Ireland: two species of *Salix* (*S. herbacea* and *S. phylicifolia*), a single species of *Betula* (*B. pubescens*), and a single species of *Dryas* (*D. octopetala*).

Ireland is not included in our treatment. Although the important symbionts *Salix herbacea* and *Dryas octopetala* are found there, their range is small and maritime. The number of symbiotic plants is too low, and we have no information about the arctic-alpine funga.

The United Kingdom belongs to the temperate Eurosiberian climate zone, but it does include small subalpine areas. Most of these are in Scotland, but a few are in England, Wales and the northern part of Ireland.

Eleven ecto-mycorrhizal symbionts are reported from the UK, including eight species of *Salix* (*S. arbuscula*, *S. herbacea*, *S. lanata*, *S. lapponum*, *S. myrsinifolia*, *S. myrsinites*, *S. phylicifolia*, and *S. reticulata*), two species of *Betula* (*B. nana* and *B. pubescens*), and a single species of *Dryas* (*D. octopetala*).

Scotland lacks a true arctic-alpine funga. Watling (1987) gave an excellent account of the funga of the Grampians and the Northwest Highlands. Important species like *Amanita nivalis* (originally described from Scotland), *Russula nana*, *R. norvegica*, and *R. pascua* occur, and species of *Cortinarius* like *C. alpinus* (syn. *C. favrei*), *C. norvegicus*, *C. gausapatus*, and *C. scotoides* are found associated with *Salix herbacea*. Definite cold climate species of *Inocybe* like *I. squamosoannulata* and *I. giacomi* also occur, as well as a number as yet unidentified species characteristic of arctic-alpine associations. However, the arctic-alpine funga is sporadic, not coherent, and not very diverse, and is therefore excluded. Small areas of England are reminiscent of an arctic-alpine biome, but nothing is known about their fungi.

Denmark has a supratemperate climate except for a small hemiboreal area. It belongs to the Eurosiberian climate zone and the Central European subatlantic subtype.

Two ecto-mycorrhizal symbiont hosts occur in Denmark, *Salix hastata* and *Betula pubescens.*

No parts of Denmark qualify as arctic-alpine. In northern Jutland *Salix hastata* reaches its southern limit, but its associated cold climate fungi have not been reported. In the dune landscapes along the North Sea a few species occur that have their main distribution in northern areas, like *Russula subrubens* and *R. norvegica*. On neighbouring heaths, *Multiclavula vernalis* and the ascomycete *Sarcoleotia globosa* occur as rare examples of arctic-alpine species. However, Denmark is excluded from this work.

Central Europe

The Netherlands. The climate is supratemperate throughout, belonging to the Eurosiberian zone and the Central European subatlantic subtype.

The only ecto-mycorrhizal symbiont recorded from the Netherlands is *Betula pubescens.*

No part of the country qualifies as arctic-alpine. Cold climate fungi associated with *Betula pubescens* are missing. A few species occur in the dune landscapes along the Atlantic that have their main distribution in northern areas, like *Russula subrubens.* On neighbouring heaths, *Multiclavula vernalis* and the ascomycete *Sarcoleotia globosa* occur as rare examples of arctic-alpine species. Like Denmark, the Netherlands are excluded from this work.

Belgium. The climate of Belgium is supratemperate throughout, belonging to the Eurosiberian zone and the Central European Subatlantic subtype.

The only ecto-mycorrhizal symbiont recorded from Belgium is *Betula pubescens.*

Belgium is comparable to Denmark and the Netherlands, and is likewise excluded.

Germany is a part of the Atlantic-Central European Eurosiberian climate zone. Small orotemperate areas of the eastern alpine subtype (Garmisch-Partenkirchen, Salzburger Kalkalpen, Bayerischer Alpen) occur along the border to Switzerland and Austria, and also in central Germany, in Thuringia and the Harz Mountains.

Seventeen ecto-mycorrhizal symbionts are recorded from Germany, including 13 species of *Salix* (*S. alpina*, *S. breviserrata*, *S. glabra*, *S. hastata*, *S. herbacea*, *S. lapponum*, *S. myrsinifolia*, *S. myrtilloides*, *S. phylicifolia*, *S. reticulata*, *S. retusa*, *S. serpillifolia*, and *S. waldsteiniana*), two species of *Betula* (*B. nana* and *B. pubescens*), a single species of *Dryas* (*D. octopetala*), and a single species of *Alnus* (*A. alnobetula*).

In southernmost Germany, alpine areas occur as the northern outlier of the Limestone Alps, which continue into Austria. The highest peaks (up to 2550 m) were investigated by Schmid-Heckel (1985), who made a comprehensive study of many arctic-alpine fungi associated with *Dryas octopetala*, *Salix retusa*, *S. reticulata*, *S. glauca* and *Alnus alnobetula*, genera like *Cortinarius*, *Inocybe*, *Naucoria*, *Russula* and *Lactarius*. Germany has a median number of arctic-alpine symbiont host species.

Poland belongs to the the Atlantic-Central European Eurosiberian climate zone. It includes small orotemperate areas in the Western Carpathians (Tatra Mountains) belonging to the Alpino-Caucasian type, the Carpathian subtype.

Fourteen ecto-mycorrhizal symbionts are recorded from Poland, including 10 species of *Salix* (*S. alpina*, *S. hastata, S. helvetica*, *S. herbacea*, *S. lapponum*, *S. myrsinifolia*, *S. myrtilloides*, *S. phylicifolia*, *S. reticulata*, and *S. retusa*), two species of *Betula* (*B. nana* and *B. pubescens*), a single species of *Dryas* (*D. octopetala*), and a single species of *Alnus* (*A. alnobetula*).

A part of the Tatra Mountains around Sarnia Scała (1377 m) was intensely studied by A. Ronikier (2012), and shown to be subalpine, and no truly Arctic-alpine symbionts were found. Poland most likely has smaller areas with alpine climate and funga.

Lithuania belongs to the Eurosiberian climate zone, Central European type, Hemiboreal Baltic subtype.

Five ecto-mycorrhizal symbionts are reported from Lithuania: three species of *Salix* (*S. lapponum*, *S. myrsinifolia*, and *S. phylicifolia*), and two species of *Betula* (*B. nana* and *B. pubescens*).

No part of Lithuania qualifies as arctic-alpine, and Lithuania is not included in this work.

Latvia belongs to the Eurosiberian climate zone, Central European type, Hemiboreal Baltic subtype.

Five ecto-mycorrhizal symbionts are reported from Latvia: three species of *Salix* (*S. lapponum*, *S. myrsinifolia*, and *S. phylicifolia*), and two species of *Betula* (*B. nana* and *B. pubescens*).

No part of Latvia qualifies as arctic-alpine, and like Lithuania it is excluded.

Estonia belongs to the Eurosiberian Climate zone, Central European type, Hemiboreal Baltic subtype. Its northeastern corner is Boreal-Subcontinental.

Five ecto-mycorrhizal symbionts are reported from Latvia: three species of *Salix* (*S. lapponum*, *S. myrsinifolia*, and *S. phylicifolia*), and two species of *Betula* (*B. nana* and *B. pubescens*).

No part of Estonia qualifies as arctic-alpine, and like the other Baltic countries it is excluded.

The Czech Republic lies in the atlantic-central European Eurosiberian climate zone. It includes small orotemperate areas in the Erzgebirge (Ore Mountains), the Šumava Mountains (Bohemian Forest), and the Sudetes.

Twelve ecto-mycorrhizal symbionts are recorded from the Czech Republic, including eight species of *Salix* (*S. alpina*, *S. hastata*, *S. helvetica*, *S. herbacea*, *S. myrsinifolia*, *S. myrtilloides*, *S. reticulata*, and *S. retusa*), two species of *Betula* (*B. nana* and *B. pubescens*), a single species of *Dryas* (*D. octopetala*), and a single species of *Alnus* (*A. alnobetula*).

The highest point in the country is Sněžka at 1603 m, with a small alpine top. We have not seen reports from this peak. The number of host symbionts in the Czech Republic (12) only marginally fits our definition of "alpine", and the country in not included in this work.

Slovakia belongs to the Eurosiberian climate zone; its western part belongs to the Atlantic-Central European subtype, and its eastern part to the Pannonio-Carpathian subtype of the Alpino-Caucasian zone. Slovakia includes large orotemperate areas in the Western Carpathians (the Vysoké Tatry or High Tatras in the Spiš region), with the highest point being Gerlachov Peak at 2665 m.

Twelve ecto-mycorrhizal symbionts are reported from Slovakia, including eight species of *Salix* (*S. alpina*, *S. hastata*, *S. herbacea*, *S. lapponum*, *S. myrsinifolia*, *S. myrtilloides*, *S. reticulata*, and *S. retusa*), two species of *Betula* (*B. nana* and *B. pubescens*), a single species of *Dryas* (*D. octopetala*), and a single species of *Alnus* (*A. alnobetula*).

Fellner & Landa (1993, 1994) reported a handful of truly alpine species from the Belaer Tatras, including *Russula dryadicola*, *R. saliceticola*, *R. pascua*, *R. norvegica*, *R. cupreola*, *Lactarius nanus* and the new *Cortinarius tatrensis*. The number of symbiont hosts in Slovakia is marginal, but we have mapped a few records due to the high mountains and the presence of true alpine species.

Ukraine belongs to the Atlantic-Central European Eurosiberian climate zone. The northern part belongs to the Sarmatian subtype, whereas the southern part belong to the Alpino-Caucasian part of the Eurosiberian climate zone, the Escitian subtype. It includes a few small orotemperate areas in the Eastern Carpathians.

Nine ecto-mycorrhizal symbionts are recorded from Ukraine, including five species of *Salix* (*S. alpina*, *S. lapponum*, *S. myrsinifolia*, *S. myrtilloides*, and *S. retusa*), two species of *Betula* (*B. nana* and *B. pubescens*), a single species of *Dryas* (*D. octopetala*), and a single species of *Alnus* (*A. alnobetula*).

The highest mountain in the Ukrainian Carpathians is Goverla at 2061 m, surrounded by alpine meadows. Due to the low number of symbiont hosts and the lack of any report of alpine fungi from the area we have excluded it.

France is in its large northwestern part situated in the Atlantic-Central European Eurosiberian climate zone. The southeastern part of France includes orotemperate areas in the Pyrenees, the Alps and some smaller enclaves in the Massif Central.

Sixteen ecto-mycorrhizal symbionts are recorded from France, including 12 species of *Salix* (*S. breviserrata*, *S. hastata*, *S. hegetschweileri*, *S. helvetica*, *S. herbacea*, *S. lapponum*, *S. myrsinifolia*, *S. phylicifolia*, *S. pyrenaica*, *S. reticulata*, *S. retusa*, and *S. serpillifolia*), two species of *Betula* (*B. nana* and *B. pubescens*), a single species of *Dryas* (*D. octopetala*), and a single species of *Alnus* (*A. alnobetula*).

France includes large alpine areas, especially in the western Alps, the core area for alpine fungi. The French part of the Pyrenees includes the highest parts of these mountains, but the alpine area is small compared to the Alps. The number of symbiont hosts is median, but numerous alpine fungi are known and described from the French Alps, especially by Kühner and Lamoure (l.c.).

ISAM IV took place in Lanslebourg in the French Alps in 1992 and was hosted by Denise Lamoure (see Petrini & Laursen 1993).

Switzerland is situated in the alpino-caucasian part of the Eurosiberian climate zone, in the western and central subzone. Most of the southern part includes orotemperate areas in the Alps.

Twenty ecto-mycorrhizal symbionts are recorded from Switzerland, including 16 species of *Salix* (*S. alpina*, *S. breviserrata*, *S. glabra*, *S. glauca*, *S. hastata*, *S. hegetschweileri*, *S. helvetica*, *S. herbacea*, *S. lapponum*, *S. myrsinifolia*, *S. myrtilloides*, *S. phylicifolia*, *S. reticulata*, *S. retusa*, *S. serpillifolia*, and *S. waldsteiniana*), two species of *Betula* (*B. nana* and *B. pubescens*), a single species of *Dryas* (*D. octopetala*), and a single species of *Alnus* (*A. alnobetula*).

Most of Switzerland is in the Alps, and the Swiss Alps are the best-known alpine area on Earth when it comes to fungi, thanks especially to Jules Favre's works (1955, 1960), and in later years that of Egon Horak and Beatrice Senn-Irlet. The greatest number of symbiont host plants are also found there, with only the amphiberingian area having more species.

ISAM II took place in Ftan in the Swiss Alps in 1984 and was hosted by Egon Horak (see Laursen et al. 1987).

Austria is situated in the alpino-caucasian part of the Eurosiberian climate zone, in the eastern subzone. Most of western Austria includes large orotemperate areas in the Alps.

The 20 ecto-mycorrhizal symbiont plants recorded from Austria are exactly the same as those recorded from Switzerland.

All of western Austria is in the Eastern Alps. These are well studied thanks to the work of Josef Poelt, Meinhard Moser, and Ursula Peintner, and they are also well covered when it comes to rusts and smuts (Poelt & Zwetko 1997, Zwetko 2000).

Southern Europe

Romania belongs to the Alpino-Caucasian part of the Eurosiberian Climate zone. It includes many smaller orotemperate areas in the Eastern Carpathians, the Southern Carpathians and the Romanian Western Carpathians.

Twelve ecto-mycorrhizal symbionts are reported from Romania, including eight species of *Salix* (*S. alpina*, *S. hastata*, *S. herbacea*, *S. lapponum*, *S. myrtilloides*, *S. phylicifolia*, *S. reticulata*, and *S. retusa*), two species of *Betula* (*B. nana* and *B. pubescens*), a single species of *Dryas* (*D. octopetala*), and a single species of *Alnus* (*A. alnobetula*).

In the Southern Carpathians a number of alpine peaks reach 2500 m, the highest being Moldoveanu at 2544 m. In the Eastern Carpathians the highest peak is Pietrosul Rodnei (2305 m). In spite of being the largest mountain massif in Europe, the Carpathians are for the most part not very tall and the number of host symbionts is quite low. Ronikier (2008) reported 24 species of fungi from the alpine zone of the Southern Carpathians, among which *Amanita nivalis*, *Lactarius brunneoviolaceus*, *L. nanus*, *Russula heterochroa*, *R. nana*, *R. saliceticola*, *Inocybe alboperonata*, and *I. microfastigiata* are typical arctic-alpine species.

Romania is close to the southern limit for alpine fungi in Europe, but is excluded due to its low number of host symbionts.

Spain lies in the Alpino-Caucasian part of the Eurosiberian Climate zone. Only the northernmost part of Spain, the Pyrenees and Galicia, includes smaller orotemperate areas of Sevenno-Pyrenean subtypes.

Eleven ecto-mycorrhizal symbionts are recorded from Spain, including eight species of *Salix* (*S. breviserrata*, *S. hastata*, *S. herbacea*, *S. lapponum*, *S. phylicifolia*, *S. pyrenaica*, *S. reticulata*, and *S. retusa*), two species of *Betula* (*B. nana* and *B. pubescens*), and a single species of *Dryas* (*D. octopetala*).

Only the central Pyrenees, where the highest peaks are situated, are included in our treatment, as this area has a rich and well investigated funga. Numerous papers by Marcel Bon, Josep Ballarà, Gilles Corriol, Fernando Esteve-Raventós, and Jordi Vila were summarized by Corriol (2008). Many alpine species have been reported: *Amanita nivalis*, *A. oreina*, *Cortinarius albonigrellus*, *C. chamaesalicis*, *C. chrysomalus*, *C. diasemospermus*, *C. alpina*, *C. phaeochrous*, *C. polaris*, *C. tenebricus*, *C. inops*, *C. minutalis*, *C. minutulus*, *C. phaeopygmaeus*, *C. scotoides*, *C. stenospermus*, *Inocybe canescens*, *I. giacomi*, *I. geraniodora*, *I. luteipes*, *I. monochroa*, *I. salicis-herbaceae*, *Lactarius brunneoviolaceus*, *L. dryadophilus*, *L. nanus*, *L. salicis-herbaceae*, *Mallocybe arthrocystis*, *M. leucoblema*, *M. leucoloma*, *M. squarrosoannulata*, *Russula nana*, *R. norvegica*, and *R. pascua*, to name a few. We have not seen reports from the small orotemporate areas of Galicia. The Pyrenees are at the southernmost limit for alpine fungi in Europe. In spite of its relatively low number of host symbionts, the Pyrenees are included in our treatment.

Portugal has a meso-temperate to mediterranean climate.

Only one ecto-mycorrhizal symbiont, *Betula pubescens*, is reported from Portugal.

The high temperatures, low mountains, and lone symbiont host do not support arctic-alpine fungi, and Portugal is not included in this treatment.

Italy. The northern part of Italy lies in the alpino-caucasian part of the Eurosiberian climate zone, whereas the southern part belongs to the mediterranean climate zone. Orotemperate areas occur in the Italian Alps, in the northern Apennines, and east of Rome in the Gran Sasso d'Italia.

Eighteen ecto-mycorrhizal symbionts are recorded from Italy, including 14 species of *Salix* (*S. alpina*, *S. breviserrata*, *S. glabra*, *S. glauca*, *S. hastata*, *S. hegetschweileri*, *S. helvetica*, *S. herbacea*, *S. myrsinifolia*, *S. phylicifolia*, *S. reticulata*, *S. retusa*, *S. serpillifolia*, and *S. waldsteiniana*), two species of *Betula* (*B. nana* and *B. pubescens*), a single species of *Dryas* (*D. octopetala*), and a single species of *Alnus* (*A. alnobetula*).

In 2006 Jamoni published "Macromiceti della zona alpina inferiore e superior, con particolare riguardo all'area del Monte Rosa". Based on this he then published "Funghi alpini delle zone alpine superiori e inferiori" (Jamoni 2008), giving a broader view of fungi in the Alps. Jamoni's fine work is a continuation of Favre's, but updated to include the many new species since Favre's era. Alpine Italy is included in our treatment.

Slovenia belongs to the Alpino-Caucasian part of the Eurosiberian climate zone, the Apennino-Balkan subtype. It includes orotemperate areas in the Julian Alps.

Twelve ecto-mycorrhizal symbionts are recorded from Slovenia, including nine species of *Salix* (*S. alpina*, *S. glabra*, *S. hastata*, *S. herbacea*, *S. myrsinifolia*, *S. reticulata*, *S. retusa*, *S. serpillifolia*, and *S. waldsteiniana*), and a single species each of *Betula* (*B. pubescens*), *Dryas* (*D. octopetala*), and *Alnus* (*A. alnobetula*).

The northern part of Slovenia neighbours the Austrian Alps and is in many ways similar, but drier and with fewer host symbionts. The highest mountain is Triglav at 2864 m, near the Italian border, followed by Grintovec at 2558 m. We have not seen reports of Slovenian alpine fungi, and the country is not included in this work.

Croatia belongs to the Alpino-Caucasian part of the Eurosiberian Climate zone, the Apennino-Balkan subtype. It includes orotemperate areas on Plješevica.

Twelve ecto-mycorrhizal symbionts are reported from Croatia, including nine species of *Salix* (*S. alpina*, *S. glabra*, *S. hastata*, *S. herbacea*, *S. myrsinifolia*, *S. reticulata*, *S. retusa*, *S. serpillifolia*, and *S. waldsteiniana*), and a single species each of *Betula* (*B. pubescens*), *Dryas* (*D. octopetala*), and *Alnus* (*A. alnobetula*).

The highest mountain is Dinara at 1830 m in the Dinaric Alps. The relatively low mountains and the warm climate are unfavourable for alpine fungi, and the country is not included in this work.

Bosnia and Herzegovina belongs to the alpino-caucasian part of the Eurosiberian climate zone, the apennino-balkan subtype. The country includes a number of orotemperate areas in the Dinaric Alps. Twelve ecto-mycorrhizal symbionts are reported, including nine species of *Salix* (*S. alpina*, *S. glabra*, *S. hastata*, *S. herbacea*, *S. myrsinifolia*, *S. reticulata*, *S. retusa*, *S. serpillifolia*, and *S. waldsteiniana*), and a single species each of *Betula* (*B. pubescens*), *Dryas* (*D. octopetala*), and *Alnus* (*A. alnobetula*).

The Dinaric Alps are low (1800 m), dry, and warm, conditions unfavourable for alpine fungi. The country is not included in this work.

Montenegro belongs to the Alpino-Caucasian part of the Eurosiberian Climate zone, the Apennino-Balkan subtype. It includes a number of orotemperate areas in the Dinaric Alps.

Twelve ecto-mycorrhizal symbionts are recorded from Montenegro, including nine species of *Salix* (*S. alpina*, *S. glabra*, *S. hastata*, *S. herbacea*, *S. myrsinifolia*, *S. reticulata*, *S. retusa*, *S. serpillifolia*, and *S. waldsteiniana*), and a single species each of *Betula* (*B. pubescens*), *Dryas* (*D. octopetala*), and *Alnus* (*A. alnobetula*).

The Dinaric Alps are generally low (1800 m) and dry, although Babotov Kuk at 2523 m is an exception. However, the warm climate is unfavourable for alpine fungi and the country is not included in this work.

Serbia belongs to the Alpino-Caucasian part of the Eurosiberian Climate zone. The western part belong to the Apennino-Balkan subtype, the eastern part to the Pannonio-Carpathian subtype. It includes orotemperate areas in the Crna Gora.

Eleven ecto-mycorrhizal symbionts are recorded from Serbia, including eight species of *Salix* (*S. alpina*, *S. glabra*, *S. herbacea*, *S. myrsinifolia*, *S. reticulata*, *S. retusa*, *S. serpillifolia*, and *S. waldsteiniana*),

The warm climate of Serbia is unfavourable for alpine fungi and the country is not included here.

Bulgaria belongs to the Alpino-Caucasian part of the Eurosiberian Climate zone, the Apennino-Balkan subtype. It includes a few orotemperate areas in Stara planina (the Balkan Mountains) east of Sofia, and in the Rila, Pirin and Rhodope Mountains south of Sofia.

Eleven ecto-mycorrhizal symbionts are reported from Bulgaria, including eight species of *Salix* (*S. hastata*, *S. herbacea*, *S. lapponum*, *S. myrsinifolia*, *S. reticulata*, *S. retusa*, and *S. waldsteiniana*), and a single species each of *Betula* (*B. pubescens*), *Dryas* (*D. octopetala*), and *Alnus* (*A. alnobetula*). The warm dry climate and the few symbiont hosts do not fit our definition of alpine.

Albania has six ecto-mycorrhizal symbionts including five species of *Salix* (*S. hastata*, *S. herbacea*, *S. reticulata*, *S. retusa*, and *S. waldsteiniana*), and a single species of *Dryas* (*D. octopetala*). The climate is too dry for alpine fungi.

Greece only includes two ecto-mycorrhizal host symbionts, *Salix lapponum* and *Dryas octopetala*. The climate is too dry for alpine fungi.

Asia

Kazakhstan is adjacent to Russia and has a dry continental climate, with high mountains with an alpine climate. Nineteen host symbionts are recorded from Kazakhstan, including 13 species of *Salix* (*S. arbuscula*, *S. arctica*, *S. krylovii*, *S. myrtilloides*, *S. glauca*, *S. lanata*, *S. lapponum*, *S. myrtilloides*, *S. phylicifolia*, *S. rectijulis*, *S. reticulata*, *S. tianschanica*, and *S. turczaninowii*), four species of *Betula* (*Betula humilis*, *B.*, a single species of *Dryas* (*D. oxyodonta*), and a single species of *Alnus* (*A. alnobetula*). *Betula karagandensis*, *B. psammophila*, and *B. saviczii* are not considered in this work.

Japan (only Hokkaido) has a subalpine climate with high annual mean temperatures (Mt. Shokanbetsu, 1492 m). Ecto-mycorrhizal symbionts include two species of *Salix* (*S. nakamurana* and *S. nummularia*), three species of *Betula* (*B. ermanii*, *B. fruticosa*, and *B. gmelinii*), a single species of *Dryas* (*D. ajanensis*), and a single species of *Alnus* (*A. alnobetula*).

ISAM X took place in Kanazawa in Honshu in Japan in 2016, hosted by Tamotsu Hoshino (see above). It is an alpine area with much precipitation in winter, but also with high annual mean temperatures. Unfortunately the weather did not permit a trip to the top of Mt. Hakusan, to see if the mountain had specific alpine fungi.

6. Habitats

The division of arctic vegetation into types and subtypes is difficult, since conditions in the Arctic are highly variable, and so is the vegetation. Substrate is an important factor, whether solid or weathered rock, soil, sand, gravel, or turf. The water regime is important, whether from the saline sea, lakes, rivers, marshes and bogs, or melting ice and snow. Sun and wind exposure affect the temperature, the speed of desiccation, and the ability of basidiomata to form. When these factors are combined the landscape becomes a mosaic, often changing within a few metres, as is the case in southern Greenland. In contrast, large areas of northern Greenland have a more uniform climate and substrate, so more homogenous ecosystems can develop over much larger areas.

The habitat types listed below can occasionally be found in pure form, but very often they are more or less mixed, often within a short distance.

Arctic habitats are all characterized by a low temperature resulting from the high latitude or altitude. This means that the summer is short and the growing season – the biologically active period – is therefore also short. This makes it difficult or impossible for larger plants to grow, and the Arctic is characterized by a lack of true forests. At 10 °C, trees will not form large stands and are restricted to scattered groups of often twisted, windblown and deformed trees of small size. These shrubs belong to arborescent species of the genus *Betula* (birch). Further north, they are replaced by smaller species like *B. nana*, *B. glandulosa*, *B. michauxii*, *B. fruticosa*, and *B. humilis*. They are distributed up to the northernmost terrestrial places like Svalbard, although birches in such areas are very small, hardly reaching knee-height. All species of *Betula* in Arctic regions form ecto-mycorrhiza.

The other and most important genus of woody plants is *Salix* (willow). It is a large and difficult genus, but extremely important in Arctic habitats. Willows range from a few cm in height (as in *S. herbacea*) up to 2-3 metres tall, slender shrubs. *Salix arctica* is the northernmost woody plant in the world, ranging north to 50 metres from the northernmost point of land (Cape Morris Jesup in Greenland). Most species of *Salix* favour more or less wet habitats, but a few are adapted to dry windblown places. We recognize 66 species of *Salix* from arctic-alpine areas, forming the World Wide Web of Willows (see p. 167). It is likely that all species of *Salix* form ecto-mycorrhiza, but for some species growing in remote areas there are no records of symbiotic fungi.

In contrast to the many species of birch and willow, only one species of alder (*Alnus alnobetula*) is found in arctic-alpine areas, but it includes five geographic subspecies. In many places alders define the limit between arctic and subarctic, and between alpine and subalpine. *Alnus alnobetula* forms ecto-mycorrhiza, but with a much more limited number of fungi than *Betula* and *Salix.*

This is also true for the only conifer genus in arctic-alpine areas, *Juniperus*. It occurs in scrubs among other trees, or more rarely in open but sheltered situations. *Juniperus* does not form ecto-mycorrhiza, but instead forms vesicular-arbuscular mycorrhiza.

Copses

Subarctic birch forests or scrubs are distributed throughout most of the North and are often used to define the Arctic boundary (see Climate, p. 44). In southern Greenland copses of *Betula pubescens*, *Salix glauca*, and *Alnus alnobetula* occur in the innermost parts of fjords, in the inner parts of valleys, and in other sheltered places with reduced wind. These shrubs are usually 1–4 m high, but in the most protected valleys *B. pubescens* can reach a record height of 10.25 m, and a height of 7–9 m is not uncommon. The shrubs become shorter in central Greenland, and in northern

Greenland become low, knee-high, and often creeping, but still with a rich association of ecto-mycorrhizal fungi. *Alnus alnobetula* becomes shorter around Nuuk, and *Betula pubescens* even further south. Copses may be dense, and in this way provide protection against desiccation for hygrophilous species, and naturally for species adapted to ecto-mycorrhizal symbiosis.

Betula scrubs

Betula pubescens scrubs consist of trees of rather normal height (7–10 m). In northern Scandinavia and other boreal regions, trees have a typical diameter of 40 cm at a height of 1 metre. Trees in the Qinnqua Valley in Greenland (60°18'N, 44°30'W) are abnormally large, the largest known on the island (Fig. 19).

Colder habitats are often dominated by *Betula pubescens* subsp. *czerepanovii*, formerly known as *B. tortuosa*. In contrast to *B. pubescens* subsp. *pubescens*, subsp. *czerepanovii* is usually only 2-3 metres high and the trunks are mostly less then 20 cm in diameter. In the European Alps and the Carpathians it is replaced by *B. carpatica*, which is often twisted and polycormic. This tree, and its siblings in northern parts of Canada (*B. alba* coll., *B. borealis* in northeastern Canada, and *B. kenaica* in Alaska) are the dominant trees in subarctic and subalpine regions in Europe, North America, and northern Asia.

The dwarf birch, *Betula nana*, is distributed in the northern parts of the same regions. Southward and also in large parts of Canada and Siberia it is replaced by *B. glandulosa* (including *B. exilis*), in the Altai Mountains by *B. divaricata* (including *B. rotundifolia,* which gives its name to *Leccinum rotundifolium*), and in northeastern Canada (Labrador) by *B. michauxii*. The "trunks" of dwarf birches may become up to a few cm thick, and the bushes grow from knee-height to one or rarely two metres.

The genus *Betula* grows in many different habitats. *Betula pubescens* is often found in warm localities on slopes with southern exposure, or forming open scrubs on poor soil at the bottom of fjords. Dwarf species of *Betula* often occur in bogs or wet heaths, where they may dominate the vegetation, growing alone or mixed with species of *Salix*.

The genus is an excellent mycorrhizal symbiont, and many species of fungi are restricted to it, or are also found with *Salix*. The large species *Betula pubescens* is host to at least 87 species (see p. 218) of mycorrhizal fungi, but we have found at least 114 symbiotic fungi (see p. 220) associated with the dwarf species *Betula nana*. Whether this difference is real, or merely reflects the much greater distribution of *B. nana* in Greenland compared to that of *B. pubescens*, is still unknown.

There is a large difference between the number of parasites and saprotrophs on the trunks and branches of these two kinds of *Betula*. In Greenland we found *B. pubescens* to be a host for 32 species of mycorrhizal fungi (Elborne & Knudsen 1990), but now we can confirm an additional 55 species, bringing the total known to us up to 87 species. On dead and living wood of *B. pubescens* we have recorded 75 species, and on "trunks" and twigs of *B. nana* only a few species. It is very evident that the diversity of species on the two kinds of birch is directly correlated with tree mass, which is not always evident when two different genera of woody plants are compared.

In *Betula pubescens* scrubs the ground layer of herbs may consist of several plants not found in more open situations, like *Anthoxanthum odoratum*, *Dechampsia flexuosa*, *Hieracium*, *Chamaenerion angustifolium*, *Nardus stricta*, *Poa pratensis*, *Rubus saxatilis*, *Angelica archangelica*, *Alchemilla*, and *Galium boreale*.

Fig. 19. The author with an unusually large specimen of *Betula pubescens*. Photo by J. H. Petersen; Greenland, Tasermiut Fjord, Qinnqua Valley, August 1983.

Elborne & Knudsen (1990) made a list of 61 species of fungi living on or forming ecto-mycorrhiza with *Betula pubescens*. Among these are a number of polypores, which need a fairly large mass of wood to form basidiomata, e.g. *Bjerkandera adusta*, *Cerrena unicolor*, *Inonotus obliquus*, *Mensularia* (*Inonotus*) *radiatus*, *Phellinus lundellii*, *Polyporus brumalis*, *Stereum rugosum*, *Tyromyces chioneus*, and the large fasciculate agaric *Pleurotus ostreatus*. Large trees of *Betula pubescens* are uncommon in Greenland, in fact they are so few that they can be counted. Normal Greenlandic specimens of *B. pubescens* are smaller, 3-6 metres tall, growing in more exposed areas, often with twisted branches strongly shaped by the wind. This size is too small for many of the larger basidiomycetes, but they still have a rich funga of smaller agarics, corticioids, small polypores, and many smaller ecto-mycorrhizal agarics.

Fig. 20. *Peniophora aurantiaca* on *Betula pubescens* in southern Greenland.

Fig. 21. *Macrotyphula contorta* (vol. 4) on branches of *Betula* in southern Greenland.

Alnus scrubs

The only naturally and regularly occurring species of *Alnus* in arctic-alpine areas is *A. alnobetula*. It grows in moist places along streams and lakes in flat areas, but also on steep slopes and in other dry situations. The northernmost populations occur in Godthåbsfjorden. In central Canada it grows abundantly on sandy soil in open forests with ericaceous plants.

Alnus alnobetula forms scrubs that are more homogeneous and denser than those of *Betula* or *Salix*. The species is subdivided into five different geographic subspecies: *A. alnobetula* subsp. *alnobetula* (*A. viridis*) in the Alps; subsp. *crispa* in Greenland and Nunavut (Canada); subsp. *sinuata* (*A. kamschatica*) in the amphiberingian area (eastern Siberia and Alaska); and subsp. *fruticosa* in Alaska, northwestern Canada, and northern Russia including Siberia, but not Chukotka. The fifth subspecies *suaveolens* is restricted to Corsica. *Alnus alnobetula* sensu lato forms a wide belt in arctic-alpine areas, absent only in Iceland and Scandinavia, but it mostly grows between the subarctic/subalpine zone and the northern boreal conifer region. The ground cover in *Alnus* scrubs is usually not very rich due to the density of the shrubs, but at the edges and in clearings within the scrubs a large number of herbs and grasses can be found.

Alnus alnobetula sensu lato has only few associated species of ecto-mycorrhizal fungi (31 recorded to date, see p. 226). *Alnus* is peculiar among most northern trees by the presence of actinomycete bacteria (*Frankia* sp.) in its roots, which form small knobby excrescences that fix atmospheric nitrogen.

The most characteristic fungal associate of *Alnus* is *Naucoria* (*Alnicola*), which has the most species connected with *Alnus*, but many genera have one or a few symbiont species, even in arctic areas (e.g., *Naucoria*, *Paxillus*, *Russula*, *Lactarius*, *Cortinarius*, *Amanita*, and *Alpova*).

Alnus incana is found throughout Europe and North America but is absent in Siberia. It may occur in sheltered situations in subarctic regions, but in this work it is considered to be predominantly boreal, and is therefore not included.

Fig. 22. The truffle *Alpova diplophloeus* is strictly symbiotic with *Alnus alnobetula.* We have found it in Greenland and in the Alps.

Fig. 23. *Cortinarius bibulus* (vol. 7) is strictly symbiotic with *Alnus alnobetula* sensu lato.

Salix scrubs

We recognize 66 species of *Salix* from arctic-alpine areas (see Table 4, p. 169), making it by far the most dominant genus of woody plants, not only in number of species, but also in importance for the environment and for the basidiomycetes. *Salix* is a component of most plant societies in these regions, except where the habitat is too dry. Willows are present in nearly all scrub vegetation, occurring along streams and lakes, in mires, bogs, and fens, in depressions and other moist places, but also creeping from crevices in barren windswept areas. In dry places, they occur in snowmelt, and in the northernmost terrain on the globe they grow on top of the hummocks formed by ice.

In most cold areas there are numerous species of *Salix*. The islands of Greenland and Iceland are exceptional in having only five species each, whereas Alaska and Canada have 22 arctic and boreal species, Siberia has 23, and arctic Europe has 12. In alpine areas the numbers are slightly lower: alpine North America and Siberia each have 19 species, and alpine Europe has 20. Altogether, *Salix* forms a continuous, omnipresent belt of utmost importance to arctic-alpine environments. Many of the species are known to form ecto-mycorrhiza with basidiomycete and ascomycete symbionts. We suspect that they all do so, but more morphological study of their roots and more published observations from nature of symbionts growing with the "missing" species are needed. Although we have scrutinised the relevant literature, we have been unable to find any records of ecto-mycorrhizal fungi for the majority of arctic-alpine *Salix* species. The explanation for this may be straightforward. Most species of *Salix* are notoriously difficult to identify, not just for mycologists, but even for botanists, and since they are probably all functional symbionts, there has been less incentive to determine precisely which species grow with which fungi. A host symbiont is most often simply reported as "willow". So far, we have recorded more than 160 species of symbiont fungi for each of the two most widely distributed species, *S. herbacea* and *S. glauca*.

Fig. 24. An opening in a *Salix* scrub with a herbaceous ground layer in Greenland.

Fig. 25. *Cytidia salicina* (vol. 4) is common in arctic and boreal regions on older branches of *Salix*.

Fig. 26. *Lentinellus micheneri*, on a "trunk" of *Salix glauca*.

The size range of arctic-alpine willows is extreme, from a few cm/leaves in *Salix herbacea* to a few metres in *S. arbutifolia* and *S. arbusculoides*. One of the most common willows, *S. glauca*, reaches three metres in suitable protected localities, but it may also be a very low prostrate shrub, hardly rising above the ground.

Arctic-alpine willows are found from the extreme north (83°N) to the Mediterranean area. South of the Pyrenees and the Alps, alpine willows strongly decrease in abundance, and eventually disappear except for a few sporadic occurrences of *S. herbacea* and *S. hastata* in central Spain, and of *S. alpina* in the northern Apennines. Global warming is melting the snow in the Alps faster than ever, resulting in smaller snow patches that disappear earlier in the year, and a consequent lack of water for both willows and their associated fungi when the mushroom season starts in August.

A number of herbs occur in protected *Salix* scrubs, e.g. *Gymnocarpium dryopteris*, *Coptis trifolia*, *Angelica archangelica*, *Streptopus amplexicaulis*, *Oxyria digyna*, *Alchemilla*, *Taraxacum*, *Chaemaenerion angustifolium*, *Arabis alpina*, *Luzula parviflora*, *Cornus suecica*, and more.

Sorbus decora (*S. groenlandica*) occurs in Greenland and eastern Canada. *Sorbus aucuparia* (rowan) occurs in the rest of the cold world. *Sorbus decora* and *S. aucuparia* do not make mature seeds in arctic areas, rather depending on migratory birds to disperse their seeds. Also, they never form large stands, and we have found no basidiomycetes specific to rowan, except for the rust *Gymnosporangium cornutum* on the leaves.

Fig. 27. *Phaeomarasmius borealis* on a branch of *Salix glauca. Phaeomarasmius erinaceus* is very similar, but differs in having larger spores.

Herb slopes and alpine meadows

In general, herb slopes are south-facing, with rich fertile soil, a meadow-like appearance, and a high diversity of herbs. Mycologically they are characterized by small saprotrophic basidiomycetes and a lack of ecto-mycorrhizal species.

The most diverse plant societies in the arctic are found on south-facing slopes with stable running or seeping water, forming hotspots of arctic diversity. Important herbs are *Angelica archangelica*, *Sedum roseum*, *Alchemilla glomerulans*, *Bartsia alpina*, *Chamaenerion angustifolium*, *Hieracium*, *Lycopodium*, *Platanthera hyperborea*, etc.

The litter of many herbs is consumed by a number of small saprobiontic agarics like *Mycena*, *Hemimycena*, *Galerina*, *Marasmius* s.l., *Clavaria* s.l., *Psilocybe*, *Psathyrella*, *Coprinopsis* and *Conocybe.*

Fig. 28. An alpine meadow in the Altai Mountains, Russia. The diversity of plants is high, but the diversity of fungi is low. There are no bushes to host symbiotic fungi, and there is not enough cellulose in the plants to host larger fungi, but *Typhula* and similar genera may be present.

Fig. 29. Herb slope with *Angelica*, *Epilobium*, and other living and dead herbs and shrubs.

Fig. 30. *Mycena adonis* (vol. 4) on a small stick from the wet and sunny locality shown above.

Fig. 31. *Typhula* sp. (vol. 4) on *Angelica archangelica*, from the same kind of locality.


Fig. 32. *Typhula* sp. (vol. 4) on the rotten stem of a herb.


Fig. 33. *Pterulicium sclerotiicola* (vol. 4) on rotten herbs in a dried-out rivulet.


Fig. 34. *Typhula* on rotten leaves in a marsh.

Snowbeds

Snowbeds occur in depressions where snow persists for a long time in spring or summer, with many mosses and small plants, and often surrounded by *Salix herbacea*.

In areas with slopes, depressions, and much wind, snow may pile up and form thick layers. During the melting of snow in spring and summer, these snow patches persist for a longer time, gradually melting throughout the summer and creating a special cold environment in their vicinity. The cold saturated ground and high ambient moisture favour a special vegetation including many mosses. For mycology, the presence of *Salix herbacea* is important, whereas the presence of particular herbs like *Cassiope hypnoides*, *Carex bigelowii*, *Sibbaldia procumbens*, *Oxyria digyna*, *Ranunculus pygmaeus*, and *Cerastium cerastioides* is less relevant.

Fig. 35. Steen A. Elborne at a snowbed in Altai. The snow acts as a water supply for fungi in the surroundings.

Grassland slopes

Grassland slopes are similar to herb slopes, but with more grasses and fewer herbs. They are dominated by grasses on rich soil, often with an “understorey” of mosses and lichens. Mycologically they are characterized by small saprotrophic basidiomycetes like *Hygrocybe* s.l., *Entoloma*, *Clitocybe*, *Melanoleuca*, *Psathyrella*, *Galerina*, *Mycena*, *Psilocybe*, and *Clavulina*.

Fig. 36. Arctic grassland with a large population of *Alchemilla*. Such meadows have the highest primary production among arctic plant societies, but few or no basidiomycetes are associated with *Alchemilla*.

Fig. 37. *Melanoleuca* (vol. 5) is saprotrophic and typically grows in grasslands.

Fig. 38. *Entoloma catalaunicum* from an alpine meadow in the Tatra Mountains in Poland.

Fig. 39. *Hygrocybe* is a large genus occurring mainly in grasslands, with a so far unknown lifestyle. They are often associated with species of *Entoloma* subgen. *Leptonia* (see above). This photo is from southern Greenland.

Fig. 40. Puffballs are easily observed in open arctic landscapes, where the white, immature "golf balls" are visible at a long distance. A brown (= mature) *Vascellum pratense* (vol. 6) is figured here.

Arctic-subarctic steppe

In continental areas where precipitation is low and winter snow cover is thin, a dry grassland or steppe may develop. This biome is characterized by grass-like plants such as *Puccinellia deschampsioides*, *Carex supina*, and *Calamagrostis purpurascens*, as well as *Primula stricta* and *Potentilla hookeriana*. In some areas where minerals from surrounding deposits may create a highly alkaline soil, species like *Gentiana detonsa*, *Braya linearis*, and others may occur. We have not found fungi in these areas, but it is possible that some small saprotrophs grow there.

Polar deserts

In northern Arctic regions, polar deserts may develop in dry areas with less than 2% vegetation. Most of northern Greenland is a polar desert, continuing into northern Canada, as are some of the Russian islands north of the Russian mainland. East Greenland north of the Low Arctic is a polar semi-desert, and in the High Arctic a true polar desert is found.

At Truelove Lowland on Devon Island in the Canadian High Arctic, 25% of the land is ice, 50% is arctic desert, and hummocks composed of plants, mosses, and lichens comprise the remaining 25% (Bliss 1977). These societies, also frequently called arctic crusts, have a low biomass and thus provide sparse food for fungi. Characteristic fungi are species of *Arrhenia* and *Galerina* on mosses, *Clitocybe dryadicola* and *Lepista multiformis* on the polygons, and species of *Lichenomphalia*, *Multiclavula*, *Typhula*, and *Mycena.* Polar deserts are one of the poorest habitats for fungi due to the lack of water and scarcity of organic matter to consume.

Fig. 41. *Galerina harrisonii* is a High Arctic *Galerina* growing near snowbeds amongst the liverwort *Anthelia juratzkana*.

Fig. 42. The lichen *Multiclavula vernalis* (vol. 4), a symbiotic organism consisting of a fungus and an alga, adapted to areas with low mineral resources. Microscopic algae live around the base of the stem, where the two organisms exchange nutrients and water.

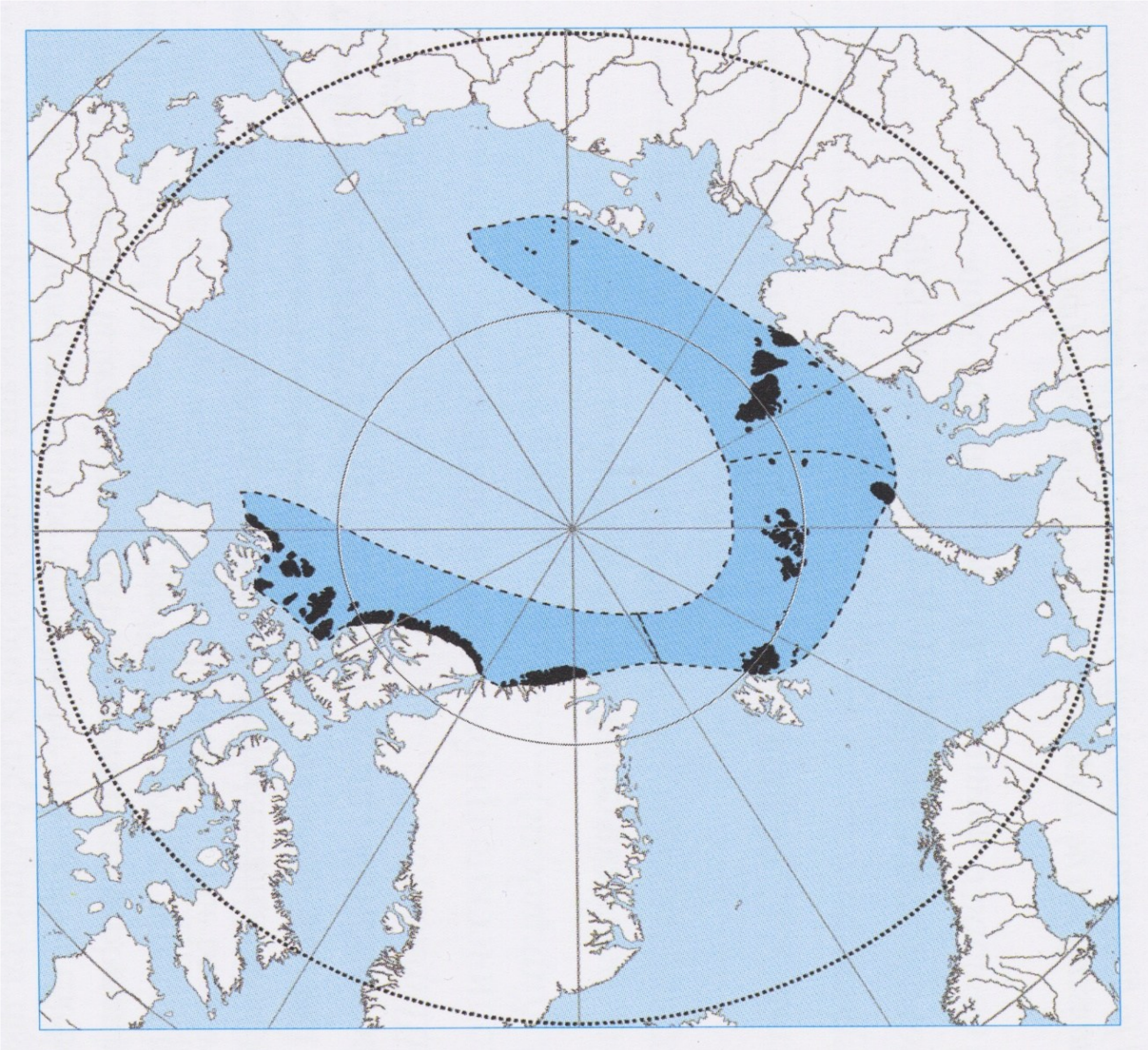


Fig. 43. Map of polar deserts (Matveyeva et al. 2015, Fig. 1). The dark blue area has an annual precipitation of around 200 mm. Precipitation in southern Greenland is very variable, from 400–1300 mm, and even up to 3000 mm in southeastern Greenland. Most polar deserts are situated in the High Arctic around 80°N (inner circle).

Tundra

The area north of the boreal forests is generally called tundra, from the Russian prefix "tundr". Tundra forms a huge part of all arctic and subarctic regions, and forms in response to the macroclimatic factors of low temperature, variable precipitation, and (often) permafrost. Plant cover is stunted, most often below one metre, and few shrubs are present, i.e. dwarf species of *Betula* and *Salix*, *Juniperus*, and many kinds of ericaceous heather. A number of herbaceous plants may also be present, depending on soil composition, pH, and moisture.

Dwarf shrub heaths (heather moors)

Ericaceous scrubs of dwarf shrubs are found on peaty soil, both wet and dry. In outer coastal areas of southern Greenland *Empetrum* and *Vaccinium uliginosum* usually dominate, whereas inland sites also include *Betula nana* or *B. glandulosa.* Further north, the heaths are more alkaline, and *Cassiope*, *Dryas*, or *Rhododendron* predominate. This kind of society is widespread and common in arctic areas and includes many fungi.

Fig. 44. Well-developed tundra with *Betula nana*, species of *Salix*, and even a conifer (middle left).

Fig. 45. Heath on granitic soil is more or less acid, with dwarf species of *Betula* constituting a fair part of the vegetation and often characterized by many ecto-mycorrhizal fungi and many specimens. As seen here, the production, i.e. turnover of organic matter, may be considerable, and the fungi are sometimes more conspicuous than the "forest"!

Species of *Rhododendron* (including *Ledum*) are woody shrubs in the heather family. In arctic areas there are only a few species, e.g. *R. lapponicum* and *R. groenlandicum*. In alpine areas a number of species are known, but since they do not form ecto-mycorrhiza, only a few basidiomycetes are associated with them. A few rusts are also parasites of *Rhododendron*, but very few fungi are associated with other species of the heather family.

Fig. 46. So-called wet tundra in northern Alaska, dominated by old rivers, old river arms, horseshoe lakes and smaller lakes. The typical vegetation is composed of grasses, cyperaceous (sedge-like) plants and *Salix* scrubs. In drier conditions, the vegetation gradually transitions to more typical ericaceous heaths, called tundra by the Russians, which further south is replaced by the "dark coniferous" forest, the taiga.

Fig. 47. *Cortinarius* (*Myxacium*) *absarokensis* from North America grows with *Betula nana.*

Fig. 48. In the Arctic most boletes belong to the genus *Leccinum*, which is symbiotic with *Betula* (vol. 4). *Betula nana* has at least 114 symbionts (see p. 220).

Fig. 49. *Amanita mortenii*, a recently described species of fly agaric from Greenland.

Fig. 50. *Russula* sect. *Polychromae* subsect. *Xerampelinae* (vol. 4).

Fig. 51. *Russula norvegica* (vol. 4) is one of the smallest and commonest of the 50-60 arctic species of *Russula*. The reddish-violaceous-blackish colors, white spores, acrid taste, and occurrence in acid soil in open situations, as seen here with *Salix herbacea*, make it easy to recognise.

Dwarf shrub heaths (calcareous tundra)

Heaths are not restricted to acidic ground. Jameson Land (central East Greenland) and the Disko Island region (central West Greenland) are both calcareous. Heaths are dominated by dwarf shrubs of the heather family (Ericaceae) like *Rhododendron lapponicum*, *Cassiope tetragona*, *C. hypnoides*, *Vaccinium uliginosum*, *V. vitis-idaea*, *Empetrum nigrum* ssp. *hermaphroditum*, *Arctostaphylos alpina*, and *Arctous uva-ursi*, and often species of *Dryas*, which is a good indicator of calcareous soil. Most Ericaceae do not form functional ecto-mycorrhiza, but *Dryas* has at least 80 known symbiotic fungi. Fungal symbionts may also occasionally be found with *A. uva-ursi* or *C. tetragona,* but never in large numbers, and no macrofungi are strictly associated with them.

The most common arctic species of Ericaceae are *Empetrum nigrum* ssp. *hermaphroditum*, especially in coastal areas on granitic bedrock, and *Cassiope tetragona*, in more continental northern areas and often on rich calcareous soil. In the heaths, *Vaccinium uliginosum* may occur everywhere, and *Rhododendron* occurs on slopes and open areas.

Ericaceae forms vast stretches of heath in arctic areas, but they are not important for the basidiomycetes, and we do not know of any ecto-mycorrhizal species associated with them, only a few saprotrophic basidiomycetes that grow on their stems and debris.

In heaths mixed with *Betula*, and especially in moist places, many *Betula* symbionts occur. Common genera are *Cortinarius*, *Inocybe*, and *Hebeloma*; less common are *Russula*, *Lactarius*, and *Amanita*.

Fig. 52. *Inocybe* sensu lato (shown here) and *Cortinarius* sensu lato (vols. 6 and 7) are the two largest genera of fleshy basidiomycetes in arctic regions, each with over 100 species. They occur in most plant communities.

Fig. 53. *Cortinarius* sp. (vol. 6) growing with *Dryas*.

Dryas is a frequent ecto-mycorrhizal host, having many fungal symbionts from many genera (see pp. 228-234), e.g. *Cortinarius. Dryas* prefers rich soil, and thus mostly hosts symbionts from genera that also (mostly) prefer rich soil, like *Inocybe.*

The genus *Dryas* is taxonomically difficult, but we recognize nine ectomycorrhizal arctic-alpine species, taken from Kew's Plants of the World Online. Four of these are more or less amphiberingian, four are endemic to Siberia or Eurasia (including *D. octopetala*, which extends to northeastern Greenland), and one is endemic to North America.

The genus generally occurs in dry open areas, on rocky slopes, barren plateaus, and sandy dune- or steppe-like areas. The ground must be alkaline, e.g. calcareous rocks, or sandy areas of old sea bottom with remnants of mussels. Similarly, *Dryas* avoids granitic areas and bedrock.

Dryas forms ecto-mycorrhiza with a large number of basidiomycetes and ascomycetes. There are a few species of fungi that are exclusively symbiotic with *Dryas*, but for most of the fungi it seems to be a matter of preference for calcareous habitats rather than a strict dependence on *Dryas*. Thus, *Dryas* has many symbionts in common with other ecto-mycorrhizal host plants. Often, *Dryas* can extend the distribution of calciphilous fungi; those occurring in temperate and boreal areas with conifers or Fagaceae often continue north with *Dryas* as their new symbiont.

We have not found fungi exclusive to only one species of *Dryas*, but our knowledge of the fungi associated with *Dryas* is still so insufficient that this level of specificity is difficult to assess. For *D. octopetala* and *D. integrifolia*, the two best-known species of *Dryas* associated with fungi, we have recorded 86 and 42 species of symbiont, respectively (see pp. 233 and 232).

Even though *Dryas* has many symbionts, these dwarf shrubs are small, so the number of saprotrophs on the stems and leaves is also small. The most well-known is *Mycetinis epidryas* (Fig. 55) growing on the small leathery leaves.

Dryas is widely distributed in cold areas, and has no northern limit, being found up to the northernmost point in Greenland at 83°N. In southern areas it is only found in mountains, except for a few very oceanic occurrences in western Ireland at sea level (The Burren).

Because it requires open areas, *Dryas* is not found in scrubs with other woody plants, but the genus may occur with prostrate willows and birches in open heaths with low vegetation.

Fig. 54. *Dryas octopetala* is symbiotic with at least 86 species of basidiomycetes.

Fig. 55. *Mycetinis epidryas* on old withered leaves of *Dryas*. It is one of the few larger saprotrophic fungi on *Dryas*, but Chlebicki & Knudsen (2001) found 33 species of microfungi on *Dryas*.

Fell-fields (abrasion fields)

Fell-fields are characterized by scattered plants on bedrock or rocky ground, in open, dry, windswept conditions. The habitat does not favor fungi, and the only species we regularly find is *Arrhenia auriscalpium*.

Fig. 56. Rocky substrates contain little or no organic food for fungi.

Beaches and dunes

On dry sandy or gravelly areas along the coast, a dune landscape may develop, which includes typical fungi from similar temperate landscapes. Riverbeds are another widespread sandy type of habitat. *Conocybe ammophila* is an arctic species described from central Greenland from calcareous dunes. Species of *Laccaria*, *Lycoperdon*, and *Calvatia*, as well as *Geastrum minimum*, are known from similar sites.

Fig. 57. Inland dunes along the river in Kangerlussuaq, Greenland.

Fig. 58. *Laccaria maritima* (vol. 6) forming ecto-mycorrhiza with *Salix* in a dune area near Constable Pynt, East Greenland.

Fig. 59. *Pseudosperma arenicola* (vol. 7) growing in sand with *Salix* in a riverbed in East Greenland.

Bogs

Arctic bogs occur on wet, often peaty, and acidic ground, with hummocks, dwarf shrubs, sedges, and many mosses. This habitat type is common and widespread in the Arctic, and it has a varied funga, partly of symbionts with dwarf birches and willows, and partly of saprobionts on mosses and other plants.

Fig. 60. *Arrhenia lobata* (vol. 5) is common on mosses in wet bogs.

Fig. 61. *Arrhenia* (vol. 5) is one of the few fungal genera where the number of species in the Arctic is larger than in temperate regions.

Hypholoma elongatum (vol. 7).

Clavaria argillacea var. *sphagnicola* (vol. 5).

Galerina sp. (vol. 7).

Psathyrella sp. (vol. 6).

Fig. 62. These four fleshy fungi occur in peat bogs.

Fig. 63. *Sphagnurus* (*Tephrocybe*) *paluster* is a parasite on *Sphagnum* in moist bogs. In temperate regions it appears in early summer, and in arctic regions in the autumn (August).

Fens and marshes

Fens and marshes occur on wet, often basic, clayey ground, with many grasses and meadow plants. In cold northern areas, heat from the sun is limited, and water from melting snow persists for longer periods in holes and depressions. Different kinds of fens and marshes develop in response to soil type, availability of nutrients, depth of water, and other factors. Due to more or less permanent hydration, habitat appropriate for fungi is restricted, and few basidiomycetes occur. Fens and marshes are dominated by sedges, rushes, and horsetails, like *Eriophorum angustifolium*, *Scirpus caespitosus*, *Carex stans*, *Equisetum variegatum*, and depending on the depth of the water, shrubs of *Vaccinium uliginosum*, *Oxycoccus quadripetalus*, and similar Ericaceae.

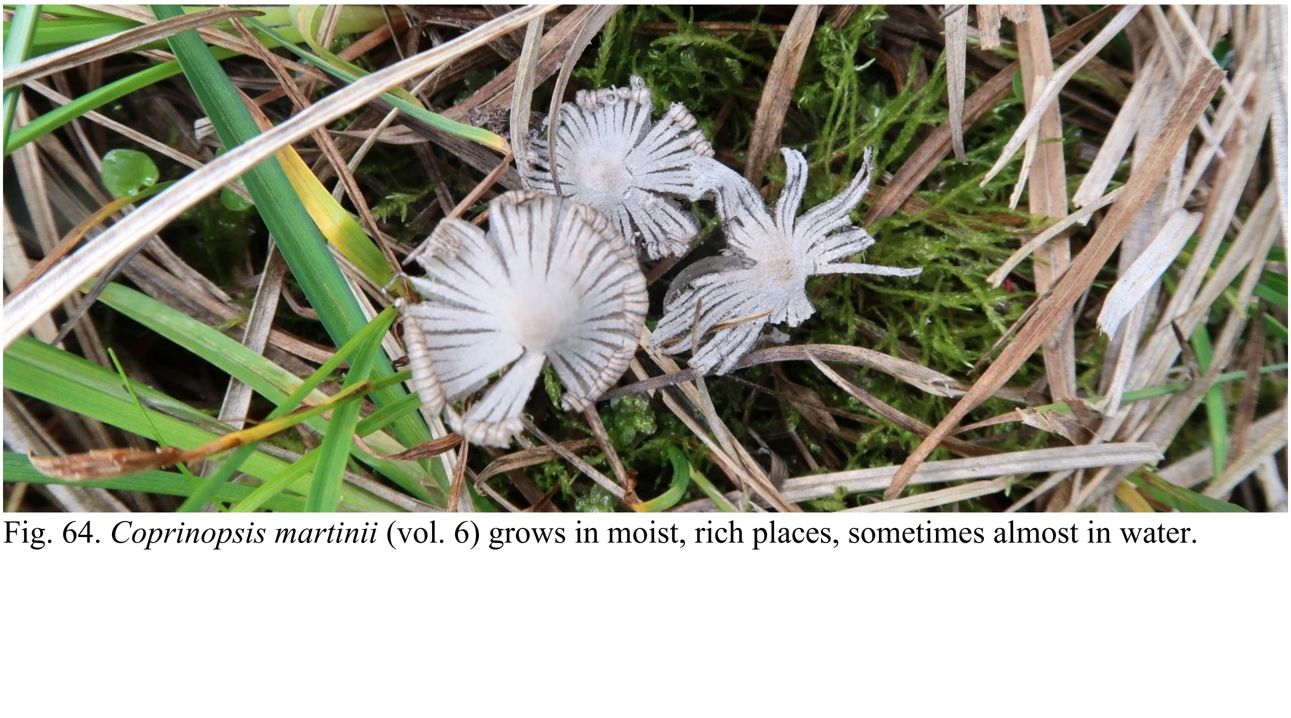


Fig. 64. *Coprinopsis martinii* (vol. 6) grows in moist, rich places, sometimes almost in water.

Fig. 65. *Lactarius pseudouvidus* grows with *Salix* in fens and at the margin of snowbeds, often in association with the yellow *Lactarius salicis-herbaceae* (vol. 4).

Fig. 66. *Thaxterogaster* (*Cortinarius*) *porphyropus* (vol. 6) is symbiotic with *Betula* on moist ground.

Solifluction soils, salt marshes, and lakes

These habitats are not known for a regular occurrence of any fungal species, but *Arrhenia auriscalpium* has been found.

Non-plant associations

Habitats like forests, bogs, mires, dunes, etc. are often characterized by the presence of certain plants. In the fungal world some extra "communities" occur, unrelated to plants, and characterized by specific fungi associated with non-plant substrates. Three of these substrates occur in arctic areas: dung, bonfires, and other fungi:

Fungi on dung

Musk ox dung has an influence on the arctic environment. Booth (1977) calculated that musk ox dung accumulation was 3.2 g/m^2 in their preferred habitat (*Salix* meadows), and was 1.3 g/m^2 on ridges. Since 3.2 g/m^2 is the average over a large area, the local density of dung at the places where the droppings actually are is much higher, which has an influence on both the plant cover and the local community of fungi. Booth also found that decomposed nutrients were utilized within a very short distance from the dung, and noted that the length of hyphae under dung was considerably larger than just a few cm away from the dung. At least some plants were favoured by the dung, e.g. plants of *Carex stans* and *C. membranacea* were darker green than those further away from the dung. Booth's conclusion was that High Arctic terrestrial ecosystems are not nutrient-poor, they are nutrient-random.

When a musk ox dies in the Arctic, bears, wolves, and foxes eat the meat, along with ravens and other birds, and finally many insects. The fur will be consumed by fungi (Onygenales and other groups), and even the keratin in the horns and hooves will be consumed by the ascomycete *Onygena equina* and related species. The decomposition of keratin is a small part of the Arctic turnaround of nutrients whereas the decomposition of the dung of these large animals by fungi is a significant part. Most dung fungi belong to the Pezizales and are not relevant in this work, but after the "phycomycetes" and ascomycetes, species of *Coprinus*, *Conocybe*, *Psathyrella*, *Psilocybe*, and *Stropharia* are also important decomposers of musk ox dung.

Repeated freezing and thawing in the winter sometimes results in the formation of a thick crust of ice, which hinders the ability of musk oxen to graze on the buds of willows. This may result in the death of a whole group from starvation. Such "graveyards" of 5–10 individuals are not rare. Their carcasses help foxes and ravens to survive, and most of the skeletons are often removed, leaving only the heavy skulls. As the skulls slowly decay and sink into the ground, *Onygena equina* consumes the underground parts of the horns and makes ascomata on the surface. This fungus was common long ago. When every village blacksmith put new shoes on horses, they cut pieces from the hooves to make them fit. These bits of hoof became food for the fungus.

Musk ox dung is large and affects the environment. Reindeer dung may have a similar ecological role, but we have not studied this substrate. Other herbivores in the Arctic, like blue hares, voles, and Norway lemmings are too small for their dung to have an influence, although they may provide a substrate for fungi. In alpine regions, chamois, wild goats, and alpine marmots similarly provide dung for fungi, but this is poorly investigated. Dung from carnivores is also decomposed by fungi, but not basidiomycetes. Birds also contribute to nutrient cycling, and members of Pezizales are common on e.g. the dung of grouse and other large herbivorous birds. *Coprinus miser* is known from dung of ptarmigan (cf. Lange in Laursen & Chmielewski 1982: 491).

Fig. 67. Large musk oxen impact the vegetation by herbivory, and their dung is a substrate for a large number of fungi. This recycling of the dung contributes minerals to the ecosystem that are taken up by growing plants.

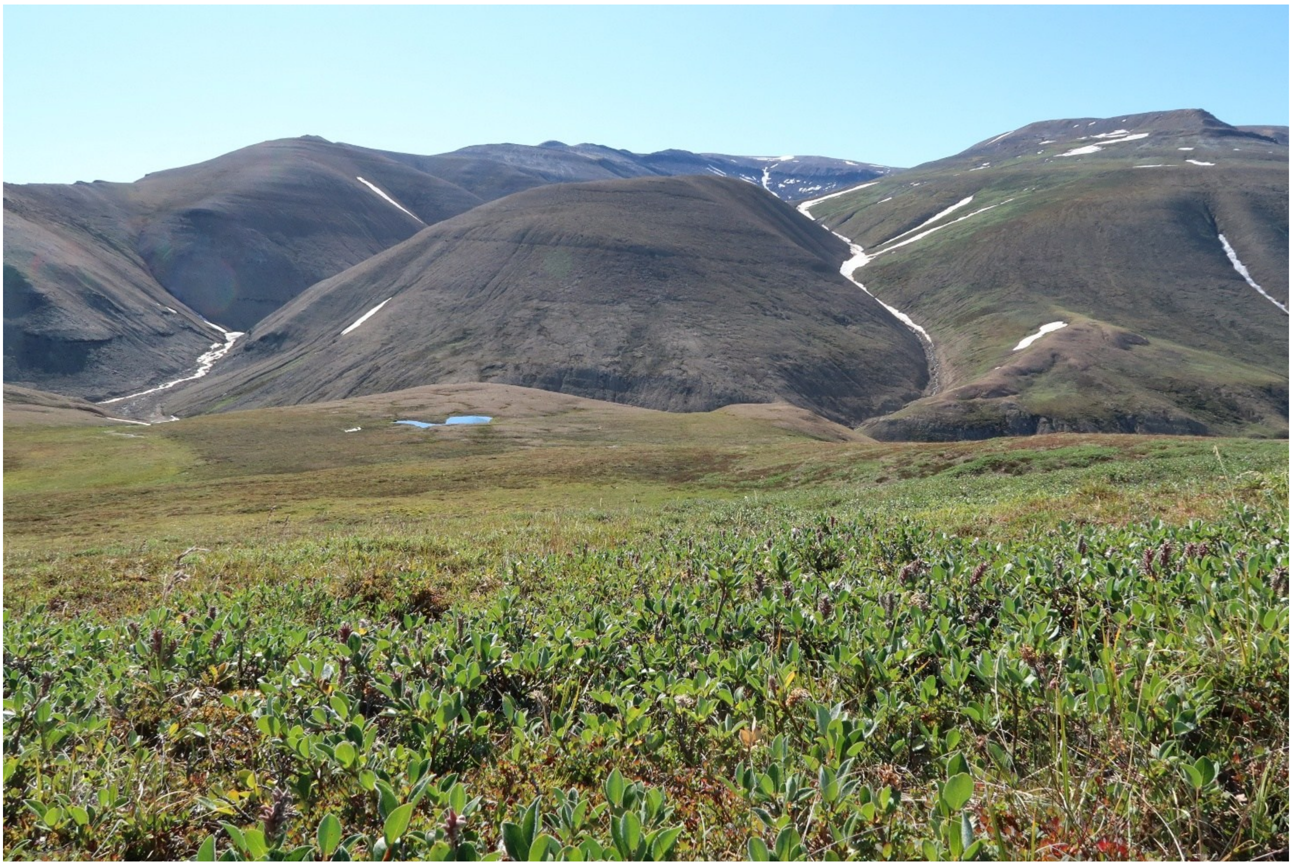


Fig. 68. Ptarmigan habitat in Jameson Land, central East Greenland.

Fig. 69. Musk ox graveyard.

Fig. 70. Skeleton of a musk ox, with a peripheral brown halo of fur decomposed by fungi of Onygenales and other Eurotiomycetes. An *Inocybe* (so far not identified) occurred in masses around this skeleton, probably fed by its nutrients. Fresh dung on soil with no mosses also stimulated the development of a ring of mosses the following year. Similarly, small mounds of dung or animal remains (e.g. that of snowy owls and lemmings) stimulate the growth of other organisms.

Fig. 71. Musk ox dung is decomposed by many fungi in a more or less strict sequence: first by phycomycetes s.l., then by ascomycetes, and finally by basidiomycetes. Two species of ascomycetes, both belonging to Pezizales, are seen here: the large *Peziza stercorea*, and a small (suspected) species of *Cheilymenia*.

Fig. 72. *Stropharia semiglobata* on horse dung, from domesticated horses in South Greenland.

Fungi on burned sites

Although devastating to most organisms, a fire in nature may produce a fungal society that literally rises from the ashes. The ashes act as a powerful fertilizer, and the heat sterilizes the ground below, so there is no competition from other organisms. In this very specific and very small ecological niche, a specific society of fungi occurs (Petersen 1975, 1977). Fire as an ecological factor is naturally rare in Arctic regions, due to the lack of wood, but even small bonfires may give rise to fungi. Most of them belong to the Pezizales, but a few pyrophilous agarics also depend on fire: *Fayodia anthracobia* and *Tephrocybe anthracophila* (vol. 5), and *Pholiota highlandensis* (vol. 7).

Fig. 73. *Tephrocybe anthracophila* is an agaric adapted to burned sites. Borgen 85.306; Greenland.

Fungi on fungi

Fungi also need to be recycled, but only few fungicolous species are found in arctic-alpine regions. *Collybia cirrata* (Fig. 74) is rather common at least in the Low Arctic, but *C. tuberosa* has also been found. *Collybia cookei* is on the contrary missing from high latitudes, as are the two species of *Asterophora*.

Fig. 74. *Collybia cirrata* (vol. 5) on the mummified remnants of a *Russula*. It commonly occurs in nutrient-poor localities.

7. Phenology

The actual time when a particular fungus appears is called its phenology. To determine whether the phenology of fungi in the Arctic differs from that of temperate regions, we made Figure 75. The x-axis shows the collecting season in Greenland, from the middle of July to the middle of September. The y-axis shows the number of collections of Greenland agarics in fungarium C made over this 62-day period (10,515 collections in total).

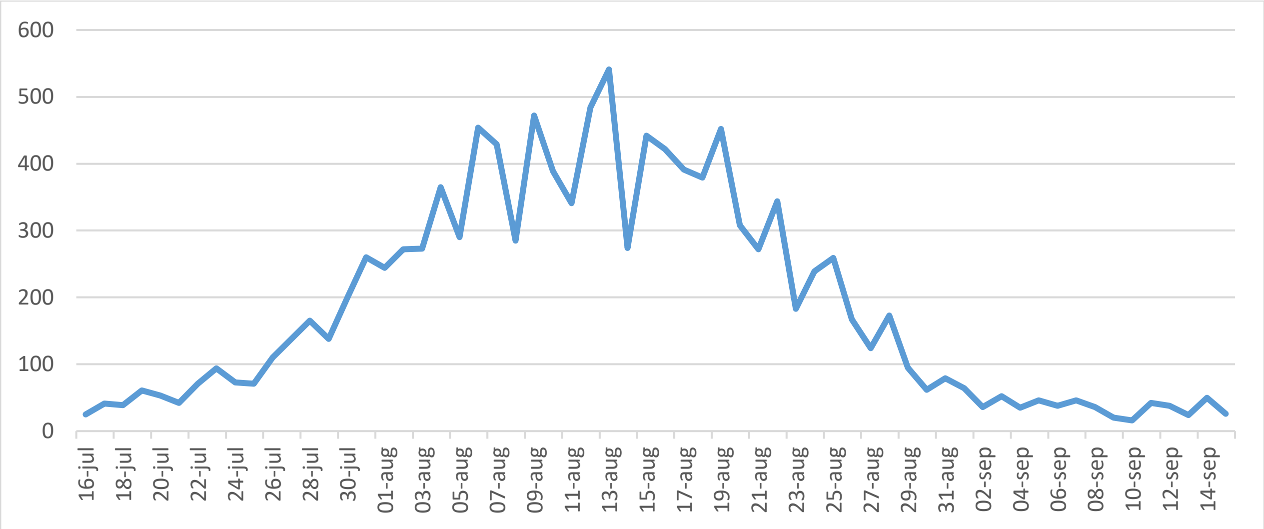


Fig. 75. Daily numbers of Greenland agarics in fungarium C.

It may be seen in Fig. 75 that August is the month in which the highest number of fungi were collected, and that yields in July and September were far lower. In spring lichenized species may occur as some of the first, e.g. species of *Lichenomphalia*. In Northern Europe, peak collecting season for agarics is roughly from mid-August to mid-October, so approximately one month later and one month longer than in Greenland. The large day-to-day variation in the middle of the season may be due to our system of collecting: one day we collect, and the next day we identify the collections.

With the compressed growing season in the Arctic, a few fungi stand out as having an aberrant phenology. One example is *Agrocybe elatella*, shown below, occurring in wet marshy areas in June and July. In contrast, *Omphaliaster asterosporus* may occur as a latecomer in the second half of September.

Fig. 76. *Myriosclerotinia vahliana* is the first larger fungus appearing in arctic areas in spring.

Fig. 77. *Agrocybe elatella* is one of the few agarics occurring early in the season (“out of season”) in both arctic and temperate regions.

Fig. 78. *Omphaliaster asterosporus* has a late season in Greenland, to the end of September.

8. Patterns of distribution

Climatic distribution types

Arctic: Not found outside Arctic areas. All species are included.

Subarctic: Species with their main distribution south of the subarctic are included if they are common in the subarctic zone. If their main distribution is to the north (Arctic) and thus the subarctic is their southern limit, they are generally included.

Alpine: Species with their main distribution in alpine areas are included. A few records may also be included from outside the alpine area.

Arctic-alpine: All species with their main distribution in arctic-alpine areas are included.

Temperate-arctic: Distributed from the temperate zone to the arctic zone, but not in alpine zones. All records from the arctic zone are included in the maps, but records from outside the arctic zone are only mentioned in the text.

Temperate-alpine: Distributed from temperate to alpine areas, but absent in the Arctic. All records from alpine areas are included in the maps, but records from non-alpine areas are only mentioned in the text.

Temperate-arctic-alpine: distributed from temperate to arctic and alpine areas. All records from alpine and arctic areas are included on the maps, but records from other areas are only mentioned in the text.

Predominantly temperate, hemiboreal or boreal: Species with their main distribution in one of these areas, even if there are a few scattered records from the arctic or alpine zones, are not included.

Geographic distribution types

Circumpolar: Occurring all around the North Pole.

Amphi-Atlantic: Occurring on both sides of the Atlantic Ocean, but not in the western USA or eastern Russia.

Amphiberingian: Occurring on both sides of the Bering Strait, but not in eastern Canada, western Siberia or Europe. The zone may extend across eastern Siberia to central Siberia (Lena), and in North America to the Yukon (Hultén & Fries 1986).

Western: Occurring in North America, but not or only in a small part of Europe.

Eastern: Occurring in Eurasia, but not or only in a small part of North America.

Cosmopolitan: Occurring all over the globe.

We use the broad distribution types above, and furthermore we have divided the distribution of basidiomycetes into 15 more specific types (see below). These types have been applied to the rusts in volume 2 and to the smut fungi and tremelloids in volume 3. We intend to continue this system in in the forthcoming volumes, and perhaps to refine it as more species are added.

Distribution types for arctic and alpine basidiomycetes

Fungi distribute themselves by spreading huge numbers of spores. They spread unpredictably depending on the wind. Since two spores from different mating types must land close to each other, even a huge number of spores may not be enough. Even when spores land in a promising place, many fungi are so specific to their substrate that they will not germinate because the substrate is not quite right. Finally, the ease with which they blow around makes it difficult for one spore to meet another spore and thus to spread to new places.

When volumes 4-7 are finished, we will be able to give a more detailed overview of the distribution types for basidiomycetes. At present we can only give a preliminary assessment.

There are four large categories (regions): two are geographic, North American (NA) and Eurasian (EU); and two are climatic, arctic (Arc) and alpine (Alp). The various combinations of these regions yield 4 × 4 = 16 different possible distribution types:

There are four possibilities for occurrence in a single region: NA, EU, Arc, Alp.

There are six possibilities for occurrence in two regions: NAArc-EUArc; EUArc-EUAlp; EUAlp-NAAlp; NAAlp-NAArc; NAArc-EUAlp; NAAlp-EUArc.

There are four possibilities for occurrence in three regions: NAArc-EUArc-EUAlp; EUArc-EUAlp-NAAlp; EUAlp-NAAlp-NAArc; NAAlp-NAArc-EUArc.

There is one possibility for occurrence in all four regions: NA-EU-Arc-Alp.

The last (16th) possibility is the situation where there are no records from any of the four regions, and therefore not interesting to us. Thus, we have divided arctic and alpine basidiomycetes into the following 15 distribution types:

Occurring in all four regions

Type 1. Both North American and Eurasian, both arctic and alpine.

Occurring in three regions

Type 2. North American arctic and alpine, Eurasian arctic.

Type 3. North American arctic and alpine, Eurasian alpine.

Type 4. Eurasian arctic and alpine, North American arctic.

Type 5. Eurasian arctic and alpine, North American alpine.

Occurring in two regions

Type 6. Arctic in both North America and Eurasia.

Type 7. Alpine in both North America and Eurasia.

Type 8. Both arctic and alpine in North America.

Type 9. Both arctic and alpine in Eurasia.

Type 10 North American arctic, Eurasian alpine.

Type 11. North American alpine, Eurasian arctic.

Occurring in only one region

Type 12. North American arctic.

Type 13. Eurasian arctic.

Type 14. North American alpine.

Type 15. Eurasian alpine.

Below, Tables 2 and 3 show the frequency of all 15 distribution types.

Type 1 (all four regions) is the most common pattern, presently 44.5% of the species.

Type 15 (Eurasian alpine) is second, presently 25.0% of species.

Type 9 (Eurasian arctic-alpine) is third, presently 14.5% of species.

Type 5 (Eurasian arctic-alpine, North American alpine) is fourth, presently 13.5% of species.

Type 4 (Eurasian arctic-alpine, North American arctic) is fifth, presently 11.5% of species.

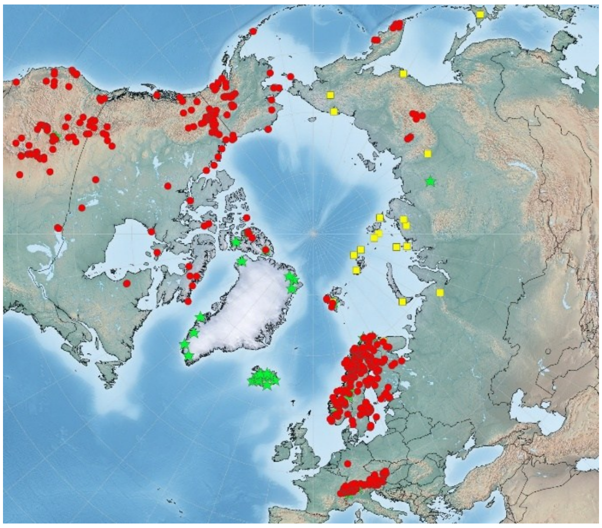
Table 2. Distribution of 142 species of rust fungi (see volume 2).

Distribution type	No. of species	% of species	
Type 1	46	32%	North American–Eurasian arctic-alpine
Type 15	25	18%	Eurasian alpine
Type 5	21	15%	North American alpine & Eurasian arctic-alpine
Type 7	12	8%	North American–Eurasian alpine
Type 9	10	7%	Eurasian arctic-alpine
Type 4	7	5%	North American arctic & Eurasian arctic-alpine
Type 13	5	4%	Eurasian arctic
Type 14	5	4%	North American alpine
Type 2	2	1%	North American arctic-alpine & Eurasian arctic
Type 3	2	1%	North American arctic-alpine & Eurasian alpine
Type 6	2	1%	North American–Eurasian arctic
Type 8	2	1%	North American arctic-alpine
Type 11	2	1%	North American alpine & Eurasian arctic
Type 10	1	1%	North American arctic & Eurasian alpine
Type 12	0	0%	North American arctic

Table 3. Distribution of 140 species of smut fungi and tremelloids (see volume 3).

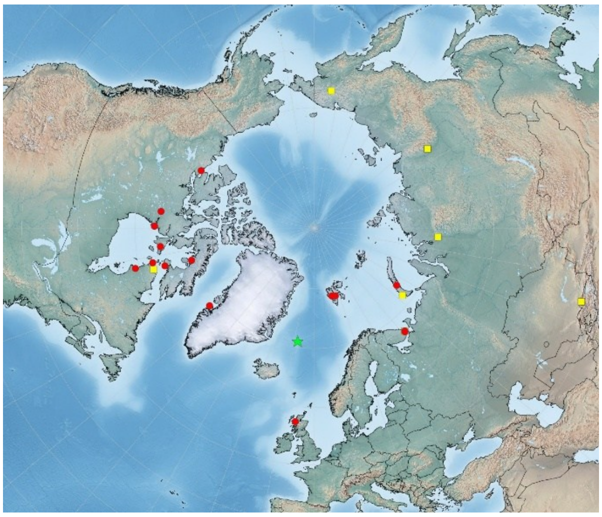
Distribution type	No. of species	% of all species	
Type 1	43	31%	North American–Eurasian arctic-alpine
Type 15	25	18%	Eurasian alpine
Type 9	19	14%	Eurasian arctic-alpine
Type 4	16	11%	North American arctic & Eurasian arctic-alpine
Type 12	8	6%	North American arctic
Type 14	7	5%	North American alpine
Type 5	6	4%	North American alpine & Eurasian arctic-alpine
Type 10	5	4%	North American arctic & Eurasian alpine
Type 3	3	2%	North American arctic-alpine & Eurasian alpine
Type 6	3	2%	North American–Eurasian arctic
Type 7	3	2%	North American–Eurasian alpine
Type 8	2	1%	North American arctic-alpine
Type 13	0	0%	Eurasian arctic
Type 2	0	0%	North American arctic-alpine & Eurasian arctic
Type 11	0	0%	North American alpine & Eurasian arctic

If the distribution types are compared by continent, then only 5% of North American rusts are not known from Eurasia, whereas 29% of Eurasian rusts are not known from North America. This difference may be due to the different sizes of the arctic-alpine regions in the two continents, but it may also reflect the somewhat greater intensity of exploration for fungi in Europe. The position of the Alps in the middle of Europe, easily accessible from many countries, has attracted many collectors, and many different collectors have reported various species and fungal aspects from the Alps. Both the size and plant diversity of the Rocky Mountains greatly exceeds those of the Alps, but the number of large mycological institutions in North America is lower. We believe it unlikely that the apparent difference is due to a real difference in rust diversity between the two areas.



Melampsora epitea is one of the most common rusts in cold regions, occurring in temperate, arctic, and alpine habitats. The map gives a good overview of collecting localities for Funga Arctica & Alpina.

Uromyces allii-sibirici grows on *Allium schoenoprasum*, which is widely distributed in temperate, boreal, and arctic regions. The rust is only known from the type locality in northernmost arctic Norway, but it may occur with the host along the Arctic Ocean.



Puccinia eutremae is a parasite of *Cochlearia* in arctic areas, and rarely in temperate regions. Although the host is common, the fungus is rarely recorded.

Puccinia soldanellae is restricted to *Soldanella*, which is itself restricted to the Alps and other alpine regions of Europe.

9. Biological interactions between plants and fungi

Parasitism

Fungi live on organic matter, but in very different ways. The most widespread way is by parasitism, i.e. directly attacking living plants, often resulting in the death of the plants. In volume 2 the arctic-alpine rusts are treated, and in volume 3 the arctic-alpine smut fungi. An overview of this phenomenon in cold areas follows, including 142 rusts and 107 smuts attacking 951 plant species. The list includes all Greenlandic plants except for introduced garden and forestry species, as well as a number of plants from other regions that are attacked by the same fungi. Plant names are only given at the species rank; infraspecific taxa and hybrids are excluded. Plant names are in black, and their accompanying fungal parasites are in red.

Families are arranged systematically, with genera and species in alphabetical order.
Plant classification, names, and authorities follow Kew's Plants of the World Online (powo.science.kew.org).

Saprotrophism

Saprotrophism is a common nutritional mode among the basidiomycetes in cold areas. Consumption of dead organic matter is the prototype of fungal life, and numerous species are adapted to this lifestyle, including those found in arctic and alpine regions.

In regions that are excessively cold or dry it may be surprising to find many saprotrophs, since the amount of organic matter is less than anywhere else. In addition, large parts of the Arctic are situated in continental areas with low precipitation and consequently a very reduced plant cover.
A list of saprotrophic fungi from cold regions arranged by substrate is given on pp. 158-165.

Ecto-mycorrhiza

Mycorrhiza are a symbiosis between a plant and a fungus, taking place in the roots, where nutrients are exchanged between the two organisms. A symbiosis is a partnership between two organisms, where both partners benefit. Generally, the plant partner (host symbiont) delivers polysaccharides to the fungus, and the fungal partner provides minerals and water to the host.

There are many types of mycorrhiza, but most are made by microscopic fungi that are not easily identified and do not form basidiomata, e.g. endomycorrhiza, ericoid mycorrhiza, or orchid mycorrhiza. These are not treated in this work.

In arctic-alpine regions, so-called ecto-mycorrhiza are frequent. This kind of symbiosis occurs between a plant (mostly trees or shrubs) and a fungus, and it is extremely important in cold areas. A list of ecto-mycorrhizal host families and genera in cold regions (Salicaceae, Betulaceae, Rosaceae, Polygonaceae, Cistaceae, Ericaceae, Primulaceae, Cyperaceae, Saxifragaceae, and Scrophulariaceae) is given on pp. 166-246.

9a. Parasitism

Parasitism is a lifestyle in which one organism exploits another. Thus, in contrast to symbiosis, where both partners benefit from the relationship, only the parasite, and not the host, benefits.

The phenomenon of parasitism in fungi is distributed in all geographic regions. This is partly a function of the obligate parasitic lifestyle of the rusts (vol. 2) and the smut fungi (vol. 3), groups that only include parasitic species. In addition to these two large groups, many other small and large groups of fleshy basidiomycetes are parasitic.

Many heterobasidiomycetous fungi are also parasitic or presumed to be parasitic. All species of *Tremella* are parasites, and three groups are parasitic on other fungi. One group is parasitic on large pyrenomycetes, one group on lichens, and one group on corticioid fungi (Diederich et al. 2022). These three groups are all represented in the Arctic: *T. karstenii* on the pyrenomycete *Diatrype* on *Juniperus*, *T. penetrans* in *Dacrymyces* spp., and *T. sibirica* (see vol. 3, p. 299) on the corticioid *Megalocystidium leucoxanthum*.

Many polypores are more or less parasitic. *Fomitopsis betulina* attacks large species of *Betula*, killing the trees before basidiomata are formed. *Fomes fomentarius* also lives on *Betula* and will also kill the tree, but basidiomata appear on the tree much earlier. Species of *Phellinus* s.l. and *Inonotus* s.l. take a longer time to kill trees, but sooner or later this does happen to trees attacked by *P. obliquus*, *P. lundellii*, *P. nigricans*, and *Mensularia* (*Inonotus*) *radiata*. The absence of large woody trunks in true arctic landscapes strongly limits the number of these parasites. On the other hand, we have often observed that a large number of trees in an arctic population were infected, possibly due to a slow rate of growth and thus a longer lifespan. We find it likely, but not certain, that the fraction of parasitized individuals in a population increases with altitude. This may be explained by the low temperatures (frost), which may occur at any time of the year, slowing growth but also prolonging lifespan. Measurements of the lifespan of *Pinus silvestris* in the alpine Ural Mountains have shown that the trees are up to 400–500 years old, some even 500–600 years. Over more seasons, the trees are more likely to be attacked by parasites. The same phenomenon may occur among the lichens, i.e. the older they are, the more likely the chance they will be attacked.

Large regions of the Arctic are covered by mosses and lichens. This is not surprising, since many lichens are small and perennial, and may start to grow as soon as temperatures are above freezing. Mosses are small simple plants that require little time to complete their life cycle, whether from spores or overwintering parts of the plants. Thus it is not surprising that many fungi living on mosses are found in arctic areas. Different basidiomycetes have different relationships with mosses, and the particular type of lifestyle – saprotrophic, parasitic or both – is not always known. Most likely the whole spectrum from obligate parasites to facultative parasites to pure saprotrophs exists. We find species of *Omphalina*, *Rickenella*, *Arrhenia*, *Hypholoma*, and *Galerina* on mosses, as well as *Cantharellula umbonata* (cf. Kuyper in Bas et al. 1995), *Lyophyllum palustre*, *Coprinus martini*, and *Psathyrella sphagnicola.* Many others grow parasitically in or on mosses, but the precise relationship between the two is rarely known.

Peat mosses (*Sphagnum* spp.) are a well-known substrate for many agarics, also in the Arctic, including *Arrhenia onisca*, *A. gerardiana*, and *A. philonotis*. Many species of *Galerina* grow on *Sphagnum*, but it is not known whether the relation is saprotrophic on the dead lower parts of the shoots, or parasitic on the green living parts. *Loreleia* on the liverwort *Marchantia polymorpha* is most likely parasitic.

Genera like *Typhula* have many representatives in northern regions. Practically all are saprotrophic, but *T. ishikariensis* is parasitic, in fact destroying grass fields in northern areas, with important consequences for northern agriculture (Hoshino et al. 1997, 1998, 2001, 2004a, 2008).

Fig. 79. Many species of mosses are attacked by parasites or saprotrophs, and it is not always known what the nature of the relationship is. *Muscinupta laevis* lives on the moss *Polytrichum*, which is otherwise rarely attacked (but see *Cantharellula umbonata* below).

Fig. 80. *Cantharellula umbonata* is a parasite on mosses, seen here growing on *Polytrichum* in Altai, Russia.

A small group of fungi are parasites or saprotrophs on other fungi. Species of *Collybia* s.str. make sclerotia from which basidiomata later develop. Species of *Asterophora* attack *Russula*, mummifying them and forming basidiomata on their caps. The basidiomata often do not mature, but grow into an anamorph stage and spread their conidia.

Lichens in northern areas are attacked by many lichenicolous fungi, but most of these are ascomycetes. Two basidiomycetes are known, *Gamundia striatula* and *Arrhenia peltigerina*, both growing on old thalli of *Peltigera*.

Finally, most species of *Galerina* are bryophilous associates of certain mosses, but it has so far not been shown whether they are parasites or saprotrophs.

List of vascular plants and their fungal parasites in cold regions

The following list comprises all Greenlandic plants attacked by rusts and smuts, excluding cultivated plants and apomicts. In cases where no parasite from these two groups is known on the plant, we offer possible reasons, which are however speculative. We assume that a number of straightforward factors have hindered the development of parasitic species.

We have included 951 arctic-alpine plants in the list (see next page). An additional 96 species are listed in the section on ecto-mycorrhiza (chapter 9c, p. 167), for a total of 1047 species. Of these, we have found that 868 (83%) may be infected by rusts or smuts, and the remaining 179 (17%) are not.

Some non-infected species actually belong to the same genus as different species that are infected in other regions, suggesting that in some cases more investigation could identify infections in these arctic-alpine species; but for some genera, infection has never been recorded because they are immune to rusts and smuts. Thus the number of species susceptible to infection may be higher than estimated here.

Some plants (154 species or 15%) are infected by two or more rusts or smuts.

In contrast, the following genera have never been found infected. Possible explanations (often more than one) could be:

Small habit: *Anemonastrum*, *Coptis*, *Halerpestes*, *Sibbaldia*, *Crucihimalaya*, *Polygala*, *Cornus*, *Chelesia*, *Sabulina*, *Diapensia*, *Hackelia*, *Limosella*, *Linnaea*, *Melanocalyx*, *Antennaria*, *Omalotheca* (*Gnaphalium*), *Tofieldia*, *Sisyrinchium*, *Eleocharis*, *Eriophorum*, *Dupontia*, *Nardus*, and *Phippsia.* These genera include species with a small leaf surface, either with small entire leaves, or with larger, compound, deeply incised leaves with very slender leaflets.

Growing in wet habitats like marshes, bogs, lakes, rivers, or brackish areas along coasts: *Comarum palustre*, *Montia fontana*, *Menyanthes trifoliata*, *Plantago maritima*, *Triglochin*, and members of Gentianaceae.

Orchid mycorrhiza: *Corallorhiza*, *Galearis*, *Neottia*, and *Pseudorchis*.

Ericoid mycorrhiza: *Cassiope*, *Kalmia*, and *Phyllodoce*.

Large habit but leaves strongly divided: *Argentina* (*Potentilla*) *anserina* and *Tripleurospermum*.

Leaves densely provided with sticky glands: *Drosera*.

Very hairy plants: *Asperugo*, *Oreomecon* (*Papaver*).

Other: *Lathyrus.*

CUPRESSACEAE

1. *Juniperus communis* L.
P: *Gymnosporangium communis*.

RANUNCULACEAE

2. *Aconitum anthora* L.
P: *Urocystis irregularis.*

3. *Aconitum columbianum* Nutt.
P: *Urocystis irregularis.*

4. *Aconitum delphiniifolium* DC.
P: *Urocystis irregularis.*

5. *Aconitum lamarckii* Rchb. ex Spreng.
P: *Urocystis irregularis.*

6. *Aconitum lycoctonum* L.
P: *Urocystis irregularis.*

7. *Aconitum napellus* L.
P: *Puccinia recondita, Urocystis irregularis.*

8. *Aconitum septentrionale* Koelle
P: *Puccinia recondita, Urocystis irregularis.*

9. *Aconitum soongaricum* (Regel) Stapf
P: *Urocystis irregularis.*

10. *Aconitum variegatum* L.
P: *Puccinia recondita.*

11. *Aconitum vulparia* Rchb.
P: *Urocystis irregularis.*

12. *Anemonastrum richardsonii* (Hook.) Mosyakin

13. *Aquilegia atrata* W.D.J. Koch
P: *Puccinia recondita.*

14. *Aquilegia chrysantha* A. Gray
P: *Puccinia recondita.*

15. *Aquilegia nigricans* Baumg.
P: *Puccinia recondita.*

16. *Aquilegia vulgaris* L.
P: *Puccinia recondita.*

17. *Callianthemum alatavicum* Freyn
P: *Urocystis callianthemi.*

18. *Callianthemum coriandrifolium* Rchb.
P: *Urocystis callianthemi.*

19. *Clematis alpina* (L.) Mill.
P: *Puccinia atragenicola, P. recondita.*

20. *Clematis drummondii* Torr. & A. Gray
P: *Puccinia recondita.*

21. *Clematis ligusticifolia* Nutt.
P: *Puccinia recondita.*

22. *Coptis trifolia* (L.) Salisb.

23. *Halerpestes cymbalaria* (Pursh) Greene

Ranunculus L.
P: *Schroeteriaster alpinus, Uromyces dactylidis, U. fischerianus.*

24. *Ranunculus acris* L.
P: *Urocystis nivalis, U. ranunculi.*

25. *Ranunculus alberti* Regel & Schmalh.
P: *Urocystis nivalis.*

26. *Ranunculus alpestris* L.
P: *Puccinia gibberulosa, Urocystis ranunculi.*

27. *Ranunculus altaicus* Laxm.
P: *Urocystis nivalis.*

28. *Ranunculus arcticus* Richardson
P: *Puccinia gibberulosa, Urocystis nivalis.*

29. *Ranunculus auricomus* L.
P: *Puccinia geranii-silvatici.*

30. *Ranunculus breyninus* Crantz
P: *Urocystis ranunculi.*

31. *Ranunculus bulbosus* L.
P: *Entyloma microsporum.*

32. *Ranunculus cardiophyllus* Hook.
P: *Puccinia gibberulosa.*

33. *Ranunculus carpaticus* Herbich
P: *Urocystis ranunculi.*

34. *Ranunculus confervoides* (Fr.) Fr.
Aquatic plant.

35. *Ranunculus glacialis* L.
P: *Urocystis ranunculi.*

36. *Ranunculus grandiflorus* L.
P: *Urocystis ranunculi.*

37. *Ranunculus hyperboreus* Rottb.
P: *Urocystis ranunculi.*

38. *Ranunculus lapponicus* L.
P: *Puccinia gibberulosa.*

39. *Ranunculus lyngei* (Harry Sm. ex Fagerst. & G. Kvist) Ericsson
This plant is only known from a handful of localities in northernmost Sweden.

40. *Ranunculus montanus* Willd.
P: *Entyloma microsporum.*

41. *Ranunculus nivalis* L.
P: *Urocystis nivalis, U. ranunculi.*

42. *Ranunculus platanifolius* L.
P: *Urocystis ranunculi.*

43. *Ranunculus polyanthemos* L.
P: *Urocystis ranunculi.*

44. *Ranunculus propinquus* C.A. Mey.
P: *Puccinia gibberulosa.*

45. *Ranunculus pseudomontanus* Schur
P: *Urocystis ranunculi.*

46. *Ranunculus pygmaeus* Wahlenb.
P: *Entyloma microsporum, Puccinia gibberulosa, Urocystis nivalis.*

47. *Ranunculus reptans* L.
A small plant with very slender leaves.

48. *Ranunculus sabinei* R. Br.
A small plant with very slender leaves.

49. *Ranunculus songaricus* Schrenk
P: *Urocystis nivalis, U. ranunculi.*

50. *Ranunculus sulphureus* Sol.
P: *Urocystis nivalis.*

51. *Ranunculus villarsii* DC.
P: *Urocystis ranunculi.*

Thalictrum Tourn. ex L.
P: *Puccinia rhytismoides, P. septentrionalis.*

52. *Thalictrum alpinum* L.
P: *Puccinia recondita, Urocystis sorosporioides.*

53. *Thalictrum aquilegiifolium* L.
P: *Puccinia recondita, Urocystis sorosporioides.*

54. *Thalictrum fendleri* Engelm. ex A. Gray
P: *Puccinia recondita, Urocystis sorosporioides.*

55. *Thalictrum flavum* L.
P: *Urocystis sorosporioides.*

56. *Thalictrum foetidum* L.
P: *Urocystis sorosporioides.*

57. *Thalictrum minus* L.
P: *Puccinia recondita, Urocystis sorosporioides.*

58. *Thalictrum simplex* L.
P: *Puccinia recondita, Urocystis sorosporioides.*

59. *Thalictrum sparsiflorum* Turcz. ex Fisch. & C.A. Mey.
P: *Urocystis sorosporioides.*

60. *Trautvetteria caroliniensis* (Walter) Vail
P: *Urocystis trautvetteriae.*

61. *Trollius europaeus* L.
P: *Puccinia recondita.*

ROSACEAE

62. *Alchemilla alpina* L.
P: *Trachyspora melospora.*

63. *Alchemilla borealis* Sam. ex Juz.
P: *Trachyspora alchemillae.*

64. *Alchemilla filicaulis* Buser
P: *Trachyspora alchemillae.*

65. *Alchemilla glabra* Neygenf.
P: *Trachyspora alchemillae.*

66. *Alchemilla glomerulans* Buser
P: *Trachyspora alchemillae.*

67. *Alchemilla hybrida* (L.) L.
P: *Trachyspora alchemillae.*

68. *Alchemilla murbeckiana* Buser
P: *Trachyspora alchemillae.*

69. *Alchemilla retropilosa* Juz.
P: *Trachyspora alchemillae.*

70. *Alchemilla sibirica* Zämelis
P: *Trachyspora alchemillae.*

71. *Alchemilla vulgaris* L.
P: *Trachyspora alchemillae.*

72. *Alchemilla wichurae* (Buser) Stefánsson
P: *Trachyspora alchemillae.*

73. *Argentina anserina* (L.) Rydb.

74. *Comarum palustre* L.
A bog plant.

Dryas, see ecto-mycorrhizal plants p. 228.

75. *Drymocallis glandulosa* (Lindl.) Rydb.
P: *Phragmidium ivesiae.*

76. *Geum glaciale* Adams ex Fisch.
P: *Puccinia urbanii.*

77. *Geum rivale* L.

78. *Geum rossii* (R. Br.) Ser.
P: *Puccinia sieversiae.*

79. *Hedlundia meinichii* (Lindeb. ex Hartm.) Sennikov & Kurtto
P: *Gymnosporangium cornutum.*

80. *Hedlundia neglecta* (Hedl.) Sennikov & Kurtto
P: *Gymnosporangium cornutum.*

81. *Potentilla argentea* L.
P: *Phragmidium potentillae.*

82. *Potentilla aurea* L.
P: *Phragmidium potentillae.*

83. *Potentilla basaltica* Tiehm & Ertter
P: *Phragmidium ivesiae.*

84. *Potentilla centigrana* Maxim.
P: *Phragmidium potentillae.*

85. *Potentilla crantzii* (Crantz) Fritsch
P: *Phragmidium biloculare, P. potentillae.*

86. *Potentilla cryptotaeniae* Maxim.
P: *Phragmidium potentillae.*

87. *Potentilla flabellifolia* Hook. ex Torr. & A. Gray
P: *Phragmidium biloculare.*

88. *Potentilla glaucophylla* Lehm.
P: *Phragmidium ivesiae.*

89. *Potentilla gracilis* Douglas ex Hook.
P: *Phragmidium ivesiae.*

90. *Potentilla hyparctica* Malte

91. *Potentilla multifida* L.
P: *Phragmidium potentillae.*

92. *Potentilla nivea* L.
P: *Phragmidium potentillae.*

93. *Potentilla norvegica* L.

94. *Potentilla pulchella* R. Br.

95. *Potentilla pulcherrima* Lehm.
P: *Phragmidium ivesiae.*

96. *Potentilla recta* L.
P: *Phragmidium ivesiae.*

97. *Potentilla reptans* L.
P: *Phragmidium potentillae.*

98. *Potentilla rubella* T.J. Sørensen

99. *Potentilla rubricaulis* Lehm.

100. *Potentilla stipularis* L.
P: *Phragmidium biloculare, P. boreale.*

101. *Potentilla stolonifera* Lehm. ex Ledeb.
P: *Phragmidium potentillae.*

102. *Potentilla thuringiaca* Bernh. ex Link
P: *Phragmidium potentillae.*

103. *Potentilla vahliana* Lehm.
This species has very small leaves.

104. *Potentilla verna* L.
P: *Phragmidium potentillae.*

105. *Potentilla virgata* Lehm.
P: *Phragmidium potentillae.*

106. *Rosa acicularis* Lindl.
P: *Phragmidium fusiforme, P. kamschatkae.*

107. *Rosa amblyotis* C.A. Mey.
P: *Phragmidium fusiforme, P. kamschatkae.*

108. *Rosa arkansana* Porter
P: *Phragmidium montivagum.*

109. *Rosa cinnamomea* L.
P: *Phragmidium fusiforme, P. kamschatkae.*

110. *Rosa davurica* Pall.
P: *Phragmidium kamschatkae, P. montivagum.*

111. *Rosa nutkana* C. Presl
P: *Phragmidium fusiforme, P. montivagum.*

112. *Rosa pendulina* L. [syn. *R. alpina* L.]
P: *Phragmidium fusiforme.*

113. *Rosa platyacantha* Schrenk
P: *Phragmidium kamschatkae.*

114. *Rosa rugosa* Thunb.
P: *Phragmidium kamschatkae, P. montivagum.*

115. *Rosa woodsii* Lindl.
P: *Phragmidium montivagum.*

116. *Rubus allegheniensis* Porter
P: *Arthuriomyces peckianus.*

117. *Rubus arcticus* L.
P: *Aculeastrum arcticum, Phragmidium arcticum.*

118. *Rubus chamaemorus* L.
P: *Arthuriomyces peckianus, Phragmidium arcticum.*

119. *Rubus idaeus* L.
P: *Arthuriomyces peckianus.*

120. *Rubus occidentalis* L.
P: *Arthuriomyces peckianus.*

121. *Rubus pubescens* Raf.
P: *Arthuriomyces peckianus, Phragmidium arcticum.*

Fig. 81. The northern mountain ash (*Sorbus decora*) becomes a few metres high in arctic areas, but often occurs as solitary individuals, without any larger impact on the vegetation, except as a host for *Gymnosporangium.* Occasionally some corticioid species are found on the wood, but none of them seem to be specialized to this host. The seeds do not mature in arctic regions, so viable seeds must be imported via bird droppings.

122. *Rubus radula* Weihe
P: *Arthuriomyces peckianus.*

123. *Rubus saxatilis* L.
P: *Arthuriomyces peckianus, Phragmidium arcticum.*

124. *Scandosorbus intermedia* (Ehrh.) Sennikov
P: *Gymnosporangium cornutum.*

125. *Sibbaldia procumbens* L.

126. *Sibbaldia tridentata* (Aiton) Paule & Soják
P: *Phragmidium potentillae.*

127. *Sorbus americana* Marshall
P: *Gymnosporangium cornutum.*

128. *Sorbus aucuparia* L.
P: *Gymnosporangium cornutum.*

129. *Sorbus decora* (Sarg.) C.K. Schneid.
P: *Gymnosporangium cornutum.*

130. *Sorbus discolor* (Maxim.) Maxim.
P: *Gymnosporangium cornutum.*

131. *Sorbus sambucifolia* (Cham. & Schltdl.) M. Roem.
P: *Gymnosporangium cornutum.*

132. *Sorbus tianschanica* Rupr.
P: *Gymnosporangium cornutum.*

CRASSULACEAE

133. *Rhodiola rosea* L.
P: *Puccinia umbilici.*

134. *Sedum acre* L.
A host for *Puccinia longissima* in warmer places in central Europe.

135. *Sedum annuum* L.

136. *Sedum villosum* L.

SAXIFRAGACEAE

137. *Boykinia richardsonii* (Hook.) Rothr.
P: *Urocystis alaskana.*

138. *Chrysosplenium alternifolium* L.
P: *Puccinia pallidomaculata.*
In Asia this rust occurs on *Chrysosplenium*, in North America on *Saxifraga* spp.

139. *Chrysosplenium tetrandrum* (N. Lund) Th. Fr.

140. *Heuchera parvifolia* Nutt.
P: *Urocystis heucherae.*

141. *Micranthes hieraciifolia* (Willd.) Haw.
P: *Melampsora arctica, Puccinia saxifragae.*

142. *Micranthes nelsoniana* (D. Don) Small
P: *Melampsora arctica, Puccinia saxifragae.*

143. *Micranthes nivalis* (L.) Small
P: *Melampsora arctica.*

144. *Micranthes punctata* (L.) Losinsk.
P: *Puccinia saxifragae.*

145. *Micranthes stellaris* (L.) Galasso et al.
P: *Melampsora arctica, Puccinia pazschkei.*

146. *Micranthes tenuis* (Wahlenb.) Small
P: *Melampsora arctica.*

147. *Micranthes tolmiei* (Torr. & A. Gray) Brouillet & Gornall
P: *Urocystis heucherae.*

148. *Micranthes unalaschcensis* (Sternb.) Gornall & H. Ohba
P: *Puccinia saxifragae.*

149. *Saxifraga adscendens* L.
P: *Melampsora arctica.*

150. *Saxifraga aizoides* L.
P: *Melampsora arctica, Puccinia fischeri, P. pazschkei.*

151. *Saxifraga androsacea* L.
P: *Melampsora arctica.*

152. *Saxifraga blepharophylla* Hayek
P: *Melampsora arctica.*

153. *Saxifraga cernua* L.
P: *Melampsora arctica*, *Puccinia saxifragae.*

154. *Saxifraga cespitosa* L.
P: *Melampsora arctica.*

155. *Saxifraga cotyledon* L.
P: *Puccinia pazschkei.*

156. *Saxifraga exarata* Vill.
P: *Melampsora arctica.*

157. *Saxifraga flagellaris* Willd.
P: *Melampsora arctica*, *Puccinia fischeri.*

158. *Saxifraga granulata* L.
P: *Puccinia saxifragae.*

159. *Saxifraga hirculus* L.
P: *Melampsora arctica*, *M. hirculus.*

160. *Saxifraga hyperborea* R. Br.
P: *Melampsora arctica.*

161. *Saxifraga hypnoides* L.
P: *Melampsora arctica.*

162. *Saxifraga oppositifolia* L.
P: *Melampsora arctica*, *Puccinia fischeri*, *P. pazschkei.*

163. *Saxifraga paniculata* Mill.
P: *Melampsora arctica*, *Puccinia pazschkei.*

164. *Saxifraga rivularis* L.
P: *Melampsora arctica.*

165. *Saxifraga rotundifolia* L.
P: *Melampsora arctica.*

166. *Saxifraga seguieri* Biehler
P: *Puccinia saxifragae.*

167. *Saxifraga serpyllifolia* Pursh
P: *Melampsora arctica.*

168. *Saxifraga sibirica* L.
P: *Puccinia saxifragae.*

169. *Saxifraga tricuspidata* Rottb.
P: *Melampsora arctica*, *Puccinia saxifragae.*

CELASTRACEAE

170. *Parnassia fimbriata* K.D. Koenig
P: *Puccinia parnassiae.*

171. *Parnassia kotzebuei* Cham. ex Spreng.

GROSSULARIACEAE

172. *Ribes alpinum* L.
P: *Puccinia caricina*, *P. ribis.*

173. *Ribes petraeum* Wulfen
P: *Puccinia ribis.*

174. *Ribes rubrum* L.
P: *Puccinia ribis.*

175. *Ribes spicatum* E. Robson
P: *Puccinia caricina*, *P. ribis.*

176. *Ribes triste* Pall.
P: *Puccinia ribis.*

FABACEAE

177. *Astragalus alopecurus* Pall.
P: *Uromyces lapponicus.*

178. *Astragalus alpinus* L.
P: *Uromyces lapponicus.*

179. *Astragalus australis* (L.) Lam.
P: *Uromyces lapponicus.*

180. *Astragalus frigidus* (L.) A. Gray
P: *Uromyces lapponicus.*

181. *Astragalus jarmolenkoi* Gontsch.
P: *Uromyces lapponicus.*

182. *Astragalus melilotoides* Pall.
P: *Uromyces lapponicus.*

183. *Astragalus ovinus* Boiss.
P*: Uromyces lapponicus.*

184. *Astragalus quisqualis* Bunge
P: *Uromyces lapponicus.*

185. *Astragalus rytidocarpus* Ledeb.
P: *Uromyces lapponicus.*

186. *Astragalus schanginianus* Pall.
P: *Uromyces lapponicus.*

187. *Astragalus sieversianus* Pall.
P: *Uromyces lapponicus.*

188. *Hedysarum gmelinii* Ledeb.
P: *Uromyces hedysari-obscuri.*

189. *Hedysarum hedysaroides* (L.) Schinz & Thell.
P: *Uromyces hedysari-obscuri.*

190. *Hedysarum occidentale* Greene
P: *Uromyces hedysari-obscuri.*

191. *Lathyrus japonicus* Willd.

192. *Oxytropis albiflora* Bunge
P: *Uromyces lapponicus.*

193. *Oxytropis campestris* (L.) DC.
P: *Uromyces lapponicus.*

194. *Oxytropis czucotica* Jurtzev
P: *Uromyces lapponicus.*

195. *Oxytropis glabra* DC.
P: *Uromyces lapponicus.*

196. *Oxytropis mertensiana* Turcz.
P: *Uromyces lapponicus.*

197. *Oxytropis middendorfii* Trautv.
P: *Uromyces lapponicus.*

198. *Oxytropis nigrescens* (Pall.) DC.
P: *Uromyces lapponicus.*

199. *Oxytropis revoluta* Ledeb.
P: *Uromyces lapponicus.*

200. *Oxytropis sordida* (Willd.) Pers.
P: *Uromyces lapponicus.*

ONAGRACEAE

201. *Epilobium alpestre* (Jacq.) Krock.
P: *Doassansia epilobii*, *Puccinia epilobii.*

202. *Epilobium alsinifolium* Vill.
P: *Doassansia epilobii*, *Puccinia epilobii*, *P. scandica*, *Pucciniastrum epilobii.*

203. *Epilobium anagallidifolium* Lam.
P: *Doassansia epilobii*, *Puccinia epilobii*, *P. scandica*, *P. veratri*, *Pucciniastrum epilobii.*

204. *Epilobium angustifolium* L.
P: *Pucciniastrum epilobii*, *Puccinia gigantea.*

205. *Epilobium arcticum* Sam.
This species has very small leaves.

206. *Epilobium ciliatum* Raf.

207. *Epilobium collinum* C.C. Gmel.
P*: Puccinia pulverulenta.*

208. *Epilobium davuricum* Fisch. ex Hornem.
P: *Puccinia epilobii.*

209. *Epilobium fleischeri* Hochst.
P: *Puccinia epilobii-flesicheri.*

210. *Epilobium hallianum* Hausskn.
This species has very small leaves.

211. *Epilobium hornemannii* Rchb.
P: *Doassansia epilobii*, *Puccinia epilobii*, *P. scandica*, *Pucciniastrum epilobii.*

212. *Epilobium lactiflorum* Hausskn.
P: *Puccinia scandica.*

213. *Epilobium latifolium* L.
P: *Pucciniastrum epilobii.*

214. *Epilobium montanum* L.
P: *Puccinia epilobii, P. pulverulenta, Pucciniastrum epilobii.*

215. *Epilobium palustre* L.
P: *Doassansia epilobii, Puccinia epilobii, Pucciniastrum epilobii.*

216. *Epilobium roseum* (Schreb.) Schreb.
P: *Puccinia epilobii.*

217. *Epilobium tetragonum* L.
P: *Puccinia epilobii.*

PAPAVERACEAE

218. *Oreomecon nudicaulis* (L.) Banfi et al.

219. *Oreomecon radicata* (Rottb.) Banfi et al.

BRASSICACEAE

220. *Arabidopsis arenicola* (Richardson ex Hook.) Al-Shehbaz et al.
P: *Puccinia holboellii.*

221. *Arabidopsis lyrata* (L.) O'Kane & Al-Shehbaz
P: *Thecaphora thlaspeos.*

222. *Arabidopsis thaliana* (L.) Heynh.
P: *Puccinia holboellii, P. thlaspeos.*

223. *Arabis alpina* L.
P: *Thecaphora thlaspeos.*

224. *Arabis sagittata* (Bertol.) DC.
P: *Thecaphora thlaspeos.*

225. *Boechera divaricarpa* (A. Nelson) Á. Löve & D. Löve
P: *Puccinia holboellii*.

226. *Boechera drummondii* (A. Gray) Á. Löve & D. Löve
P: *Puccinia holboellii*.

227. *Boechera holboellii* (Hornem.) Á. Löve & D. Löve
P: *Puccinia holboellii*.

228. *Boechera lyallii* (S. Watson) Dorn
P: *Puccinia aberrans, P. holboellii.*

229. *Boechera platysperma* (A. Gray) Al-Shehbaz
P: *Puccinia holboellii*.

230. *Boechera retrofracta* (Graham) Á. Löve & D. Löve
P: *Puccinia holboellii*.

231. *Braya humilis* (C.A. Mey.) B.L. Rob.
P: *Puccinia holboellii.*

232. *Braya linearis* Rouy

233. *Braya purpurascens* (R. Br.) Ledeb.

234. *Braya thorild-wulffii* Ostenf.

235. *Cakile edentula* (Bigelow) Hook.
A succulent plant growing along salty coasts.

236. *Cardamine bellidifolia* L.
P: *Puccinia cruciferarum, Thecaphora thlaspeos.*

237. *Cardamine cordifolia* A. Gray
P: *Puccinia cruciferarum.*

238. *Cardamine polemonioides* (Rouy) T. Durand & B.D. Jacks.

239. *Cardamine pratensis* L.
P: *Puccinia cruciferarum.*

240. *Cardamine resedifolia* L.
P: *Puccinia cruciferarum.*

241. *Cochlearia groenlandica* L.
P: *Puccinia eutremae.*

242. *Cochlearia officinalis* L.
P: *Puccinia eutremae.*

243. *Crucihimalaya bursifolia* (DC.) D.A. German & A.L. Ebel

244. *Descurainia sophia* (L.) Webb ex Prantl
P: *Puccinia epilobii.*

245. *Draba aizoides* L.
P: *Puccinia drabae, Thecaphora thlaspeos.*

246. *Draba alpina* L.
P: *Puccinia drabae, Thecaphora thlaspeos.*

247. *Draba altaica* (C.A. Mey.) Bunge
P: *Puccinia drabae.*

248. *Draba arctica* J. Vahl
A small plant with small leaves.

249. *Draba arctogena* (Ekman) Ekman
A small plant with small leaves.

250. *Draba aurea* Vahl ex Hornem.
P: *Puccinia drabae.*

251. *Draba cinerea* Adams
P: *Puccinia drabae.*

252. *Draba corymbosa* R. Br. ex DC.
P: *Puccinia drabae.*

253. *Draba crassifolia* Graham
A small plant with small thick leaves.

254. *Draba daurica* DC.
P: *Puccinia drabae.*

255. *Draba fladnizensis* Wulfen
P: *Puccinia drabae.*

256. *Draba glabella* Pursh

257. *Draba glacialis* Adams
P: *Puccinia drabae.*

258. *Draba hirta* L.
P: *Puccinia drabae.*

259. *Draba incana* L.
P: *Puccinia drabae, Thecaphora thlaspeos.*

260. *Draba lactea* Adams
P: *Puccinia drabae.*

261. *Draba lanceolata* Royle
P: *Puccinia drabae.*

262. *Draba nivalis* Lilj.
P: *Puccinia drabae.*

263. *Draba norvegica* Gunnerus
P: *Puccinia drabae, Thecaphora thlaspeos.*

264. *Draba oblongata* R. Br. ex DC.
A small plant.

265. *Draba oxycarpa* Sommerf.

266. *Draba pauciflora* R. Br.

267. *Draba sibirica* (Pall.) Thell.
A small plant on moist ground.

268. *Draba subcapitata* Simmons
A small plant.

Erysimum Tourn. ex L.
P: *Puccinia holboellii.*

269. *Erysimum cheiranthoides* L.
P: *Puccinia aberrans.*

270. *Erysimum odoratum* Ehrh.
P: *Puccinia thlaspeos.*

271. *Erysimum redowskii* Weinm.
A small plant.

272. *Eutrema edwardsii* R. Br.
P: *Puccinia eutremae.*

273. *Eutrema integrifolium* (DC.) Bunge
P: *Puccinia drabae.*

274. *Noccaea caerulescens* (J. Presl & C. Presl) F.K. Mey.
P: *Puccinia thlaspeos, Thecaphora thlaspeos.*

275. *Noccaea cochleariformis* (DC.) Á. Löve & D. Löve
P: *Puccinia thlaspeos.*

276. *Noccaea fendleri* (A. Gray) Holub
P: *Puccinia thlaspeos.*

277. *Noccaea granatensis* (Boiss. & Reut.) R. Kr. Singh et al.
P: *Puccinia thlaspeos.*

278. *Noccaea macrantha* (Lipsky) F.K. Mey.
P: *Puccinia thlaspeos.*

279. *Noccaea montana* (L.) F.K. Mey.
P: *Puccinia oudemansii.*

280. *Noccaea praecox* (Wulfen) F.K. Mey.
P: *Puccinia thlaspeos.*

281. *Parrya rydbergii* Botsch.
P: *Puccinia oudemansii.*

282. *Parrya turkestanica* (Korsh.) N. Busch
P: *Puccinia oudemansii.*

283. *Physaria arctica* (Wormsk. ex Hornem.) O'Kane & Al-Shehbaz
P: *Puccinia cruciferarum*, *P. drabae.*

284. *Polyctenium fremontii* (S. Watson) Greene
P: *Puccinia aberrans.*

285. *Rorippa islandica* (Oed.) Borb.
Growing on wet ground.

286. *Sisymbrium linifolium* (Nutt.) Nutt.
P: *Puccinia holboellii.*

287. *Smelowskia americana* Rydb.
P: *Puccinia aberrans.*

288. *Smelowskia calycina* (Willd.) C.A. Mey.
P: *Puccinia holboellii.*

289. *Subularia aquatica* L.
Small aquatic plant.

290. *Teesdalia nudicaulis* (L.) W.T. Aiton
P: *Puccinia oudemansii.*

VIOLACEAE

291. *Viola biflora* L.
P: *Puccinia alpina*, *Uredo alpestris.*

292. *Viola canina* L.

293. *Viola epipsila* Ledeb.
P: *Melampsora lapponum*, *Puccinia fergussonii.*

294. *Viola labradorica* Schrank

295. *Viola langsdorfii* Fisch. ex Ging.
P: *Puccinia fergussonii.*

296. *Viola odorata* L.
P: *Puccinia alpina.*

297. *Viola palustris* L.
P: *Melampsora lapponum.*

298. *Viola pinnata* L.
P: *Puccinia alpina.*

299. *Viola selkirkii* Pursh ex Goldie
P: *Puccinia fergussonii.*

300. *Viola suecica* Fr.
P: *Melampsora lapponum*, *Puccinia fergussonii*.

301. *Viola turkestanica* Regel & Schmalh.
P: *Puccinia alpina.*

302. *Viola vaginata* Maxim.
P: *Puccinia alpina.*

DROSERACEAE

303. *Drosera rotundifolia* L.
A small plant found in wetlands.

GERANIACEAE

304. *Geranium albiflorum* Ledeb.
P: *Puccinia geranii-silvatici.*

305. *Geranium collinum* Stephan ex Willd.
P: *Puccinia geranii-silvatici.*

306. *Geranium erianthum* DC.
P: *Puccinia geranii-silvatici.*

307. *Geranium rectum* Trautv.
P: *Puccinia geranii-silvatici.*

308. *Geranium saxatile* Kar. & Kir.
P: *Puccinia geranii-silvatici.*

309. *Geranium sylvaticum* L.
P: *Puccinia geranii-silvatici*, *P. morthieri.*

EUPHORBIACEAE

310. *Euphorbia alatavica* Boiss.
P: *Uromyces striolatus.*

311. *Euphorbia cyparissias* L.
P: *Uromyces alpestris*, *U. striolatus.*

312. *Euphorbia soongarica* Boiss.
P: *Uromyces striolatus.*

POLYGALACEAE

313. *Polygala serpyllifolia* Hosé

CORNACEAE

314. *Cornus canadensis* L.

315. *Cornus suecica* L.

APIACEAE

316. *Angelica archangelica* L.
P: *Puccinia bistortae*; *P. mei-mamillata.*

317. *Angelica sylvestris* L.
P: *Puccinia bistortae*; *P. mei-mamillata.*

318. *Anthriscus sylvestris* (L.) Hoffm.
P: *Puccinia dolomitica*; *P. svendsenii.*

319. *Astrantia minor* L.
P: *Puccinia bistortae.*

320. *Athamanta cretensis* L.
P: *Puccinia athamantina.*

321. *Carum carvi* L.
P: *Puccinia bistortae.*

322. *Chaerophyllum villarsii* W.D.J. Koch
P: *Puccinia enormis.*

323. *Conopodium majus* (Gouan) Loret
P: *Puccinia bistortae.*

324. *Ligusticum mutellina* (L.) Crantz
P: *Puccinia mei-mamillata.*

325. *Ligusticum scothicum* L.
P: *Puccinia bistortae*, *P. halosciadis.*

326. *Peucedanum ostruthium* (L.) W.D.J. Koch
P: *Puccinia imperatoriae.*

327. *Peucedaum verticillare* (L.) DC.
P: *Puccinia terrieri.*

328. *Pimpinella major* (L.) Huds.
P: *Puccinia bistortae.*

329. *Pleurospermum uralense* Hoffm.
P: *Puccinia bistortae.*

SALICACEAE is treated in the ecto-mycorrhiza section, p. 167.

BETULACEAE is treated in the ecto-mycorrhiza section, p. 217.

SANTALACEAE

330. *Thesium alatavicum* Kar. & Kir.
P: *Puccinia mougeotii.*

331. *Thesium alpinum* L.
P: *Puccinia mougeotii.*

POLYGONACEAE

332. *Bistorta bistortoides* (Pursh) Small
P: *Microbotryum bistortarum, M. marginale.*

333. *Bistorta carnea* (K. Koch) Kom.
P: *Microbotryum marginale.*

334. *Bistorta elliptica* (Willd. ex Spreng.) V.V. Petrovsky et al.
P: *Microbotryum bistortarum, M. marginale, M. pustulatum.*

335. *Bistorta officinalis* Delarbre
P: *Microbotryum bistortarum, M. marginale, M. pustulatum.*

336. *Bistorta plumosa* (Small) Greene
P: *Microbotryum bistortarum, M. marginale.*

337. *Bistorta vivipara* (L.) Delarbre
P: *Microbotryum pustulatum, Puccinia bistortae, P. mei-mammillata, P. septentrionalis.*
See also the ecto-mycorrhiza section, p. 237.

338. *Koenigia alpina* (All.) T.M. Schust. & Reveal
P: *Microbotryum bosniacum, M. piperi, Puccinia bistortae.*

339. *Koenigia coriaria* (Grig.) T.M. Schust. & Reveal
P: *Microbotryum bosniacum.*

340. *Koenigia davisiae* (W.H. Brewer ex A. Gray) T.M. Schust. & Reveal
P: *Puccinia bistortae.*

341. *Koenigia islandica* L.
P: *Microbotryum koenigiae, M. picaceum, Puccinia bistortae, P. polygoni-alpini.*

342. *Koenigia ocreata* (L.) T.M. Schust. & Reveal
P: *Microbotryum bosniacum.*

343. *Koenigia phytolaccifolia* (Meisn. ex Small) T.M. Schust. & Reveal
P: *Microbotryum piperi.*

344. *Koenigia songarica* (Schrenk) T.M. Schust. & Reveal
P: *Microbotryum bosniacum, M. piperi.*

345. *Koenigia tripterocarpa* (A. Gray) T.M. Schust. & Reveal
P: *Microbotryum bosniacum, M. piperi.*

346. *Oxyria digyna* (L.) Hill
P: *Microbotryum vinosum, Puccinia oxyriae.*

347. *Rumex acetosa* L.
P: *Microbotryum goeppertianum.*

348. *Rumex acetosella* L.

349. *Rumex alpinus* L.
P: *Schroeteriaster alpinus.*

350. *Rumex arcticus* Trautv.
P: *Microbotryum warmingii.*

351. *Rumex arifolius* All.
P: *Microbotryum goeppertianum.*

352. *Rumex graminifolius* Georgi ex Lamb.

353. *Rumex lapponicus* (Hiitonen) Czernov
P: *Microbotryum goeppertianum.*

354. *Rumex longifolius* DC.
P: *Microbotryum warmingii.*

MONTIACEAE

355. *Claytonia acutifolia* Pall. ex Willd.
P: *Microbotryum claytoniae, Puccinia claytoniae.*

356. *Claytonia arctica* Adam
P: *Puccinia claytoniae.*

357. *Claytonia joanneana* Schult.
P: *Microbotryum claytoniae, Puccinia claytoniae.*

358. *Claytonia lanceolata* Pursh
P: *Puccinia claytoniicola.*

359. *Montia fontana* L.
Aquatic plant.

360. *Montia linearis* (Douglas) Greene
P: *Microbotryum claytoniae.*

CARYOPHYLLACEAE

361. *Arenaria biflora* L.
P: *Microbotryum stellariae.*

362. *Arenaria ciliata* L.
P: *Puccinia arenariae.*

363. *Arenaria humifusa* Wahlenb.
Growing on moist ground.

364. *Arenaria multicaulis* L.
P: *Microbotryum stellariae.*

365. *Arenaria pseudofrigida* (Ostenf. & O.C. Dahl) Steffen

366. *Cerastium arcticum* Lange

367. *Cerastium arvense* L.
P: *Melampsorella elatina.*

368. *Cerastium carinthiacum* Vest
P: *Puccinia hysteriiformis.*

369. *Cerastium davuricum* Fisch. ex Spreng.
P: *Puccinia arenariae.*

370. *Cerastium fontanum* Baumg.
P: *Puccinia arenariae.*

371. *Cerastium maximum* L.
P: *Puccinia arenariae.*

372. *Cerastium regelii* Ostenf.
P: *Puccinia arenariae.*

373. *Cherleria biflora* (L.) A.J. Moore & Dillenb.
A small plant.

374. *Dianthus orientalis* Adams
P: *Puccinia arenariae.*

375. *Dichodon cerastoides* (L.) Rchb.
P: *Melampsorella elatina.*

376. *Eremogone capillaris* (Poir.) Fenzl
P: *Puccinia arenariae.*

377. *Eremogone congesta* (Nutt.) Ikonn.
P: *Puccinia hysteriiformis.*

378. *Eremogone kingii* (S. Watson) Ikonn.
P: *Puccinia hysteriiformis.*

Gypsophila L.
P: *Puccinia hysteriiformis.*

379. *Heliosperma pusillum* (Waldst. & Kit.) Rchb.
P: *Microbotryum heliospermatis.*

380. *Honckenya peploides* (L.) Ehrh.
P: *Puccinia arenariae.*

381. *Mesostemma kotschyanum* (Fenzl ex Boiss.) Vved.
P: *Puccinia hysteriiformis.*

382. *Minuartia recurva* (All.) Schinz & Thell.
P: *Microbotryum minuartiae.*

383. *Sabulina rossii* (Richardson) Graebn.
Small plant.

384. *Sabulina rubella* (Wahlenb.) Dillenb. & Kadereit
A small plant.

385. *Sabulina stricta* (Sw.) Rchb.
A small plant.

386. *Sabulina verna* (L.) Rchb.
P: *Puccinia hysteriiformis*, *P. arenariae.*

387. *Sabulina villarii* (Balb.) Rchb.
P: *Microbotryum minuartiae.*

388. *Sagina cespitosa* Lange
A small plant.

389. *Sagina nivalis* (Lindblom) Fr.
P: *Microbotryum nivale.*

390. *Sagina nodosa* (L.) Fenzl
A small plant.

391. *Sagina procumbens* L.
P: *Puccinia arenariae.*

392. *Sagina saginoides* (L.) H. Karst.
P: *Puccinia arenariae.*

393. *Silene acaulis* (L.) Jacq.
P: *Microbotryum silenes-acaulis.*

394. *Silene adenopetala* Raikova
P: *Microbotryum adenopetalae.*

395. *Silene dioica* (L.) Clairv.
P: *Puccinia arenariae.*

396. *Silene involucrata* (Cham. Schltdl.) Bocquet

397. *Silene sorensensis* (B. Boivin) Bocquet

398. *Silene uralensis* (Rupr.) Bocquet
P: *Microbotryum arcticum, M. savilei.*

399. *Silene vulgaris* (Moench) Garcke
P: *Microbotryum lagerheimii, M. violaceoirregulare.*

400. *Silene wahlbergella* Chowdhuri

401. *Spergularia canadensis* (Pers.) G. Don

Stellaria L.
P: *Melampsorella elatina, Puccinia hysteriiformis.*

402. *Stellaria borealis* Bigelow
P: *Microbotryum stellariae.*

403. *Stellaria calycantha* (Ledeb.) Bong.
P: *Microbotryum stellariae.*

404. *Stellaria crassipes* Hult.
P: *Microbotryum stellariae.*

405. *Stellaria edwardsii* R. Br.
P: *Puccinia arenariae, Microbotryum stellariae.*

406. *Stellaria eschscholtziana* Fenzl
P: *Microbotryum stellariae.*

407. *Stellaria graminea* L.
P: *Microbotryum stellariae, Puccinia arenariae.*

408. *Stellaria humifusa* Rottb.

409. *Stellaria laeta* Richardson
P: *Microbotryum stellariae.*

410. *Stellaria longifolia* Muhl. ex Willd.
P: *Microbotryum stellariae.*

411. *Stellaria longipes* Goldie
P: *Puccinia arenariae, Microbotryum stellariae.*

412. *Stellaria nemorum* L.
P: *Puccinia arenariae.*

413. *Stellaria peduncularis* Bunge
P: *Microbotryum stellariae.*

414. *Stellaria soongorica* Roshev
P: *Puccinia arenariae.*

415. *Viscaria alpina* (L.) G. Don
P: *Microbotryum lagerheimii.*

416. *Viscaria vulgaris* Bernh.
P: *Microbotryum lagerheimii.*

417. *Wilhelmsia physodes* (Fisch. ex Ser.) McNeill
P: *Puccinia arenariae.*

PLUMBAGINACEAE

418. *Armeria maritima* (Mill.) Willd.
Growing in salt meadows.

PRIMULACEAE

419. *Androsace chamaejasme* Wulfen
P: *Puccinia dubyi.*

420. *Androsace helvetica* (L.) All.
P: *Puccinia dubyi.*

421. *Androsace obtusifolia* All.
P: *Puccinia dubyi.*

422. *Androsace septentrionalis* L.
P: *Puccinia dubyi*, *P. volkartiana.*

423. *Lysimachia arvensis* (L.) U. Manns & Anderb.

424. *Lysimachia borealis* (Raf.) U. Manns & Anderb. [= *Trientalis borealis* Raf.]
P: *Puccinia karelica.*

425. *Lysimachia europaea* (L.) U. Manns & Anderb.
P: *Puccinia karelica*, *Urocystis trientalis.*

426. *Primula egaliksensis* Wormsk.

427. *Primula integrifolia* L.
P: *Uromyces primulae-integrifoliae.*

428. *Primula matthioli* (L.) V.A. Richt.
P: *Urocystis cortusae.*

429. *Primula nutans* Georgi [syn. *P. sibirica* Jacq.]
P: *Puccinia arctica.*

430. *Soldanella alpina* L.
P: *Puccinia soldanellae.*

431. *Soldanella hungarica* Simonk.
P: *Puccinia soldanellae.*

432. *Soldanella montana* Willd.
P: *Puccinia soldanellae.*

433. *Soldanella pusilla* Baumg.
P: *Puccinia soldanellae.*

ERICACEAE

434. *Andromeda polifolia* L.
P: *Pucciniastrum sparsum.*

435. *Arctostaphylos uva-ursi* (L.) Spreng.
P: *Pucciniastrum sparsum.*

436. *Arctous alpina* (L.) Nied.
P: *Pucciniastrum sparsum.*

437. *Arctous rubra* (Rehder & E.H. Wilson) Nakai
P: *Pucciniastrum sparsum.*

438. *Cassiope* (*Harrimanella*) *hypnoides* (L.) D. Don

439. *Cassiope tetragona* (L.) D. Don

440. *Chaemaedaphne calyculata* (L.) Moench
P: *Chrysomyxa cassandrae.*

441. *Empetrum nigrum* L.
P: *Chrysomyxa empetri.*

442. *Kalmia procumbens* (L.) Galasso et al.
A small plant.

443. *Moneses uniflora* (L.) A. Gray
P: *Pucciniastrum pyrolae*, *Rossmanomyces pyrolae.*

444. *Orthilia secunda* (L.) House
P: *Rossmanomyces pyrolae.*

445. *Phyllodoce caerulea* (L.) Bab.

446. *Pyrola chlorantha* Sw.
P: *Pucciniastrum pyrolae.*

447. *Pyrola elliptica* Nutt.
P: *Pucciniastrum pyrolae.*

448. *Pyrola grandiflora* Radius
P: *Rossmanomyces pyrolae.*

449. *Pyrola media* Sw.
P: *Pucciniastrum pyrolae.*

450. *Pyrola minor* L.
P: *Pucciniastrum pyrolae*, *Rossmanomyces pyrolae.*

451. *Pyrola picta* Sm.
P: *Pucciniastrum pyrolae.*

452. *Pyrola rotundifolia* L.
P: *Pucciniastrum pyrolae.*

Rhododendron L.
P: *Chrysomyxa reticulata.*

453. *Rhododendron aureum* Georgi
P: *Chrysomyxa succinea.*

454. *Rhododendron brachycarpum* G. Don
P: *Chrysomyxa succinea.*

455. *Rhododendron canadense* (L.) Torr.
P: *Chrysomyxa rhododendri.*

456. *Rhododendron* (*Ledum*) *columbianum* (Piper) Harmaja
P: *Chrysomyxa ledi.*

457. *Rhododendron ferrugineum* L.
P: *Chrysomyxa rhododendri.*

458. *Rhododendron* (*Ledum*) *groenlandicum* (Oeder) Kron & Judd
P: *Chrysomyxa ledi*; *C. ledicola*; *C. nagodhii.*

459. *Rhododendron hirsutum* L.
P: *Chrysomyxa rhododendri.*

460. *Rhododendron japonoheptamerum* Kitam.
P: *Chrysomyxa succinea.*

461. *Rhododendron lapponicum* (L.) Wahlenb.
P: *Chrysomyxa rhododendri.*

462. *Rhododendron maximum* L.
P: *Chrysomyxa rhododendri.*

463. *Rhododendron minus* Michx.
P: *Chrysomyxa rhododendri.*

Fig. 82. *Ledum groenlandicum*. Ericoid mycorrhiza are found in most heath plants. The fungal symbionts are often the same as in orchid mycorrhiza, e.g. *Sebacina*, *Tomentella*, and *Thelephora*.

464. *Rhododendron periclymenoides* (Michx.) Shinners
P: *Chrysomyxa succinea.*

465. *Rhododendron* (*Ledum*) *tomentosum* Harmaja
P: *Chrysomyxa ledi, C. ledicola.*

466. *Vaccinium membranaceum* Torr.
P: *Naohidemyces vaccinii.*

467. *Vaccinium myrtillus* L.
P: *Naohidemyces vaccinii.*

468. *Vaccinium oxycoccos* L.
P: *Naohidemyces vaccinii.*

469. *Vaccinium uliginosum* L.
P: *Naohidemyces vaccinii.*

470. *Vaccinium vitis-idaea* L.
P: *Naohidemyces vaccinii.*

DIAPENSIACEAE

471. *Diapensia lapponica* L.

GENTIANACEAE

472. *Comastoma tenellum* (Rottb.) Toyok.

473. *Gentiana nivalis* L.
P: *Microbotryum nannfeldtii.*

474. *Gentianella amarella* (L.) Börner

475. *Gentianella aurea* (L.) Harry Sm.

476. *Gentianopsis detonsa* (Rottb.) Ma

477. *Lomatogonium rotatum* (L.) Fr.

478. *Swertia connata* Fisch. & C.A. Mey.
P: *Puccinia swertiae.*

479. *Swertia lactea* Bunge
P: *Puccinia swertiae.*

480. *Swertia perennis* L.
P: *Puccinia swertiae.*

481. *Swertia petiolata* D. Don
P: *Puccinia swertiae.*

482. *Swertia thomsonii* C.B. Clarke
P: *Puccinia swertiae.*

MENYANTHACEAE

483. *Menyanthes trifoliata* L.

Fig. 83. *Menyanthes trifoliata*. Many aquatic plants are not attacked by rusts and smuts.

POLEMONIACEAE

484. *Polemonium boreale* Adams
P: *Entyloma lapponicum, Puccinia polemonii.*

485. *Polemonium villosum* Georgi
P: *Entyloma lapponicum.*

BORAGINACEAE

486. *Asperugo procumbens* L.

487. *Hackelia floribunda* (Lehm.) I.M. Johnst.
P: *Puccinia hydrophylli.*

488. *Hydrophyllum capitatum* Benth.
P: *Puccinia hydrophylli.*

489. *Hydrophyllum occidentale* (S. Watson) A. Gray
P: *Puccinia hydrophylli.*

490. *Hydrophyllum virginianum* L.
P: *Puccinia hydrophylli.*

491. *Mertensia arizonica* Greene
P: *Puccinia hydrophylli.*

492. *Mertensia ciliata* (Torr.) G. Don
P: *Puccinia hydrophylli.*

493. *Mertensia maritima* (L.) Gray
P: *Puccinia hydrophylli.*

494. *Mertensia oblongifolia* (Nutt.) G. Don
P: *Puccinia hydrophylli.*

495. *Mertensia sibirica* (L.) G. Don
P: *Puccinia hydrophylli.*

496. *Mertensia viridis* (A. Nelson) A. Nelson
P: *Puccinia hydrophylli.*

Myosotis L.
P: *Puccinia myosotidis.*

497. *Phacelia hastata* Douglas ex Lehm.
P: *Puccinia recondita.*

498. *Phacelia heterophylla* Pursh
P: *Puccinia recondita.*

499. *Phacelia secunda* J.F. Gmel.
P: *Puccinia recondita.*

LAMIACEAE

500. *Thymus praecox* Opiz
P: *Puccinia thymi.*

501. *Thymus serpyllum* L.
P: *Puccinia thymi.*

SCROPHULARIACEAE

502. *Limosella aquatica* L.
A small aquatic plant.

OROBANCHACEAE

503. *Pedicularis capitata* Adams
P: *Puccinia helicalis.*

504. *Pedicularis flammea* L.

Fig. 84. *Pedicularis flammea* from Altai, Russia. We suspect this genus to be ecto-mycorrhizal, at least under some circumstances (see p. 246). In contrast, the genus is rarely attacked by rusts, perhaps due to the narrowly divided leaves with little surface area.

505. *Pedicularis groenlandica* Retz.

506. *Pedicularis labradorica* Wirsing
P: *Puccinia lapponica.*

507. *Pedicularis lanata* Cham. & Schlecht.

508. *Pedicularis langsdorfii* Fisch. ex Steven

509. *Pedicularis lapponica* L.
P: *Puccinia lapponica.*

510. *Pedicularis oederi* L.
P: *Puccinia pedicularis.*

511. *Rhinanthus minor* L.

LENTIBULARIACEAE

512. *Pinguicula alpina* L.
P: *Microbotryum alpinum.*

513. *Pinguicula grandiflora* Lam.
P: *Microbotryum pinguiculae.*

514. *Pinguicula leptoceras* Rchb.
P: *Microbotryum pinguiculae.*

515. *Pinguicula macroceras* Pall. ex Link
P: *Microbotryum pinguiculae.*

516. *Pinguicula spathulata* Ledeb.
P: *Microbotryum liroi.*

517. *Pinguicula villosa* L.
P: *Microbotryum liroi.*

518. *Pinguicula vulgaris* L.
P: *Microbotryum pinguiculae.*

PLANTAGINACEAE

519. *Lagotis glauca* Gaertn.
P: *Puccinia gymnandrae.*

520. *Lagotis yunnanensis* W.W. Sm.
P: *Puccinia gymnandrae.*

521. *Plantago maritima* L.
In wet saline habitats.

522. *Veronica alpina* L.
P: *Puccinia albulensis.*

523. *Veronica aphylla* L.
P: *Puccinia albulensis.*

524. *Veronica bellidioides* L.
P: *Puccinia rhaetica.*

525. *Veronica cusickii* A. Gray
P: *Puccinia albulensis.*

526. *Veronica fruticans* Jacq.

527. *Veronica longifolia* L.
P: *Puccinia albulensis.*

528. *Veronica wormskjoldii* Roem. & Schult.
P: *Puccinia albulensis.*

RUBIACEAE

529. *Galium anisophyllon* Vill.
P: *Puccinia lagerheimii.*

530. *Galium noricum* Ehrend.
P: *Puccinia lagerheimii.*

531. *Galium saxatile* L.
P: *Puccinia lagerheimii.*

CAPRIFOLIACEAE

532. *Linnaea borealis* L.
A small plant.

533. *Scabiosa columbaria* L.
P: *Microbotryum intermedium.*

534. *Scabiosa lucida* Vill.
P: *Microbotryum intermedium.*

CAMPANULACEAE

Campanula L.
P: *Puccinia novae-zembliae.*

535. *Campanula gieseckiana* Vest ex Schult. (“*giesekiana*”)

536. *Campanula rotundifolia* L.
P: *Puccinia campanulae.*

537. *Jasione montana* L.
P: *Puccinia campanulae.*

538. *Melanocalyx uniflora* (L.) Morin

539. *Phyteuma betonicifolium* Vill.
P: *Uromyces caricis-sempervirentis.*

540. *Phyteuma confusum* A. Kern.
P: *Uromyces caricis-sempervirentis.*

541. *Phyteuma hemisphaericum* L.
P: *Uromyces caricis-sempervirentis.*

542. *Phyteuma orbiculare* L.
P: *Uromyces caricis-sempervirentis.*

543. *Phyteuma ovatum* Honck.
P: *Uromyces caricis-sempervirentis.*

544. *Phyteuma spicatum* L.
P: *Uromyces caricis-sempervirentis.*

ASTERACEAE

545. *Achillea millefolium* L.
P: *Puccinia cnici-oleracei*; *P. dioicae.*

546. *Achillea ptarmica* L.
P: *Puccinia cnici-oleracei.*

547. *Adenostyles alliariae* (Gouan) Kern.
P: *Uromyces cacaliae.*

548. *Adenostyles alpina* (L.) Bluff & Fingerh.
P: *Uromyces cacaliae.*

549. *Agoseris aurantiaca* (Hook.) Greene
P: *Puccinia columbiensis.*

550. *Agoseris glauca* (Pursh) Raf.
P: *Puccinia columbiensis*, *P. dioicae*, *P. hieracii.*

551. *Agoseris parviflora* (Nutt.) D. Dietr.
P: *Puccinia dioicae.*

552. *Antennaria alpina* (L.) Gaertn.
A small plant.

553. *Antennaria bocheriana* A.E. Porsild
A small plant.

554. *Antennaria canescens* Malte
A small plant.

555. *Antennaria friesiana* (Trautv.) Ekman
A small plant.

556. *Antennaria monocephala* DC.
A small plant.

557. *Antennaria porsildii* E. Ekman
A small plant.

558. *Antennaria rosea* Greene
A small plant.

Arnica L.
P: *Puccinia arnicae-scorpioidis.*

559. *Arnica angustifolia* Vahl
P: *Arnica chamissonis.*

560. *Arnica cordifolia* Hook.
P: *Entyloma arnicale*; *Puccinia arnicalis.*

561. *Arnica gracilis* Rydb.
P: *Entyloma arnicale.*

562. *Arnica griscomii* Fernald
P: *Puccinia arnicalis.*

563. *Arnica latifolia* Bong.
P: *Entyloma arnicale.*

564. *Arnica longifolia* D.C. Eaton
P: *Entyloma arnicale.*

565. *Arnica louiseana* Farr
P: *Puccinia arnicalis.*

566. *Arnica mollis* Hook.
P: *Entyloma arnicale.*

567. *Arnica rydbergii* Greene
P: *Entyloma arnicale.*

568. *Artemisia abrotanum* L.
P: *Puccinia cnici-oleracei.*

569. *Artemisia campestris* L.
P: *Puccinia cnici-oleracei.*

570. *Artemisia carruthii* J.H. Carruth
P: *Puccinia dioicae.*

571. *Artemisia richardsoniana* Besser
P: *Puccinia artemisiae-norvegicae.*

572. *Artemisia vulgaris* L.
P: *Puccinia cnici-oleracei.*

573. *Centaurea jacea* L.
P: *Puccinia dioicae, P. hieracii.*

574. *Centaurea phrygia* L.
P: *Puccinia hieracii.*

575. *Centaurea subtilis* Bertol.
P: *Puccinia dioicae.*

576. *Cicerbita alpina* (L.) Wallr.
P: *Puccinia mulgedii.*

577. *Cicerbita azurea* (Ledeb.) Beauverd
P: *Puccinia mulgedii.*

578. *Cicerbita rosea* (Popov & Vved.) Krasch. ex Kovalevsk.
P: *Puccinia mulgedii.*

579. *Cichorium intybus* L.
P: *Puccinia hieracii.*

580. *Cirsium acaulon* (L.) Scop.
P: *Puccinia dioicae, P. laschii.*

581. *Cirsium arvense* (L.) Scop.
P: *Puccinia laschii.*

582. *Cirsium canescens* Nutt.
P: *Puccinia laschii.*

583. *Cirsium coloradense* (Rydb.) Daniels
P: *Puccinia laschii.*

584. *Cirsium congestissimum* Kitam.
P: *Puccinia laschii.*

585. *Cirsium discolor* (Willd.) Spreng.
P: *Puccinia laschii.*

586. *Cirsium flodmanii* Arthur
P: *Puccinia laschii.*

587. *Cirsium helenioides* (L.) Hill
P: *Puccinia cnici-oleracei.*

588. *Cirsium heterophyllum* (L.) Hill
P: *Puccinia cnici-oleracei, P. dioicae, P. laschii.*

589. *Cirsium hookerianum* Nutt.
P: *Puccinia laschii.*

590. *Cirsium japonicum* DC.
P: *Puccinia dioicae.*

591. *Cirsium longistylum* R.J. Moore & Frankton
P: *Puccinia laschii.*

592. *Cirsium muticum* Michx.
P: *Puccinia laschii.*

593. *Cirsium nipponicum* Makino
P: *Puccinia laschii.*

594. *Cirsium oleraceum* (L.) Scop.
P: *Puccinia cnici-oleracei, P. laschii.*

595. *Cirsium parryi* Petr.
P. *Puccinia laschii.*

596. *Cirsium pitcheri* Torr. & A. Gray
P: *Puccinia laschii.*

597. *Cirsium scariosum* Nutt.
P: *Puccinia laschii.*

598. *Cirsium spicatum* Matsum.
P: *Puccinia dioicae.*

599. *Cirsium spinosissimum* (L.) Scop.
P: *Puccinia laschii.*

600. *Cirsium tioganum* (Congdon) Petr.
P: *Puccinia laschii.*

601. *Cirsium tuberosum* (L.) All.
P: *Puccinia dioicae.*

602. *Cirsium undulatum* (Nutt.) Spreng.
P: *Puccinia hieracii.*

603. *Crepis acuminata* Nutt.
P: *Puccinia crepidicola.*

604. *Crepis alpestris* (Jacq.) Tausch
P: *Puccinia crepidicola.*

605. *Crepis aurea* (L.) Cass.
P: *Puccinia crepidicola.*

606. *Crepis biennis* L.
P: *Puccinia dioicae.*

607. *Crepis blattarioides* (L.) Vill.
P: *Puccinia crepidicola.*

608. *Crepis capillaris* (L.) Wallr.
P: *Puccinia crepidicola.*

609. *Crepis dioscoridis* L.
P: *Puccinia crepidicola.*

610. *Crepis foetida* L.
P: *Puccinia crepidicola.*

611. *Crepis neglecta* L.
P: *Puccinia crepidicola.*

612. *Crepis occidentalis* Nutt.
P: *Puccinia crepidicola.*

613. *Crepis pleurocarpa* A. Gray
P: *Puccinia crepidicola.*

614. *Crepis pontana* (L.) Dalla Torre
P: *Puccinia crepidicola.*

615. *Crepis pyrenaica* (L.) Greuter
P: *Puccinia crepidicola.*

616. *Crepis rubra* L.
P: *Puccinia crepidicola.*

617. *Crepis setosa* Haller f.
P: *Puccinia crepidicola.*

618. *Crepis vesicaria* L.
P: *Puccinia crepidicola.*

619. *Endocellion glaciale* (Ledeb.) Toman
P: *Puccinia conglomerata.*

Erigeron L.
P: *Puccinia dioicae.*

620. *Erigeron acris* L.
P: *Entyloma erigerontis*, *Puccinia dovrensis.*

621. *Erigeron alpinus* L.
P: *Entyloma erigerontis*, *Puccinia dovrensis.*

622. *Erigeron aurantiacus* Regel
P: *Entyloma erigerontis.*

623. *Erigeron borealis* Simmons
P: *Entyloma erigerontis*, *Puccinia dovrensis.*

624. *Erigeron compositus* Pursh

625. *Erigeron eriocephalus* J. Vahl
P: *Entyloma erigerontis.*

626. *Erigeron glabratus* Hoppe & Hornsch.
ex Bluff & Fingerh.
P: *Entyloma erigerontis.*

627. *Erigeron glacialis* (Nutt.) A. Nelson
P: *Entyloma erigerontis.*

628. *Erigeron humilis* Graham
P: *Entyloma erigerontis*, *Puccinia dovrensis.*

629. *Erigeron philadelphicus* L.
P: *Puccinia dioicae.*

630. *Erigeron politus* Fr.
P: *Entyloma erigerontis*, *Puccinia dovrensis*.

631. *Erigeron schleicheri* Gremli
P: *Entyloma erigerontis.*

632. *Erigeron speciosus* (Lindl.) DC.
P: *Entyloma erigerontis.*

633. *Erigeron uniflorus* L.
P: *Entyloma erigerontis*, *Puccinia dovrensis*.

634. *Erigeron ursinus* D.C. Eaton
P: *Entyloma erigerontis.*

635. *Eurybia macrophylla* (L.) Cass.
P: *Puccinia dioicae.*

636. *Eurybia sibirica* (L.) G.L. Nesom
P: *Puccinia dioicae.*

637. *Euthamia graminifolia* (L.) Nutt.
P: *Puccinia dioicae.*

638. *Galatella linosyris* (L.) Rchb. f.
P: *Puccinia cnici-oleracei.*

Hieracium L. (including all apomictic species)
P: *Puccinia columbiensis*, *P. hieracii*; *P. uralensis.*

Fig. 85. *Hieracium* sp. The 146 species of Asteraceae we include here are with few exceptions all infected by rusts. Exceptions are the genera *Antennaria* and *Omalotheca* (*Gnaphalium*), characterized by their very small flowering heads.

639. *Homogyne alpina* (L.) Cass.
P: *Puccinia conglomerata.*

640. *Homogyne discolor* Cass.
P: *Puccinia conglomerata.*

641. *Hymenoxys hoopesii* (A. Gray) Bierner
P: *Puccinia poarum.*

642. *Jacobaea alpina* (L.) Moench
P: *Puccinia conglomerata.*

643. *Jacobaea pseudoarnica* (Less.) Zuev
P: *Puccinia dioicae.*

644. *Klasea nudicaulis* (L.) Fourr.
P: *Puccinia hieracii.*

645. *Krigia biflora* (Walter) S.F. Blake
P: *Puccinia columbiensis.*

646. *Lactuca canadensis* L.
P: *Puccinia minussensis.*

647. *Lactuca indica* L.
P: *Puccinia minussensis.*

648. *Lactuca oblongifolia* Nutt.
P: *Puccinia dioicae, P. minussensis.*

649. *Lactuca raddeana* Maxim.
P: *Puccinia minussensis.*

650. *Lactuca sativa* L.
P: *Puccinia minussensis.*

651. *Lactuca sibirica* (L.) Benth. ex Maxim.
P: *Puccinia dioicae, P. minussensis.*

652. *Leontodon hispidus* L.
P: *Entyloma leontodontis.*

653. *Lycoseris trinervis* (D. Don) S.F. Blake
P: *Puccinia dioicae.*

654. *Lygodesmia grandiflora* Torr. & A. Gray
P: *Puccinia hieracii.*

655. *Nabalus hastatus* (Less.) A. Heller
P: *Puccinia hieracii.*

656. *Nabalus racemosus* (Michx.) Hook.
P: *Puccinia columbiensis.*

657. *Nabalus trifoliolatus* Cass.
P: *Puccinia columbiensis.*

658. *Omalotheca norvegica* (Gunnerus) F.W. Schultz & Sch. Bip.

659. *Omalotheca supina* (L.) DC.

660. *Packera aurea* (L.) Á. Löve & D. Löve
P: *Puccinia conglomerata.*

661. *Parasenecio hastatus* (L.) H. Koyama
P: *Puccinia uralensis.*

662. *Petasites frigidus* (L.) Fr.
P: *Puccinia conglomerata, P. poarum.*

663. *Picris hieracioides* L.
P: *Puccinia hieracii.*

Prenanthes L.
P: *Puccinia conglomerata, P. variabilis.*

664. *Saussurea alpina* (L.) DC.
P: *Puccinia vaginatae.*

665. *Scorzoneroides autumnalis* (L.) Moench
P: *Entyloma leontodontis, Puccinia hieracii.*

666. *Scorzoneroides helvetica* (Mérat) Holub
P: *Entyloma leontodontis.*

667. *Scorzoneroides pyrenaica* (Gouan) Holub
P: *Entyloma leontodontis.*

668. *Senecio doronicum* (L.) L.
P: *Puccinia conglomerata.*

669. *Senecio lugens* Richardson
P: *Puccinia conglomerata.*

670. *Senecio nemorensis* L.
P: *Puccinia conglomerata.*

671. *Senecio ovatus* (G. Gaertn., B. Mey & Scherb.) Willd.
P: *Puccinia conglomerata.*

672. *Senecio taraxacoides* (A. Gray) Greene
P: *Puccinia conglomerata.*

673. *Serratula tinctoria* L.
P: *Puccinia hieracii.*

674. *Solidago altissima* L.
P: *Puccinia virgae-aureae.*

675. *Solidago chilensis* Meyen
P: *Puccinia virgae-aureae.*

676. *Solidago puberula* Nutt.
P: *Puccinia virgae-aureae.*

677. *Solidago rugosa* Mill.
P: *Puccinia virgae-aureae.*

678. *Solidago virgaurea* L.
P: *Puccinia virgae-aureae.*

679. *Stephanomeria pauciflora* (Torr.) A. Nelson
P: *Puccinia hieracii.*

680. *Symphyotrichum adscendens* (Lindl.) G.L. Nesom
P: *Puccinia dioicae.*

681. *Symphyotrichum drummondii* (Lindl.) G.L. Nesom
P: *Puccinia dioicae.*

682. *Symphyotrichum foliaceum* (DC.) G.L. Nesom
P: *Puccinia dioicae.*

683. *Tamingasa yatabei* (Matsum. & Koidz.) C. Ren & Q.E. Yang
P: *Puccinia uralensis.*

684. *Tanacetum parthenium* (L.) Sch. Bip.
P: *Puccinia cnici-oleracei.*

Taraxacum F.H. Wigg (including all names)
P: *Puccinia dioicae, P. hieracii, P. variabilis.*

685. *Tephroseris integrifolia* (L.) Holub
P: *Puccinia senecionis.*

686. *Tephroseris palustris* (L.) Rchb.
P: *Puccinia senecionis.*

687. *Tripleurospermum ambiguum* (Ledeb.) Franch. & Sav.
A plant with slender filiform leaves.

688. *Tripleurospermum inodorum* (L.) Sch. Bip.
A plant with slender filiform leaves.

689. *Tripleurospermum maritimum* (L.) W.D.J. Koch
A plant with slender filiform leaves.

690. *Tripolium pannonicum* (Jacq.) Dobrocz.
P: *Puccinia cnici-oleracei, P. dioicae.*

691. *Tussilago farfara* L.
P: *Puccinia poarum.*

THYMELAEACEAE

692. *Dirca palustris* L.
P: *Puccinia dioicae.*

PHRYMACEAE

693. *Phryma leptostachya* L.
P: *Puccinia dioicae.*

TOFIELDIACEAE

694. *Tofieldia coccinea* Richardson

695. *Tofieldia pusilla* (Michx.) Pers.

Fig. 86. *Streptopus amplexifolius* (L.) belongs to the Liliaceae, and as such is rarely attacked.

LILIACEAE

696. *Streptopus amplexifolius* (L.) DC.

MELANTHIACEAE

697. *Anticlea elegans* (Pursh) Rydb.
P: *Urocystis flowersii.*

698. *Toxicoscordion venenosum* (S. Watson) Rydb.

P: *Urocystis flowersii.*

699. *Veratrum album* L.
P: *Uromyces veratri.*

AMARYLLIDACEAE

700. *Allium victorialis* L.
P: *Puccinia japonensis.*

701. *Allium ochotense* Prokh.
P: *Puccinia japonensis.*

IRIDACEAE

702. *Sisyrinchium groenlandicum* Böcher

Fig. 87. *Listera cordata*. Nearly all species of orchids form endo-mycorrhiza, often called orchid mycorrhiza. The fungal partner may be a species of *Sebacina*, *Tulasnella*, or another heterobasidiomycete, or a homobasidiomycete like *Thelephora*, *Tomentella*, or *Russula* (all in vol. 4).

ORCHIDACEAE

703. *Corallorhiza trifida* Châtel

704. *Galearis rotundifolia* (Banks ex Pursh) R.M. Bateman

705. *Neottia cordata* (L.) Rich.

706. *Platanthera hyperborea* (L.) Lindl.
P: *Melampsora epitea.*

707. *Pseudorchis albida* (L.) Á. Löve & D. Löve

JUNCACEAE

708. *Juncus alpinoarticulatus* Chaix

709. *Juncus arcticus* Willd.
P: *Urocystis junci.*

710. *Juncus biglumis* L.
P: *Stegocintractia lidii, Urocystis junci, U. tothii.*

711. *Juncus bufonius* L.

712. *Juncus castaneus* Sm.

713. *Juncus filiformis* L.
P: *Urocystis junci.*

714. *Juncus gerardi* Loisel.

715. *Juncus ranarius* Songeon & E.P. Perrier

716. *Juncus squarrosus* L.

717. *Juncus subtilis* E. Mey.

718. *Juncus triglumis* L.

719. *Luzula alpinopilosa* (Chaix) Breistr.
P: *Stegocintractia spadicea.*

720. *Luzula campestris* (L.) DC.
P: *Stegocintractia luzulae.*

721. *Luzula confusa* Lindeb.
P: *Stegocintractia hyperborea.*

722. *Luzula groenlandica* Böcher

723. *Luzula multiflora* (Ehrh.) Lej.
P: *Stegocintractia luzulae.*

724. *Luzula nivalis* (Laest.) Spreng.
P: *Stegocintractia hyperborea.*

725. *Luzula nivea* (L.) DC.
P: *Stegocintractia luzulae.*

726. *Luzula parviflora* (Ehrh.) Desv.

727. *Luzula spicata* (L.) DC.
P: *Stegocintractia luzulae.*

728. *Luzula sudetica* (Willd.) Schult.
P: *Stegocintractia luzulae.*

729. *Luzula wahlenbergii* Rupr.
P: *Stegocintractia luzulae.*

730. *Oreojuncus trifidus* (L.) Záv. Drábk. & Kirschner

CYPERACEAE

731. *Carex adelostoma* V.I. Krecz.
P: *Anthracoidea buxbaumii.*

732. *Carex alatauensis* S.R. Zhang
P: *Anthracoidea lindebergiae.*

733. *Carex alba* Scop.
P: *Anthracoidea inclusa.*

734. *Carex aquatilis* Wahlenb.
P: *Anthracoidea bigelowii, A. heterospora, A. liroi, Schizonella melanogramma.*

735. *Carex atherodes* Spreng.
P: *Anthracoidea americana.*

736. *Carex atrata* L.
P: *Anthracoidea atratae, Schizonella melanogramma, Urocystis fischeri.*

737. *Carex atrofusca* Schkuhr
P: *Anthracoidea misandrae.*

738. *Carex baldensis* L.
P: *Anthracoidea baldensis.*

739. *Carex bicolor* Bellardi ex All.
P: *Anthracoidea paniceae.*

740. *Carex bigelowii* Torr. ex Schwein.
P: *Anthracoidea bigelowii, A. liroi, Schizonella melanogramma, Urocystis fischeri.*

741. *Carex boecheriana* Á. Löve et al.
P: *Anthracoidea capillaris.*

742. *Carex borealipolaris* S.R. Zhang
P: *Anthracoidea elynae.*

743. *Carex brunnescens* (Pers.) Poir.
P: *Anthracoidea karii, Orphanomyces arcticus.*

744. *Carex buxbaumii* Wahlenb.
P: *Anthracoidea buxbaumii.*

745. *Carex canescens* L.
P: *Anthracoidea fischeri, A. karii, Orphanomyces arcticus.*

746. *Carex capillaris* L.
P: *Anthracoidea capillaris, Orphanomyces arcticus, Urocystis fischeri.*

747. *Carex capillifolia* (Decne.) S.R. Zhang
P: *Anthracoidea elynae.*

748. *Carex capitata* Sol.

749. *Carex cespitosa* L.
P: *Anthracoidea heterospora, A. liroi.*

750. *Carex chordorrhiza* L. f.
P: *Anthracoidea aspera, A. fischeri, Puccinia chordorrhiza.*

751. *Carex curvula* All.
P: *Anthracoidea curvulae, Schizonella melanogramma.*

752. *Carex cusickii* Mack.
P: *Anthracoidea fischeri.*

753. *Carex dacica* Heuff.
P: *Schizonella melanogramma.*

754. *Carex davalliana* Sm.
P: *Orphanomyces arcticus.*

755. *Carex deasyi* (C.B. Clarke) O. Yano & S.R. Zhang
P: *Anthracoidea elynae.*

756. *Carex deflexa* Hornem.
P: *Anthracoidea caricis.*

757. *Carex diandra* Schrank
P: *Anthracoidea aspera.*

758. *Carex dioica* L.
P: *Anthracoidea turfosa.*
759. *Carex disperma* Dewey

760. *Carex disticha* Huds.
P: *Anthracoidea fischeri.*

761. *Carex ebenea* Rydb.
P: *Anthracoidea verrucosa, Orphanomyces arcticus.*

762. *Carex eburnea* Boott
P: *Orphanomyces arcticus.*

763. *Carex eleusinoides* Turcz. ex Kunth
P: *Anthracoidea heterospora.*

764. *Carex elynoides* Holm
P: *Anthracoidea nardinae.*

765. *Carex enervis* C.A. Mey.
P: *Anthracoidea pseudofoetidae.*

766. *Carex ericetorum* Pollich
P: *Schizonella melanogramma, Urocystis fischeri.*

767. *Carex ferruginea* Scop.
P: *Anthracoidea ferrugineae, Schizonella melanogramma.*

768. *Carex firma* Mygind ex Host
P: *Schizonella melanogramma.*

769. *Carex fischeri* K. Schum.
P: *Anthracoidea fischeri.*

770. *Carex flacca* Schreb.
P: *Anthracoidea pratensis, Urocystis fischeri.*

771. *Carex foetida* All.
P: *Anthracoidea foetida.*

772. *Carex fuliginosa* Schkuhr
P: *Anthracoidea altera, A. misandrae, Schizonella melanogramma.*

773. *Carex glacialis* Mack.

774. *Carex glareosa* Schkuhr ex Wahlenb.
P: *Anthracoidea aspera, Orphanomyces arcticus.*

775. *Carex globularis* L.
P: *Schizonella melanogramma.*

776. *Carex gmelinii* Hook. & Arn.
P: *Anthracoidea gmelinii.*

777. *Carex heleonastes* Ehrh. ex L. f.
P: *Anthracoidea karii.*

778. *Carex holostoma* Drejer

779. *Carex hoodii* Boott
P: *Anthracoidea verrucosa.*

780. *Carex karii* (Liro) Nannf.
P: *Anthracoidea echinata.*

781. *Carex kitaibeliana* Degen ex Bech.
P: *Anthracoidea kitaibelianae.*

782. *Carex kokanica* (Regel) S.R. Zhang
P: *Anthracoidea lindebergiae.*

783. *Carex krascheninnikovii* V.I. Krecz.
P: *Anthracoidea atratae.*

784. *Carex lachenalii* Schkuhr
P: *Orphanomyces arcticus.*

785. *Carex lapponica* O. Lang
P: *Anthracoidea fischeri, A. karii.*

786. *Carex lasiocarpa* Ehrh.
P: *Anthracoidea lasiocarpae, Urocystis fischeri.*

787. *Carex laxa* Wahlenb.
P: *Anthracoidea laxae.*

788. *Carex lazarei* Jac. Koopman et al.
P: *Schizonella melanogramma.*

789. *Carex ledebouriana* Trevir.
P: *Anthracoidea capillaris.*

790. *Carex lenticularis* Michx.
P: *Anthracoidea heterospora.*

791. *Carex limosa* L.
P: *Anthracoidea limosae.*

792. *Carex liparocarpos* Gaudin
P: *Schizonella melanogramma.*

793. *Carex livida* (Wahlenb.) Willd.
P: *Anthracoidea paniceae.*

794. *Carex loliacea* L.
P: *Anthracoidea karii.*

795. *Carex lyngbyei* Hornem.
P: *Anthracoidea liroi, Urocystis fischeri.*

796. *Carex mackenziei* V.I. Krecz.

797. *Carex macloviana* d'Urv.
P: *Anthracoidea verrucosa, Orphanomyces arcticus.*

798. *Carex macrochaeta* Holm
P: *Anthracoidea atratae.*

799. *Carex magellanica* Lam.
P: *Anthracoidea magellanica, Puccinia karelica.*

800. *Carex marina* Dewey
P: *Anthracoidea karii.*

801. *Carex maritima* Gunnerus
P: *Anthracoidea pseudofoetidae, Orphanomyces arcticus, Planetella lironis, Urocystis littoralis.*

802. *Carex membranacea* Hook.
P: *Urocystis fischeri.*

803. *Carex microglochin* Wahlenb.

804. *Carex micropoda* C.A. Mey.
P: *Moreaua apicis.*

805. *Carex montana* L.
P: *Anthracoidea caricis, Urocystis fischeri.*

806. *Carex myosuroides* Vill.
P: *Anthracoidea elynae, Schizonella elynae.*

807. *Carex nardina* (Hornem.) Fr.
P: *Anthracoidea nardinae, Schizonella melanogramma.*

808. *Carex nigra* (L.) Reichard
P: *Anthracoidea heterospora, A. liroi, Urocystis fischeri.*

809. *Carex norvegica* Retz.
P: *Anthracoidea savilei.*

810. *Carex obtusata* Lilj.
P: *Anthracoidea obtusatae.*

811. *Carex oederi* Retz.

812. *Carex ornithopoda* Willd.
P: *Anthracoidea irregularis, Schizonella melanogramma.*

813. *Carex paleacea* Schreb. ex Wahlenb.
P: *Anthracoidea heterospora.*

814. *Carex pallescens* L.
P: *Urocystis fischeri.*

815. *Carex panicea* L.
P: *Anthracoidea paniceae, Urocystis fischeri.*

816. *Carex parallela* (Læst.) Sommerf.
P: *Anthracoidea turfosa.*

817. *Carex pediformis* C.A. Mey.
P: *Anthracoidea irregularis, Schizonella melanogramma.*

818. *Carex phaeocephala* Piper
P: *Anthracoidea verrucosa.*

819. *Carex pilulifera* L.
P: *Anthracoidea caricis.*

820. *Carex pluriflora* Hultén
P: *Puccinia karelica.*

821. *Carex podocarpa* R. Br.
P: *Anthracoidea atratae, Schizonella melanogramma.*

822. *Carex praticola* Rydb.

823. *Carex preslii* Steud.
P: *Anthracoidea verrucosa.*

824. *Carex pulicaris* L.
P: *Anthracoidea pulicaris.*

825. *Carex pyrenaica* Wahlenb.
P: *Moreaua apicis.*

826. *Carex rariflora* (Wahlenb.) Sm.
P: *Anthracoidea limosae.*

827. *Carex raynoldsii* Dewey
P: *Anthracoidea atratae, Schizonella melanogramma.*

828. *Carex rossii* Boott
P: *Anthracoidea caricis.*

829. *Carex rostrata* Stokes
P: *Anthracoidea americana, A. inclusa, Urocystis fischeri.*

830. *Carex rotundata* Wahlenb.
P: *Schizonella melanogramma.*

831. *Carex rufina* Drejer

832. *Carex rupestris* All.
P: *Anthracoidea rupestris, Puccinia rupestris, Schizonella melanogramma.*

833. *Carex sabynensis* Less. ex Kunth
P: *Schizonella melanogramma.*

834. *Carex salina* Wahlenb.
P: *Anthracoidea liroi, A. salina.*

835. *Carex saxatilis* L.
P: *Anthracoidea lasiocarpae.*

836. *Carex schmidtii* Meinsh.
P: *Anthracoidea liroi.*

837. *Carex scirpoidea* Michx.
P: *Anthracoidea scirpoideae, Schizonella melanogramma.*

838. *Carex scopulorum* Holm
P: *Anthracoidea bigelowii.*

839. *Carex sempervirens* Vill.
P: *Anthracoidea sempervirens, Schizonella melanogramma, Uromyces caricis-sempervirentis.*

840. *Carex simpliciuscula* Wahlenb.
P: *Anthracoidea lindebergiae.*

841. *Carex stenocarpa* Turcz. ex V.I. Krecz.
P: *Schizonella melanogramma.*

842. *Carex stenophylla* Wahlenb.
P: *Orphanomyces arcticus.*

843. *Carex stylosa* C.A. Mey.

844. *Carex subspathacea* Hornem.
P: *Anthracoidea subspathacea, Urocystis fischeri.*

845. *Carex supina* Willd. ex Wahlenb.

846. *Carex trisperma* Dewey

847. *Carex umbellata* Willd.

848. *Carex umbrosa* Host
P: *Anthracoidea umbrosa, Schizonella melanogramma.*

849. *Carex ursina* Dewey

850. *Carex utriculata* Boott
P: *Anthracoidea americana.*

851. *Carex vaginata* Tausch
P: *Anthracoidea paniceae, Puccinia vaginatae, Schizonella melanogramma.*

852. *Eleocharis acicularis* (L.) Roem. & Schult.
An aquatic plant.

853. *Eleocharis palustris* (L.) Roem. & Schult.
An aquatic/marsh plant.

854. *Eleocharis quinqueflora* (Hartmann) O. Schwarz
An aquatic/marsh plant.

855. *Eleocharis uniglumis* (Link) Schult.
A marsh plant.

856. *Eriophorum angustifolium* Honck.
An aquatic/marsh plant.

857. *Eriophorum callitrix* C.A. Mey.
A marsh plant.

858. *Eriophorum scheuchzeri* Hoppe
A marsh plant.

859. *Eriophorum triste* (Th. Fr.) Hadac & Á. Löve
A marsh plant.

860. *Eriophorum vaginatum* L.
A marsh plant.

Fig. 88. *Eriophorum scheuchzeri* and most other species of *Eriophorum* are not attacked by rusts.

861. *Trichophorum cespitosum* (L.) Hartm.
P: *Anthracoidea scirpi.*

POACEAE

862. *Achnatherum calamagrostis* (L.) P. Beauv.
P: *Puccinia recondita.*

863. *Acrospelion alpestre* (Host) Barberá & Quintanar
P: *Urocystis triseti.*

Agrostis L.
P: *Ustilago striiformis*.

864. *Agrostis canina* L.
P: *Puccinia recondita.*

865. *Agrostis capillaris* L.

866. *Agrostis gigantea* Roth
P: *Puccinia recondita.*

867. *Agrostis idahoensis* Nash
P: *Puccinia recondita.*

868. *Agrostis mertensii* Trin.
P: *Puccinia recondita.*

869. *Agrostis scabra* Willd.
P: *Puccinia poarum.*

870. *Agrostis stolonifera* L.

871. *Agrostis vinealis* Schreb.

Alopecurus L.
P: *Uromyces dactylidis, Stegocintractia luzulae.*

872. *Alopecurus aequalis* Sobol.

873. *Alopecurus magellanicus* Lam.

874. *Anthoxanthum monticola* (Bigelow) Veldkamp

875. *Anthoxanthum nitens* (Weber) Y. Schouten & Veldkamp
P: *Puccinia recondita.*

876. *Anthoxanthum odoratum* L.
P: *Puccinia brachypodii, P. recondita, Stegocintractia luzulae, Urocystis roivainenii.*

877. *Arctagrostis latifolia* (R. Br.) Griseb.
P: *Puccinia brachypodii, Urocystis agropyri, Ustilago striiformis.*

878. *Arrhenatherum elatius* (L.) P. Beauv. ex J. Presl & C. Presl
P: *Puccinia brachypodii.*

Avenella Bluff ex Drejer
P: *Ustilago striiformis.*

879. *Avenella flexuosa* (L.) Drejer

Beckmannia Host
P: *Ustilago striiformis.*

880. *Brachypodium pinnatum* (L.) P. Beauv.
P: *Puccinia brachypodii.*

881. *Brachypodium rupestre* (Host) Roem. & Schult.
P: *Puccinia brachypodii.*

882. *Brachypodium sylvaticum* (Huds.) P. Beauv.
P: *Puccinia brachypodii.*

Bromus L.
P: *Ustilago striiformis.*

883. *Bromus anomalus* Rupr. ex E. Fourn.
P: *Puccinia recondita.*

884. *Bromus arvensis* L.
P: *Puccinia recondita.*

885. *Bromus ciliatus* L.
P: *Puccinia recondita.*

886. *Bromus tectorum* L.
P: *Puccinia recondita.*

887. *Calamagrostis lapponica* (Wahlenb.) Hartm.

888. *Calamagrostis purpurascens* R. Br.

889. *Calamagrostis purpurea* (Trin.) Trin.
P: *Ustilago calamagrostidis.*

890. *Calamagrostis stricta* (Timm) Koeler
P: *Puccinia recondita, Ustilago scrobiculata.*

891. *Dactylis glomerata* L.
P: *Uromyces dactylidis*

892. *Danthonia spicata* (L.) Roem. & Schult.
P: *Ustilago striiformis.*

Deschampsia P. Beauv.
P: *Puccinia brachypodii, Uromyces airae-flexuosae, Ustilago striiformis.*

893. *Deschampsia cespitosa* (L.) P. Beauv.

894. *Dupontia fisheri* R. Br.
A bog plant with slender filiform leaves.

895. *Dupontia fulva* (Trin.) Röser & Tkach
A marsh plant.

Elymus L.
P: *Ustilago striiformis.*

896. *Elymus arizonicus* (Scribn. & J.G. Sm.) Gould
P: *Puccinia recondita.*

897. *Elymus canadensis* L.
P: *Urocystis agropyri.*

898. *Elymus ciliaris* (Trin.) Tzvelev
P: *Puccinia brachypodii.*

899. *Elymus elymoides* (Raf.) Swezey
P: *Puccinia recondita.*

900. *Elymus glaucus* Buckley
P: *Urocystis agropyri.*

901. *Elymus macrourus* (Steud.) Tzvelev
P: *Puccinia recondita, Urocystis agropyri.*

902. *Elymus repens* (L.) Gould
P: *Puccinia recondita.*

903. *Elymus sajanensis* (Nevski) Tzvelev

904. *Elymus smithii* (Rydb.) Gould
P: *Urocystis agropyri.*

905. *Elymus violaceus* (Hornem.) J. Feilberg
P: *Puccinia recondita, Urocystis agropyri.*

Festuca Tourn. ex L.
P: *Uromyces dactylidis, Ustilago striiformis.*

906. *Festuca arizonica* Vasey
P: *Puccinia poarum.*

907. *Festuca baffinensis* Polunin

908. *Festuca brachyphylla* Schult. & Schult. f.

909. *Festuca hyperborea* Holmen

910. *Festuca rubra* L.

911. *Festuca sororia* Piper
P: *Puccinia poarum.*

912. *Festuca vivipara* (L.) Sm.

Helictochloa Romero Zarco
P: *Ustilago striiformis.*

913. *Koeleria pyramidata* (Lam.) P. Beauv.
P: *Puccinia brachypodii, Ustilago striiformis.*

914. *Koeleria spicata* (L.) Barberá et al.
P: *Puccinia brachypodii, Urocystis triseti.*

915. *Leymus arenarius* (L.) Hochst.
P: *Urocystis agropyri.*

916. *Leymus mollis* (Trin.) Pilg.
P: *Urocystis agropyri.*

917. *Leymus triticoides* (Buckley) Pilg.
P: *Puccinia recondita.*

918. *Leymus villosissimus* (Scribn.) Tzvelev
P: *Urocystis agropyri.*

Melica L.
P: *Ustilago striiformis.*

919. *Milium effusum* L.
P: *Puccinia brachypodii.*

920. *Nardus stricta* L.

921. *Phippsia algida* (Sol.) R. Br.
A marsh plant.

922. *Phleum alpinum* L.

923. *Pleuropogon sabinei* R. Br.
P: *Ustilentyloma pleuropoginis.*

Poa L.
P: *Puccinia brachypodii, Uromyces dactylidis.*

924. *Poa abbreviata* R. Br.

925. *Poa alpigena* Lindm.
P: *Puccinia poarum.*

926. *Poa alpina* L.
P: *Puccinia poarum.*

927. *Poa annua* L.
P: *Puccinia poarum.*

928. *Poa arctica* R. Br.

929. *Poa glauca* Vahl

930. *Poa hartzii* Gand.

931. *Poa nemoralis* L.
P: *Puccinia poarum.*

932. *Poa palustris* L.
P. *Ustilago striiformis.*

933. *Poa pratensis* L.
P: *Puccinia poarum.*

934. *Poa trivialis* L.
P: *Puccinia poarum.*

Podagrostis (Griseb.) Scribn. & Merr.
P: *Ustilago striiformis.*

935. *Pseudoroegneria spicata* (Pursh) Á. Löve
P: *Urocystis agropyri.*

Puccinellia Parl.
P: *Ustilago striiformis.*

936. *Puccinellia andersonii* Swallen
This grass grows on coastal shores.

937. *Puccinellia angustata* (R. Br.) E.L. Rand & Redfield
On moist sandy-clayey ground near the coast.

938. *Puccinellia distans* (Jacq.) Parl.

939. *Puccinellia groenlandica* T.J. Sørensen
In clayey-sandy marshes near fjord margins.

940. *Puccinellia maritima* (Huds.) Parl.
On moist sandy-clayey ground near the coast.

941. *Puccinellia neoarctica* (Á. Löve & D. Löve) Böcher et al.

942. *Puccinellia nutkaensis* (J. Presl) Fernald & Weath.

943. *Puccinellia nuttalliana* (Schult.) Hitchc.
Growing on sandy-clayey saline lake margins.

944. *Puccinellia phryganodes* (Trin.) Scribn. & Merr.
Growing in salt marshes and coastal shores.

945. *Puccinellia porsildii* T.J. Sørensen

946. *Puccinellia tenella* (Lange) Holmb.
Growing on damp coastal shores.

947. *Puccinellia vaginata* (Lange) Fernald & Weath.
This plant is found by mud volcanoes.

948. *Puccinellia vahliana* (Liebm.) Scribn. & Merr.
On moist sandy-clayey ground near the coast.

Sesleria Scop.
P: *Ustilago striiformis.*

Sibirotrisetum Barberá et al.
P: *Ustilago striiformis.*

949. *Trisetum flavescens* (L.) P. Beauv.
P: *Urocystis triseti.*

950. *Vahlodea atropurpurea* (Wahlenb.) Fr.
P: *Ustilago striiformis.*

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951. *Triglochin palustris* L.
Clayey beaches around fjords and lakes, salt marshes.

9b. Saprotrophic fungi and their substrates

The most diverse genera of saprotrophic fungi (represented by 10 or more species) are *Clitocybe*, *Cystoderma*, *Entoloma*, *Galerina* (if they are not parasitic), *Gymnopus*, *Hemimycena*, *Hygrocybe*, *Melanoleuca*, *Mycena*, *Psilocybe*, *Psathyrella*, and *Typhula*. But in the arctic-alpine region, high species diversity is not characteristic; instead, a large number of smaller saprotrophic genera occur.

Another characteristic – and expected – feature of arctic-alpine saprotrophs is the rarity of species with large basidiomata. One of the more notable exceptions is *Lepista multiformis* (Fig. 14), a High Arctic species occurring around the margin of polygons and other places rich in organic matter. In dry regions, the occurrence of species of *Calvatia* is remarkable; they resemble white golf balls and are often easily seen at a distance in open areas.

Plants in arctic areas are generally small, primarily due to the short growing season and low temperatures, which do not allow large plants to develop. In light of the low overall biomass of the vegetation, it may be expected that the fungi living on these plants are also small. *Mycena* and *Galerina* are present, with many species occurring on diverse flowering plants and mosses, and a level of diversity similar to that of temperate areas. *Galerina* may even be more diverse, due to the more extensive moss cover in arctic-alpine regions. Another genus of small saprotrophic agarics is *Hemimycena*, with small basidiomata occurring on various kinds of plant debris. Examples of very small saprotrophic genera of agarics and cyphelloids are *Typhula*, *Pterulicium*, *Flagelloscypha*, *Glabrocyphella*, *Mucronella*, *Rimbachia*, *Arrhenia*, *Stromatocyphella*, *Merismodes* and *Gloiocephala*.

Clitocybe and *Gymnopus* are the most common larger saprotrophs, but they rarely occur in the large masses seen in temperate regions. The largest species of arctic-alpine saprotrophic agarics belong to the genera *Melanoleuca*, *Lepista*, *Calvatia*, and *Agaricus*. These are uncommon, as they demand more debris than other genera. *Melanoleuca cognata* was regularly found in a calcareous field covered with *Cassiope tetragona*, which produced much debris, and was associated with the ecto-mycorrhizal species *Tricholoma scalpturatum* and *T. hemisulphureum*.

Most saprotrophs occur in moist areas, in scrubs along small streams, on herb slopes, and in other places with much organic matter, but they are also found in areas seemingly without organic matter. In fell-fields the wind can be harsh and few plants survive; they are generally prostrate, creeping along the surface of the stony ground. In rainy seasons, it is however still possible to find fungi on the underside of their woody stems, surviving on the debris in the moist mm-narrow zone between the ground and the woody creeping stem.

On various kinds of wood (generalist saprotrophs)

Only a few fungi belong to this group, since most species are specific to *Salix* or *Betula* and thus are treated below. Corticioid or resupinate fungi predominate among the generalist saprotrophs. These are a large group of >50 species of pale, white, beige, or yellowish, thin fungi, often referred to as "white paint". Almost all of them grow on more or less decayed wood of *Alnus*, *Betula* and *Salix*, some preferring specific stages of decay, and others occurring more randomly. Similarly, some species require a specific host substrate, whereas others consume any host. It is often difficult to identify the host, especially if the bark has disappeared.

Most Arctic corticioids are restricted to the southern Arctic, since solid pieces of wood are necessary for their growth, but a few may be found at higher latitudes on the underside of old *Salix*.

A few other agarics and polypores that are indifferent to host species also belong here, e.g. *Kuehneromyces mutabilis*, *Hypholoma capnoides*, and *Lentinus* (*Polyporus*) *brumalis*. On introduced conifers, the dangerous (for the trees) genus *Armillariella* has been found. The most commonly recorded corticioids are species of *Hyphoderma*, *Trechispora*, *Tubulicrinis* and *Tulasnella*. Less common are *Botryobasidium*, *Hyphodontia*, and others we have only found once.

Fig. 89. *Kuehneromyces mutabilis* grows on a wide variety of substrates.

Fig. 90. A species of *Entoloma* subgen. *Leptonia*. The basidiomata are often found in the same localities as species of *Hygrocybe*, related genera, and club fungi. Their nutritional mode is still unknown, but it is unlikely that they are ecto-mycorrhizal members of the genus (cf. Fig. 100).

Fig. 91. The Arctic climate is cold, often windswept, and dry. Dead, decorticated, and completely dry ruins of junipers and willows occur. On the underside, there may be a narrow space between the ruin and the ground, where there is oxygen and moisture from precipitation running down the ruin onto the ground. In this narrow space with high humidity and wet wood, small saprotrophs can develop, like *Crepidotus*, *Pellidiscus*, and others (see e.g. Senn-Irlet 1992).

On wood of *Salix*

Salix glauca is one of the dominant species of willows in cold areas that has stems and trunks large enough to support many fungi. The polypore *Ceriporia varia* is common, as are *Picipes badius*, *P. melanopus*, and the northern *P. tubaeformis*. Other species are *Resiniporus resinascens* and *R. pseudogilvescens.* Common fungi that demand less wood are the stereoid and corticioid species *Hydnoporia tabacina*, *Laetocorticium roseum*, *Peniophora polygonia*, *Cytidia salicina* (Fig. 25), *Megalocystidium leucoxanthum*, and *Aleurodicus lapponicus*. Among the agarics specific to *Salix* are the cold-tolerant species *Lentinellus micheneri* and *Flammulina velutipes*, and the small *Phaeomarasmius borealis* (Fig. 27). These are a few of the most characteristic, but *Salix* is a very versatile substrate.

On wood of *Betula*

In subarctic and subalpine regions, *Betula pubescens* is sufficiently large to be the host for many fungi growing on wood. Typical large species are *Fomitopsis* (*Piptoporus*) *betulina*, *Inonotus obliquus*, *Mensularia* (*Inonotus*) *radiata*, *Phellinus lundellii*, *P. laevigatus*, *Postia chionea*, *P. tephroleuca*, *Cerrena unicolor* and *Tyromyces kmetii.* The large fungus *Stereum rugosum* is common in southern Greenland. *Panellus ringens* is found on standing dead trunks. The peculiar species *Macrotyphula contorta* (see Fig. 21) is only one to a few cm high, while the closely related *M. fistulosa* is 10–15 cm high.The other arctic-alpine species of birch have “trunks” so small that they are rarely a substrate for larger fungi.

Fig. 92. *Chondrostereum purpureum* is common on *Betula pubescens* in southern Greenland.

Fig. 93. *Trechispora* is a common corticioid fungus in southern Greenland.

On soil and debris

Grasslands are a variable habitat, depending on the mineral composition of the ground and on the vegetation. Typical temperate grasslands are also found in arctic-alpine regions, and they include many of the same species, e.g. *Chromosera citrinopallida*, *C. lilacina*, *C. xanthochroa*, *Cuphophyllus cinerellus*, *C. colemammnianus*, *C. esteriae*, *C. hygrocyboides*, *C. lacmus*, *C. virgineus*, *Gliophorus laetus*, *G. psittacinus*, *Hygrocybe acutoconica*, *H. biminiata*, *H. cantharellus*, *H. conica* s.l., *H. constricta*, *H. glacialis*, *H. miniata*, *H. reidii*, *H. rubrolamellata*, *H. salicis-herbaceae*, and *H. turunda*, to name a few.

Two other groups usually accompany waxcaps in grasslands, i.e., *Entoloma* and *Clavaria* s.l. Clavarioids are represented by e.g. *Clavaria argillacea*, *C. fragilis*, *Clavulinopsis corniculata*, *C. fusiformis*, *C. laeticolor*, and *Clavicorona pyxidata*. *Entoloma* has not yet been comprehensively reviewed, but some examples are *E. porphyrophaeum*, *E. sericellum*, *E. sericeum*, *E. serratulum*, and *E. xanthochroum.*

Genera like *Panaeolus*, *Psilocybe*, *Hypholoma* and *Stropharia* also commonly occur, as well as gastroid species of *Calvatia*, *Lycoperdon*, *Bovista*, and others.

Fig. 94. *Entoloma milleri* from Jameson Land, central East Greenland. This species was described from calcareous tundra in Svalbard (Noordeloos & Gulden 2004).

Fig. 95. *Calocybe onychina*, a rare white-spored agaric known from coniferous montane-alpine areas, and shown here from calcareous tundra in Jameson Land, central East Greenland.

Fig. 96. *Cystoderma amianthinum* on assorted debris in open land.

On herbs

It is not surprising that herbs with little mass when dry are only attacked by small basidiomycetes, and even more by many small ascomycetes. Similarly, large basidiomycetes live on the large masses of cellulose found in the trunks and branches of woody plants. The basidiomycetes found on herbs are common but small, and thus often overlooked unless specifically sought. *Typhula* is one of the most frequent genera (Figs. 31, 32, and 34) of saprotrophs on herbs. Other club-shaped species are *Ceratellopsis acuminata* (below) and *Pterulicium sclerotiicola* (Fig. 33). Among the agarics, species of *Hemimycena* like *H. hirsuta*, *H. mauretanica*, and *H. subimmaculata* are found on herbs. *Mycena adonis* grows on sticks (Fig. 30), and *M. smithiana* on leaves of *Salix*, whereas most species of *Mycena* live on unrecognizable debris. Cyphelloid genera are also well represented on herbs, including *Glabrocyphella*, *Rimbachia*, *Stromatocyphella, Flagelloscypha*, *Merismodes*, and the tiny clavarioid species of *Mucronella*.

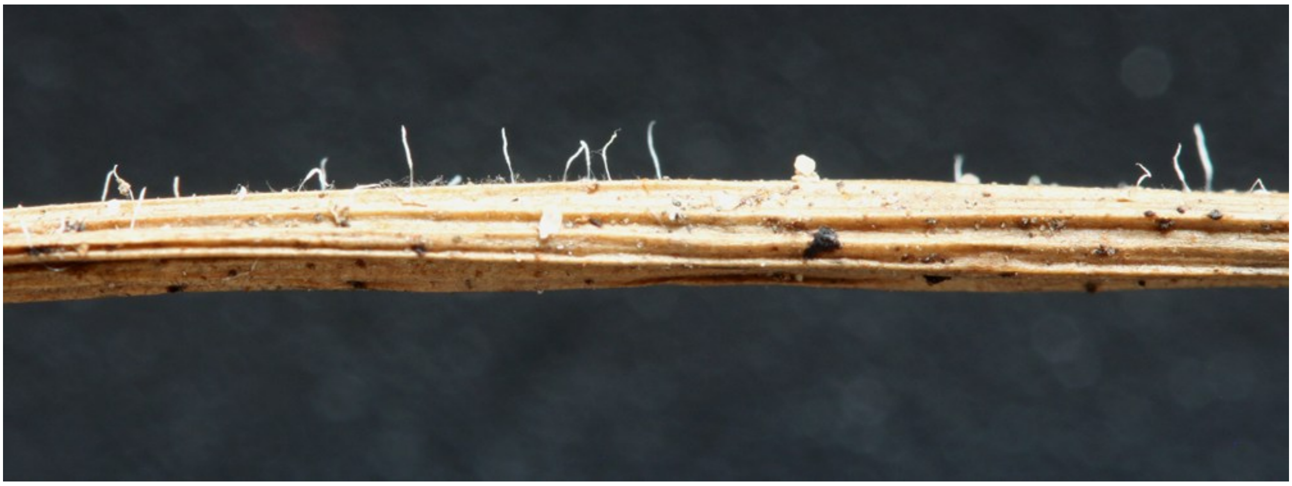


Fig. 97. *Ceratellopsis acuminata* has a stem 0.1 mm thick and grows on dead stems of herbs.

On mosses

The cold northern climate naturally prohibits the occurrence of many plant species. Feilberg (1984) registered 346 species of vascular plants from southern Greenland, whereas Bay (1992) only registered 218 species (63 %) from northern Greenland. In a small country with a temperate climate like Denmark, ca. 2000 species are known, but this includes a number of introduced plants. This "absence" of vascular plants in the North has led to conditions better suited to other organisms, and large areas in northern Greenland are – if there is life at all – covered by mosses, lichens and terrestrial algae.

The genus *Galerina* (Fig. 41) has exploited this. More than 30 species of *Galerina* are adapted to cold areas, most of them living on mosses, a few on wood or other debris. Whether or not they are parasites is still an open question. Other fungi on mosses are species of *Hypholoma* (Fig. 62), *Arrhenia* (Figs. 60, 61, and 98), *Rimbachia neckerae* on *Antitrichia curtipendula*, *Rickenella*, *Loreleia* on the liverwort *Marchantia polymorpha*, *Cantharellula umbonata* on *Polytrichum* (Fig. 80), and others, but without definite information about the kind of relationship between the fungi and the mosses.

Another, even more exceptional kind of symbiosis is found in the biotrophic triple symbiosis between the agaric *Blasiphalia pseudogrisella*, the liverwort *Blasia pusilla*, and the cyanobacterium *Nostoc*. Such unorthodox symbioses are most likely an adaptation to the harsh climate.

Fig. 98. *Arrhenia retiruga* is the smallest *Arrhenia*, lacking stem and gills, and thus resembling a discomycete.

9c. Ecto-mycorrhiza

Ecto-mycorrhization was discovered more than a century ago and identified as an important symbiosis between a vascular plant and a fungus (Hesselmann 1900). Early observations of ecto-mycorrhiza involved a basidiomycete, usually an agaric, but as more fungi were examined the symbiosis was also found between vascular plants and ascomycetes, and in other groups of basidiomycetes like polypores, *Ramaria*, *Clavulina*, *Hydnum*, *Cantharellus*, *Sebacina*, *Tomentella*, *Thelephora*, *Coltricia*, *Hymenogaster*, *Albatrellus* s.l., etc.

It is not only the identity of the organisms involved in the symbiosis, but subsequently also the types of mycorrhiza that have been better defined and understood. The majority of mycorrhiza in plants are found in herbs. In fact, most of the world's species of mycorrhizal fungi (90%) form arbuscular mycorrhiza with a herb, with the notorious exception of the family Brassicaceae. Another notable exception is the large family Orchidaceae, where in general all species of orchids (ca. 28,000) have mycorrhiza from groups of lower fungi. A third group of mycorrhizal fungi form specialized ericoid mycorrhiza with species from the heather family (Ericaceae).

Besides these well-known types of symbiosis, a number of divergent ecto-mycorrhizal symbioses take place in arctic and alpine regions. One could guess that ecto-mycorrhiza with these plants from herbaceous families could represent a protective adaptation against the harsh climate, the mineral-poor conditions, and slow nutrient cycling.

In arctic and alpine regions *Cortinarius* is the most widespread fungal symbiont. Other common symbionts include generalist genera like *Sebacina*, *Inocybe*, *Russula*, *Suillus*, and *Tomentella* (Jumpponen et al. 2002, Kernaghan & Currah 1998, Kernaghan & Harper 2001, Krpata et al. 2007, Nara 2006). Among these we have not found any *Suillus* basidiomata, since they are ecto-mycorrhizal with conifers that are by definition excluded from our investigations. When it comes to *Sebacina* we have found basidiomata of *Sebacina* s.l. (vol. 3) on *Betula* and *Salix*, but the taxonomy of the resupinate species of Sebacinaceae needs more scrutiny and comparison between the results from DNA studies of soil samples and the basidiomata themselves.

The diversity of *Tomentella* s.l. (including *Odontia*, *Polyozellus*, *Thelephora*, *Tomentellina*, and *Tomentellopsis*) is underestimated. These fungi differ from the corticioids (p. 158) in having brown or grey-brown colours, as well as a totally different lifestyle. They grow on wood, but only to support the basidiomata. This group has been detected in large numbers in DNA analyses of soil samples. The Danish specialist Knud Hauerslev estimated that the genus includes ca. 40 species in temperate regions, of which ca. 30 were included in Hauerslev et al. (1997). In Greenland we have found 16 species, sometimes on stones, since no trees were around!

In this chapter, an overview of ecto-mycorrhiza in arctic-alpine regions is given, based on the number of hosts (vascular plants) and the number of symbionts (fungi). Only basidiomycetes are included. The ecto-mycorrhizal relationship is confirmed either by the presence of a host and a nearby symbiont (in the field), or by experimental proof in a laboratory, where the symbiont forms a hyphal sheath around the root tips of a host.

Ecto-mycorrhizal host plants

Plant families with the largest number of symbionts are listed first. Within a genus, host species are organized first by distribution (those with the widest distribution first), and second by number of symbionts (those with the most symbionts first). For each host plant, the name and author is given, then the main arctic and alpine distributional regions. Names are taken from Kew's Plants of the World Online, without accounting for infraspecific taxa or hybrids. Distribution outside of arctic-alpine regions is not considered. Symbionts found in our studies are listed first, followed by symbionts reported in the literature (*), with references. Where not otherwise noted, photos of dry plants are from specimens in the herbarium of the Natural History Museum of Denmark (C).

SALICACEAE Mirb. – World Wide Web of Willows

The genus *Salix* (willow) includes 468 species according to Kew's Plants of the World Online (powo.science.kew.org). It is a huge genus native to all parts of the world except Australia and some isolated tropical islands. Mycorrhization is suspected for all or at least most species. In cold regions the genus is extremely common, and there is hardly a place where there is not a *Salix*, excepting very dry and very steep sites. One species or another occurs all the way around the North Pole from 83°N–70°N. Southward, some species are replaced by others in alpine regions.

There can be no doubt that the large number of *Salix* species and the extensive area they cover represents the most important factor driving the occurrence of basidiomycetes in arctic-alpine areas. From reference to Flora of North America, vol. 7 (Argus 2010), Illustrierte Flora von Mitteleuropa (Hegi 1981), Willows of Russia (Skvortsov 1999), and Plants of the World Online, we have designated 66 species of *Salix* as arctic-alpine, i.e., having their main distribution within these cold regions or at least commonly found in them. The genus occurs in all cold areas, being the woody plants found furthest north, i.e. *Salix arctica* at Cape Morris Jesup in Greenland (83°38'N), and it is also found at the highest elevations in alpine sites, up to 3300 m in the Alps (*S. herbacea*) and in the central Asian mountains (2200–3200 m), or even higher in the American Rocky Mountains (3500–4000 m).

Of the 66 arctic-alpine species, 25 are confirmed to be ecto-mycorrhizal, but we suspect that all of them are. A number of non-arctic-alpine species are also reported to form ecto-mycorrhiza: *Salix alba*, *S. amplexicaulis*, *S. atrocinerea*, *S. aurita*, *S. babylonica*, *S. caprea*, *S. cinerea*, *S. fragilis*, *S. repens*, and also (cf. Harley & Harley 1987) *Salix pentandra*, *S. purpurea*, *S. triandra* and *S. viminalis*. Of these, *Salix repens* is a well-known and frequently reported symbiont from northwestern Europe associated with many fungi, whereas many of the large tree-like species are only rarely reported with associated fungi.

There have been several similar suggestions for a subdivision of *Salix*. Argus (2010) suggested five subgenera: *Salix*, *Protitea*, *Longifoliae*, *Chamaetia*, and *Vetrix*. The first three subgenera contain tree-like species not found in arctic-alpine areas, and so far only one is definitely known to form ecto-mycorrhiza (*Salix babylonica*). Numerous species of subgenera *Chamaetia* and *Vetrix* occur in arctic-alpine areas. Most of these are shrubs, from a few metres to only a few centimetres high, as opposed to the other three subgenera found in warmer areas.

Malloch & Malloch (1981) postulated that the whole genus was probably ecto-mycorrhizal. Harley & Harley (1987) found that all investigated British species were ecto-mycorrhizal, but also that many of them could alternatively form vesicular-arbuscular (VA) mycorrhiza. They listed 19 ecto-mycorrhizal species, mainly from confirmed samples of roots from the UK with ecto-mycorrhizal features. Harley & Harley included seven of the 66 species we list for arctic-alpine areas in their review. In our own field studies we have found 20 species definitely associated with mycorrhizal fungi. Five more species are reported in the literature, so all in all, 25 species are confirmed to have ecto-mycorrhiza. Although this number represents only 38% of arctic-alpine willows, we subscribe to Malloch & Malloch's view that all cold-area willows form ecto-mycorrhiza with basidiomycetes. Of the 17 most widely distributed willows in arctic-alpine areas (Table 4), only five have not (yet) been reported with ecto-mycorrhizal fungi.

Among the 66 species, 30 occur in arctic North America, 28 in alpine North America, 18 in arctic Europe, 22 in alpine Europe, 31 in arctic Asia and 30 in alpine Asia (Table 4). The lower diversity in Europe is usually attributed to the effects of the last glaciation. In total, Europe has 30 arctic-alpine species, Asia has 38, and North America 35. In Europe, only ten species are both arctic and alpine, eight are only arctic, and 12 are only alpine. In Asia, 23 species are common to both regions, eight are only arctic and seven are only alpine. In North America, 23 species are both arctic and alpine, seven are only arctic, and five are only alpine. Again, the long glaciation in Europe may account for the small overlap between arctic and alpine species. By the same token, most species in North America are common to both zones, and fewer are restricted to one zone (Table 4).

The two islands of Greenland and Iceland each have only five species of *Salix*, but in mainland Arctic regions the number is much higher, often 10–25 species. Although the diversity of *Salix* in Greenland and Iceland is low, the most widely distributed species (*S. glauca*) is found in both places. This species is among those with the largest diversity of symbionts, including at least 166 species of fungi. It is just surpassed by *S. herbacea* with ca. 170 species of symbionts. On the other end of the spectrum, many species of *Salix* have still not been reported as a host for any fungus. This may be due to their remote distributions, as they grow in places not often visited by mycologists; and also to the notorious difficulty in identifying willows (both for botanists and mycologists), which are often reported only as "*Salix* sp." The frequent occurrence of hybridisation is one character that makes species of *Salix* difficult to identify, although it is evidently a successful strategy for plants growing in cold areas.

In the table below, we have separated them into three main groups of species: North American, European and Asian. Each of these are further divided into arctic and alpine species. The floristic overlap between the two large continents (North America and Eurasia) is as might be expected small, only about half of that between the two geographically closer regions of Europe–Asia and North America–Asia. This seems logical in that the latter region in its beringian parts (Alaska and Chukotka) has the highest diversity of *Salix* species anywhere in the Arctic.

Kohn & Stasovski (1994) classified six plants from a High Arctic Canadian site as ecto-mycorrhizal. We found both *Salix arctica* and *Dryas integrifolia* with many symbionts, but we have not found any symbionts associated with *Pedicularis capitata*, *Saxifraga oppositifolia*, *Cassiope tetragona*, or *Carex* (*Kobresia*) *myosuroides*. See more in the discussion of plant families below.

Table 4. Arctic-alpine species of *Salix* and their distribution in three geographical areas. Two species are found in all six zones, five are found in five zones, 11 in four zones, six in three zones, 18 in two zones, and 24 are endemic to one zone. Many species of *Salix* are difficult to recognise, even for phanerogamic botanists, let alone mycologists. Fortunately, many of them are local, or endemic to an area, so it has more often been possible to name them, as local mycologists may be familiar with local willows.

	CONTINENT	North America		Europe		Asia	
	Salix species	Arctic	Alpine	Arctic	Alpine	Arctic	Alpine
1.	*S. glauca*	X	X	X	X	X	X
2.	*S. reticulata*	X	X	X	X	X	X
3.	*S. arctica*	X	X	X		X	X
4.	*S. polaris*	X	X	X		X	X
5.	*S. hastata*	X		X	X	X	X
6.	*S. lanata*	X	X	X		X	X
7.	*S. phylicifolia*	X	X	X		X	X
8.	*S. herbacea*	X	X	X	X		
9.	*S. lapponum*			X	X	X	X
10.	*S. alaxensis*	X	X			X	X
11.	*S. myrsinifolia*			X	X	X	X
12.	*S. pulchra*	X	X			X	X
13.	*S. arbusculoides*	X	X	X	X		
14.	*S. fuscescens*	X	X			X	X
15.	*S. vestita*	X	X			X	X
16.	*S. myrtilloides*			X	X	X	X
17.	*S. recurvigemmata*			X	X	X	X
18.	*S. nummularia*	X		X		X	X
19.	*S. rotundifolia*	X	X			X	
20.	*S. sphenophylla*	X				X	X
21.	*S. arbuscula*			X	X		X
22.	*S. barclayi*	X	X			X	
23.	*S. niphoclada*	X	X			X	
24.	*S. jenisseensis*			X		X	X
25.	*S. arctophila*	X	X				
26.	*S. planifolia*	X	X				
27.	*S. calcicola*	X	X				
28.	*S. barrattiana*	X	X				
29.	*S. brachycarpa*	X	X				
30.	*S. commutata*	X	X				
31.	*S. farriae*	X	X				
32.	*S. stolonifera*	X	X				
33.	*S. chamissonis*	X				X	
34.	*S. ovalifolia*	X				X	
35.	*S. phlebophylla*	X				X	
36.	*S. reptans*			X		X	
37.	*S. caesia*				X		X
38.	*S. erythrocarpa*					X	X
39.	*S. krylovii*					X	X
40.	*S. nakamurana*					X	X

Table 4, continued.

	CONTINENT	North America		Europe		Asia	
	Salix species	Arctic	Alpine	Arctic	Alpine	Arctic	Alpine
41.	*S. rectijulis*					X	X
42.	*S. turczaninowii*					X	X
43.	*S. retusa*				X		
44.	*S. serpillifolia*				X		
45.	*S. foetida*				X		
46.	*S. helvetica*				X		
47.	*S. pyrenaica*				X		
48.	*S. alpina*				X		
49.	*S. uva-ursi*	X					
50.	*S. tschuktschorum*					X	
51.	*S. cascadensis*		X				
52.	*S. eastwoodiae*		X				
53.	*S. monticola*		X				
54.	*S. nivalis*		X				
55.	*S. tweedyi*		X				
56.	*S. myrsinites*			X			
57.	*S. breviserrata*				X		
58.	*S. glabra*				X		
59.	*S. hegetschweileri*				X		
60.	*S. laggeri*				X		
61.	*S. waldsteiniana*				X		
62.	*S. berberifolia*						X
63.	*S. divaricata*						X
64.	*S. kochiana*						X
65.	*S. sajanensis*						X
66.	*S. tianschanica*						X
TOTAL		**30**	**28**	**18**	**22**	**31**	**30**

Table 5. Numbers of *Salix* species in the arctic and alpine regions of the Northern Hemisphere. Compare with *Betula* (birch) below, with far fewer species.

Total number in the Northern Hemisphere	66	
North America + Eurasia	35 + 52	
North America + Europe + Asia	35 + 30 + 38	
Common to North America, Europe and Asia	2	(2/66 = 3%)
Common to North America and Europe	10	(10/66 = 15%)
Common to North America and Asia	19	(19/66 = 29%)
Common to Europe and Asia	16	(16/66 = 24%)
Endemic to North America	17	(17/35 = 49%)
Endemic to Europe	12	(12/30 = 40%)
Endemic to Asia	11	(11/38 = 29%)

The total number of willow species in each of the three different regions is surprisingly similar. In spite of similar environments, only two species (*Salix glauca* and *S. reticulata*) are circumpolar. It can be indirectly seen from Table 5 that the Bering Strait area has the highest number of species, in some places over 20, and thus 29% of arctic-alpine species are common to North America and Asia. In contrast, only 15% of species are common to North America and Europe. The amphi-Atlantic gap is physically wider than the amphiberingian gap, resulting in much less similarity between the willows of North America and Europe than between those of North America and Asia.

Arctic diversity is strikingly similar across North America and Asia (28 and 29 species), but is remarkably lower in Europe (17 species). This could simply be due to the much smaller arctic area of Europe, and its long history of glaciation compared to the other two much larger and less glaciated regions. This is also reflected in number of species occurring in both arctic and alpine areas: 23 in North America (66%), 10 in Europe (33%) and 23 in Asia (61%). The glaciation, which isolated the Alps from northern Europe for a long time, may also be responsible for the relatively many (12) exclusively alpine species in Europe, as opposed to only five in North America and six in Asia. The fact that 49% of North American species are endemic is also noteworthy, most likely the result of “missing” glaciation in the southern part of the continent.

Table 6. Arctic-alpine plants with the most symbionts. The next ten species of *Salix* on the list have 1-3 symbionts, while 41 species of *Salix* have no known symbionts thus far.

Salix herbacea	167	*Betula nana*	114
S. glauca	162	*B. glandulosa*	97
S. arctica	77	*B. pubescens*	87
S. reticulata	66	*Dryas octopetala*	86
S. retusa	60	*D. integrifolia*	44
S. polaris	44	*Alnus alnobetula* s.l.	19
S. arctophila	38		
S. serpillifolia	14		
S. foetida	10		
S. helvetica	10		
S. pyrenaica	8		
S. planifolia	7		
S. lapponum	7		
S. hastata	6		
S. alaxensis	4		

The numbers in Table 6 will likely increase when large symbiont genera such as *Cortinarius*, *Inocybe*, and *Russula* are more closely evaluated (in vols. 4, 6 and 7).

Nine willows, viz., *Salix arbusculoides* (Canada, Alaska), *S. fuscescens* (Alaska, Canada, Chukotka), *S. nummularia* (Alaska, Russia), *S. vestita* (Canada, USA, central Asia), *S. barclayi* (eastern Siberia, western Alaska), *S. niphoclada* (eastern Sibiria, western Alaska), *S. myrtilloides* (northeastern Europe, Siberia), *S. jenisseensis* (Siberia), and *S. recurvigemmata* (Siberia), are among those with the widest distribution, yet they have no known symbionts. A likely explanation may be that they grow in regions with few people, and thus few mycologists and few observations.

Arctic and alpine symbiotic plants and their fungal partners

In the following list of ecto-mycorrhizal arctic and alpine plants, we have also listed the fungi that we know to form symbioses with them. Names from our own collections are cited first, followed by names from the literature, which are marked with an asterisk (*) and the literature citation. The names from our fungarium are partly updated to reflect current nomenclature, but the names from the literature are given as they appear in the literature. Thus some of the names may be synonyms, which we will update as the forthcoming volumes (4-7) are published. Also, a name may be repeated if it is cited by more than one source. We plan to eliminate such repetition in conjunction with our forthcoming treatments.

1. *Salix glauca* L. (including *S. glaucosericea*); Central Asia, Russia, Altai.

North American arctic-alpine; **Eurasian arctic-alpine**. Circumpolar, except for Svalbard. Alpine: Canada (Newfoundland & Labrador), USA (Rocky Mountains), Norway, Sweden, Finland, Russia, France (the Alps), Switzerland (the Alps), Austria (the Alps), Italy (the Alps), Kazakhstan.

Examples of ecto-mycorrhizal symbionts:

Amanita *arctica*, *battarrae*, *friabilis*, *groenlandica*, *mortenii*, *nivalis*. **Amanita nivalis*, *Amanita* sp. (treated in Cripps & Horak 2008 as *A. absarokensis* ad int., close to *A. groenlandica*).

Cortinarius *absarokensis*, *acutus*, *anomalus*, *calopus*, *caninus*, *caperatus*, *casimiri*, *cinnamomeoluteus*, *croceoconus*, *croceus*, *decipiens*, *delibutus*, *diasemospermus*, *duracinus*, *erythrinus*, *favrei*, *flexipes*, *glandicolor*, *hemitrichus*, *hinnuleus*, *huronensis*, *malicorius*, *mucosus*, *norvegicus*, *obtusus*, *parvannulatus*, *porphyropus*, *psammouraceus*, *raphanoides*, *saniosus*, *saturninus*, *septentrionalis*, *subtorvus*, *talus*, *trivialis*, *uliginosus*, *valgus*, *violaceus*. **Cortinarius absarokensis* (Peintner 2008).

****Hebeloma**** *alpinicola*, *alpinum*, *arcticum*, *aurantioumbrinum*, *colvinii*, *dunense*, *excedens*, *fuscatum*, *geminatum*, *helodes*, *hiemale*, *hygrophilum*, *ingratum*, *leucosarx*, *louiseae*, *marginatulum*, *mesophaeum*, *minus*, *nigellum*, *oreophilum*, *polare*, *pusillum*, *spetsbergense*, *subconcolor*, *vaccinum*, *velutipes* (Eberhardt et al. 2021).

Inocybe *albofibrillosa*, *alpigenes*, *asterospora*, *borealis*, *calamistrata*, *fastigiata*, *flocculosa*, *geophylla*, *lacera*, *maritima*, *pruinosa*, *rimosa.*

Laccaria *bicolor*, *laccata*, *maritima*, *montana*, *pumila*, *trullissata.*

Lactarius *aurantiacus*, *brunneohepaticus*, *brunneoviolaceus*, *cyathuliformis*, *dryadophilus*, *duplicatus*, *fuscus*, *glyciosmus*, *griseus*, *lanceolatus*, *musteus*, *nanus*, *obscuratus*, *pseudouvidus*, *pubescens*, *repraesentaneus*, *robertianus*, *rufus*, *salicis-herbaceae*, *salicis-reticulatae*, *subcircellatus*, *tabidus*, *torminosus*, *torminosulus*, *trivialis*, *uvidus.*

Leccinum *rotundifoliae*, *variicolor.*

Mallocybe *abruptibulbosa*, *dulcamara*, *fuscomarginata*, *lagenicystidiata*, *latispora*, *leucoblema*, *leucoloma*, *paludosa*, *pseudodulcamara*, *pygmaea.*

Naucoria *amarescens*, *bohemica*, *sphagneti.*

Russula *altaica*, *amoenipes*, *amoenoides*, *aquosa*, *chamiteae*, *citrinochlora*, *claroflava*, *clavipes*, *decolorans*, *delica*, *depallens*, *emetica*, *favrei*, *fragilis*, *gracillima*, *graveolens*, *medullata*, *nana*, *nitida*, *norvegica*, *obscura*, *ochracea*, *pascua*, *pubescens*, *purpurata*, *saliceticola*, *subrubens*, *versicolor*, *vinosa*, *violaceoincarnata*, *xerampelina.* **Russula pascua* (Cripps & Horak 2008).

Xerocomus *subtomentosus*.

Fig. 99. *Hebeloma colvinii* grows in sand with different species of *Salix*.

2. ***Salix reticulata*** L.; H. Knudsen, 2021; Alps.

North American arctic-alpine; **Eurasian arctic-alpine**. Circumpolar, but missing in Greenland. Alpine: USA (Colorado), most European countries, Russia, Kazakhstan.

Examples of ecto-mycorrhizal symbionts:

Amanita *nivalis*. **Amanita* sp. (treated in Cripps & Horak 2008 as *A. absarokensis* ad int., close to *A. groenlandica*).

Cortinarius *albonigrellus*, *alpinus*, *anomalus*, *cedriolens*, *chamaesalicis*, *comatus*, *fulvescens*, *gausapatus*, *hinnuleus*, *inops*, *minutalis*, *pauperculus*, *phaeopygmaeus*, *purpureoluteus*, *rusticellus*, *stenospermus*, *subtilior*, *subtorvus*. **Cortinarius alpinus*, *cinnamomeoluteus* (Senn-Irlet 1988a). *Cortinarius alpicola* (Jamoni 2008). *Cortinarius alpinus* (Peintner 2008).

****Hebeloma*** *alpinum*, *marginatulum* (Senn-Irlet 1988, Jamoni 2008). *Hebeloma hiemale* (Beker et al. 2010). *Hebeloma alpinum*, *dunense*, *mesophaeum*, *minus*, *oreophilum* (Beker et al. 2016).

Inocybe *calamistrata*, *concinnula*, *dulcamaroides*, *eutheles*, *friesii*, *geophylla*, *geraniodora*, *heterocystis*, *immaculipes*, *microfastigiata*, *mundula*, *oreina*, *paludosa*, *subbrunnea*, *subfusca*, *tenerella*. **Inocybe egenula* (Senn-Irlet 1988a). *Inocybe auricomella* (Bon 1989).

Laccaria *laccata*. **Laccaria pumila* (Senn-Irlet 1988a).

Lactarius *dryadophilus*, *salicis-herbaceae*, *salicis-reticulatae*. **Lactarius nanus*, *salicis-reticulatae* (Jamoni 2008).

Mallocybe *fuscomarginata*, *squamosoannulata*, *umbrinofusca*. **Mallocybe umbrinofusca* (Bon 1991b).

Naucoria *chamiteae*.

Russula *nana*, *pascua*, *saliceticola*. **Russula delica*, *nana* (Senn-Irlet 1988a). *Russula norvegica* (Kühner & Lamoure 1986).

Thelephora *caryophyllea* (Jamoni 2008).

Tricholoma *hemisulphureum* (Bon 1989).

3. ***Salix arctica*** Pall.; leg. S. Funder; Greenland, Constable Bugt, 83°34'N, 31°00'W.

North American arctic-alpine; **Eurasian arctic-alpine**. Circumpolar, except for Europe. Alpine: Alaska, Canada, USA (Oregon), Kazakhstan, Russia (Altai, Buryatia, Kamchatka).

Examples of ecto-mycorrhizal symbionts:

Amanita *groenlandica*. **Amanita nivalis* (Cripps & Horak 2008).

Cortinarius *alpinus*, *anomalus*, *delibutus*, *favrei*, *multiformis*, *polaris*, *psammouraceus*. **Cortinarius absarokensis* (Peintner 2008).

Hebeloma *alpinicola*, *alpinum*, *aurantioumbrinum*, *dunense*, *fuscatum*, *grandisporum*, *hiemale*, *hygrophilum*, *louiseae*, *marginatulum*, *mesophaeum*, *nigellum*, *nigromaculatum*, *oreophilum*, *pubescens*, *pusillum*, *spetsbergense*, *vaccinum*, *velutipes* (Eberhardt et al. 2021).

Inocybe *alpigenes*, *fastigiata*, *favrei*, *giacomi*, *lacera*, *rimosa*, *vulpinella*.

Laccaria *laccata*, *montana*, *proximella*, *pumila*.

Lactarius *aurantiacus*, *brunneoviolaceus*, *dryadophilus*, *lanceolatus*, *nanus*, *pseudouvidus*, *pubescens*, *robertianus*, *salicis-herbaceae*, *salicis-reticulatae*, *torminosulus*. **Lactarius nanus*, *repraesentaneus* (Cripps & Horak 2008).

Mallocybe *abruptibulbosa*, *fulvipes*, *latifolia*, *latispora*, *paludosa*, *pygmaea*, *squamosoannulata*.

Naucoria *amarescens*, *tantilla*.

Russula *altaica*, *amoenipes*, *amoenoides*, *delica*, *depallens*, *dryadicola*, *graveolens*, *heterochroa*, *medullata*, *nana*, *nitida*, *norvegica*, *pascua*, *saliceticola*, *subrubens*. **Russula nana* (Laursen & Chmielewski 1982; Moser & McKnight 1987).

Tricholoma *scalpturatum*.

4. *Salix polaris* Wahlenb.; leg. D. F. Murray & B. M. Murray; Canada, Yukon Territory, 60°48'N, 138°40'W.

North American; **Eurasian**. Circumarctic except for Greenland and Iceland. Alpine: Alaska, Canada (British Columbia); Norway, Sweden, Finland, Russia.

Examples of ecto-mycorrhizal symbionts:

Amanita *groenlandica*.

Cortinarius *subtorvus*. **Cortinarius alpinus*, *cinnamomeoluteus*, *simulatus* (Ohenoja 1971). *Cortinarius alpinus* (Gumińska et al. 1991). *Cortinarius alpinus*, *polaris*, *subtorvus* (Gulden & Torkelsen 1996). *Cortinarius cinnamomeoluteus* (Karatygin et al. 1999). *Cortinarius alpinus* (Peintner 2008).

****Hebeloma*** *alpinum*, *aurantioumbrinum*, *fuscatum*, *hiemale*, *louiseae*, *marginatulum*, *mesophaeum*, *minus*, *oreophilum*, *pallidolabiatum*, *perexiguum*, *salicicola*, *spetsbergense*, *velutipes* (Beker et al. 2016).

Inocybe *geophylla*, *helobia*, *praetervisa*, *rimosa*, *saliceticola*.

Laccaria *proxima*.

****Lactarius*** *brunneoviolaceus*, *lanceolatus*, *nanus*, *pseudouvidus*, *robertianus*, *torminosulus* (Gulden & Jenssen 1988, Gulden & Torkelsen 1996).

****Mallocybe*** *leucoblema* (Huhtinen 1987a).

****Naucoria*** *tantilla* (Gulden & Jenssen 1988).

Paxillus *involutus*.

Russula *gracillima*, *graveolens*, *nana*, *norvegica*, *pubescens*, *renidens*, *saliceticola*. **Russula nana* (Gulden & Torkelsen 1996).

5. ***Salix hastata*** L.; leg. H. Lindberg; Finland, Kuusamo.

North American arctic-alpine; **Eurasian arctic-alpine**. Arctic: Alaska, Canada (Yukon, Northwest Territories), Norway, Finland, Russia. Alpine: Many European countries, Russia, Kazakhstan.

Examples of ecto-mycorrhizal symbionts:

****Cortinarius*** *albonigrellus* (Kühner & Lamoure 1986).

****Inocyb****e concinnula*, *squarrosoannulata*, *subbrunnea* (Kühner & Lamoure 1986).
Inocybe leucoloma (Cripps et al. 2010).

****Naucoria*** *cholea* (Kühner & Lamoure 1986).

6. ***Salix lanata*** L.; S. A. Elborne; Germany.

North American; **Eurasian**. Circumarctic, except for Greenland. Alpine: northern Europe, Russia, Kazakhstan.

Examples of ecto-mycorrhizal symbionts:

****Cortinarius*** *chrysomallus* (Lindström et al. 2008)

****Hebeloma*** *vaccinum* (Beker et al. 2016).

7. ***Salix phylicifolia*** L.; H. F. Gøtzsche 81.10; Iceland, Thingvallavatn.

Found in many European countries, but not outside Europe.

Example of ecto-mycorrhizal symbiont:

Records of *Cortinarius absarokensis* from Wyoming reported in Peintner (2008) are doubtful on this host, which does not occur in North America according to Kew's "Plants of the World Online".

8. *Salix herbacea* L.; H. Knudsen; Greenland.

North American arctic-alpine; **Eurasian arctic-alpine**. Arctic: Canada (Northwest Territories, Nunavut), Greenland, Iceland, Norway, Finland, Russia (NW part of European part). Alpine: most countries in Europe.

Examples of ecto-mycorrhizal symbionts:

Amanita *arctica*, *groenlandica*, *hyperborea*, *mortenii*, *nivalis.* **Amanita nivalis* (Kühner & Lamoure 1986; Knudsen & Mukhin 1998). *Amanita fulva* (Watling 1992).

Cortinarius *acutus*, *alpinus*, *anomalus*, *bibulus*, *cinnamomeoluteus*, *cinnamomeus*, *croceus*, *diasemospermus*, *favrei*, *flexipes*, *hemitrichus*, *hinnuleus*, *inops*, *norvegicus*, *obtusus*, *ochroleucus*, *paleaceus*, *pauperculus*, *phaeopygmaeus*, *polaris*, *raphanoides*, *rufostriatus*, *saniosus*, *subtorvus.* **Cortinarius scotoides* (Gulden & Lange 1971). *Cortinarius albonigrellus*, *alpinus*, *bresadolae*, *caesionigrellus*, *chamaesalicis*, *chrysomallus*, *cinnamomeoluteus*, *diasemospermus*, *fallax*, *galerinoides*, *gausapatus*, *hemitrichus*, *hinnuleus*, *inops*, *minutalis*, *paleifer*, *pauperculus*, *phaeopygmaeus*, *pulchripes*, *purpureoluteus*, *rusticellus*, *subtilior*, *tenebricus* (Kühner & Lamoure 1986). *Cortinarius alpinus*, *lepidopus*, *pertristis* (Watling 1987). *Cortinarius polaris* (Bon 1989). *Cortinarius alpicola*, *chrysomallus*, *cinnamomeoluteus*, *croceoconus*, *hinnuleus*, *polaris* (Jamoni 2008). *Cortinarius chrysomallus* (Lindström et. al. 2008). *Cortinarius alpinus* (Peintner 2008).

Hebeloma *alpinicola*, *alpinum*, *aurantioumbrinum*, *clavulipes*, *collariatum*, *dunense*, *fuscatum*, *hiemale*, *islandicum*, *kuehneri*, *marginatulum*, *nigellum*, *oreophilum*, *pubescens*, *pusillum subconcolor* (Eberhardt et al. 2021). **Hebeloma minus*, *nigellum* (Kühner & Lamoure 1986). *Hebeloma marginatulum* (Jamoni 2008). *Hebeloma alpinum*, *dunense*, *hiemale*, *islandicum*, *marginatulum*, *mesophaeum*, *minus*, *nigellum*, *salicicola*, *subconcolor* (Beker et al. 2016).

****Hymenogaster*** *saliciphilus* (Bon & Cheype 1995).

Inocybe *acuta*, *alpigenes*, *alpina*, *asterospora*, *borealis*, *calamistrata*, *favrei*, *flocculosa*, *grammata*, *inodora*, *lacera*, *leiocephala*, *mixtilis*, *monochroa*, *napipes*, *rennyi*, *rimosa*, *salicis*, *salicis-herbaceae*, *soluta.* **Inocybe geophylla* (Lange & Skifte 1967). *Inocybe calamistrata*, *canescens*, *friesii*, *geophylla*, *godfrinioides*, *mundula*, *oreina*, *rimosa*, *salicis-herbaceae*, *squarrosoannulata*, *subbrunnea*, *umbrinofusca* (Kühner & Lamoure 1986). *Inocybe mixtilis* (Senn-Irlet 1987a). *Inocybe aurea*, *egenula*, *giacomi*, *pratervisa* (Horak 1987b). *Inocybe bulbosissima*, *dulcamaroides*, *hebelomoides*, *microfastigiata* (Bon 1992b). *Inocybe tetragonospora* (Graf & Horak 1993). *Inocybe arthrocystis*, *calamistrata*, *favrei*, *lacera*, *microfastigiata*, *rufofusca*, *squamosoannulata* (Jamoni 2008).

Laccaria *laccata*, *proxima*, *pumila.* **Laccaria bicolor* (Watling 1987). *Laccaria montana*, *proximella* (Jamoni 2008).

Lactarius *brunneoviolaceus*, *cyathuliformis*, *dryadophilus*, *duplicatus*, *lanceolatus*, *nanus*, *pseudouvidus*, *repraesentaneus*, *salicis-herbaceae.* **Lactarius nanus*, *pseudouvidus*, *salicis-herbaceae*, *uvidus* (Kühner & Lamoure 1986). *Lactarius nanus*, *pseudouvidus*, *salicis-herbaceae* (Jamoni 2008).

Mallocybe *arthrocystis*, *dulcamara*, *fulvipes*, *malenconii.* **Mallocybe paludosa* (Bon 1992b).

Naucoria *amarescens*, *bohemica*, *tantilla.* **Naucoria bohemica* (Kühner 1981). *Naucoria chamiteae* (Kühner & Lamoure 1986). *Naucoria tantilla* (Jamoni 2008).

****Pseudosperma*** *guttuliferum* (Bon 1992b).

Russula *alpina*, *altaica*, *amoenipes*, *amoenoides*, *barlae*, *chamiteae*, *citrinochlora*, *cremeoavellanea*, *delica*, *medullata*, *nana*, *norvegica*, *ochracea*, *pascua*, *saliceticola*, *subrubens*, *violaceoincarnata.* **Russula saliceticola* (Schmid-Heckel 1985). *Russula alpina*, *chamiteae*, *nana*, *norvegica* (Kühner & Lamoure 1986). *Russula nana*, *norvegica*, *pascua* (Watling 1987). *Russula chamiteae*, *felleicolor*, *laccata*, *saliceticola* (Jamoni 2008).

Fig. 100. For most genera the kind of mycorrhiza is known, but in *Entoloma* it is still not generally known, in spite of some hints, and of certain kinds of mycorrhiza in some groups. This *Entoloma* growing in the middle of *Salix herbacea* is most likely ecto-mycorrhizal, but this is only an assumption. Other members of the genus are saprotrophic on soil or on wood.

9. *Salix lapponum* L.; leg. B. Fredskild; Norway, Valdres, 1200 m.
Eurasian arctic-alpine. Arctic: northern Europe. Alpine: most of Europe, Kazakhstan.

Examples of ecto-mycorrhizal symbionts:

****Cortinarius*** *aureomarginatus* (Lindström et al. 2008).
****Hebeloma*** sp. (Milne et al. 2006).
****Hymenogaster*** *tener* (Kers 1981).
****Inocybe*** *rimosa* (Gulden & Lange 1971).
****Laccaria*** *proxima* (Milne et al. 2006).
****Lactarius*** *salicis-herbaceae* (as *flavidus*) (Gulden & Lange 1971).
****Thelephora*** *terrestris* (Milne et al. 2006)

10. ***Salix alaxensis*** (Andersson) Coville; S. Cannings (CC); Canada, Yukon Territory, 63°15'N, 138°20'W.

North American arctic-alpine; **Eurasian arctic-alpine**. Arctic: Alaska, most of Canada, Russia (Yakutia, Chukotka). Alpine: Canada (most provinces), Russia (Buryatia, Kamchatka).

Examples of ecto-mycorrhizal symbionts:

****Amanita*** *regalis* (Miller 1982).

****Cortinarius*** *subtorvus* (Ammirati & Laursen 1982).

****Lactarius*** *lanceolatus*, *torminosus* (Laursen & Ammirati 1982, Ohenoja & Ohenoja 1993).

11. ***Salix myrsinifolia*** Salisb. (*S. nigricans* Sm.); leg. G. Engegård, R. Parks & O. Skifte; Norway, Nordland, Gildeskål.

Eurasian arctic-alpine. Arctic: northern Europe. Alpine: most European countries.

Examples of ecto-mycorrhizal symbionts:

****Cortinarius*** *aureomarginatus* (Lindström et al. 2008)

****Lactarius*** *pubescens* (Laursen & Ammirati 1982).

12. ***Salix pulchra*** Cham.; leg. Eschscholtz; Alaska, Kotzebue Sound.

North American arctic-alpine; **Eurasian arctic-alpine**. Arctic: Alaska, Canada, Russia (Chukotka, northwestern Russia).

Example of ecto-mycorrhizal symbiont:

Hebeloma mesophaeum.

13. ***Salix arbusculoides*** Andersson; leg. A. E. Porsild; Canada, Northwest Territories, 68°40–55'N.

North American arctic-alpine. Arctic: Alaska, Canada. Alpine: Alaska.

We found no examples of ecto-mycorrhial symbionts.

14. ***Salix fuscescens*** Andersson; leg. E. A. Viereck & E. L. Little; USA, Alaska, 60°48'N, 161°45'W.

North American arctic-alpine; **Eurasian arctic-alpine**. Arctic: Alaska, Canada (Yukon, Northwest Territories, Nunavut, Manitoba), Russia (Central Siberia, Yakutia, Chukotka). Alpine: Russia (Sakhalin), Japan.

We found no reports of ecto-mycorrhizal symbionts.

15. ***Salix vestita*** Pursh; leg. V. Siljaivisskij; Russia, Buryatia, Barguzin.

North American arctic-alpine; **Eurasian arctic-alpine**. Alpine: eastern Canada (British Columbia and Alberta), northwestern USA, Russia (Yakutia, Buryatia, Altai, Tuva).

We found no reports of ecto-mycorrhizal symbionts.

16. ***Salix myrtilloides*** L.; leg. A. Kurtto & S. Vuokko; Finland, Kemi Lapland.

Eurasian arctic-alpine. Arctic: missing in western Europe and Central Siberia.

We found no examples of ecto-mycorrhizal symbionts.

17. ***Salix recurvigemmata*** A.K. Skvortsov; leg. T. Norin & A. K. Skvortsov; Russia, Yakutia, near Lena.

Eurasian arctic-alpine. Arctic-alpine: Russia (western Siberia, Altai, northern European part of Russia).

We found no examples of ecto-mycorrhizal symbionts.

18. ***Salix nummularia*** Andersson; leg. A.K. Skvortsov; Russia, Ural Mts., River Lebi.

North American arctic-alpine; **Eurasian arctic-alpine**. Arctic: Alaska, Russia. Alpine: Russia.

We found no examples of ecto-mycorrhial symbionts.

19. ***Salix rotundifolia*** Trautv.; leg. K. Holmen; USA, Alaska, Barrow, 71°20'N, 156°40'W.

North American arctic-alpine; **Eurasian arctic-alpine**. Amphiberingian, but also in alpine regions of the USA (Montana, Wyoming).

Examples of ecto-mycorrhizal symbionts:

Cortinarius *alpinus*. **Cortinarius alpinus* (Peintner 2008).

*Hebeloma *pusillum* (Antibus et al. 1981).

****Russula*** *nana* (Moser & McKnight 1987).

See also Laursen & Chmielewski (1982) and Linkins & Antibus (1982).

20. ***Salix sphenophylla*** A.K. Skvortsov; Herb. Turczaninov; Russia, Bargusinsk, 1834.

North American arctic-alpine; **Eurasian arctic-alpine**. Arctic: Alaska, Canada (Yukon, Northwest Territories); Russia (Yakutia, Chukotka, Kamchatka, Buryatia).

Example of ecto-mycorrhizal symbiont:

****Amanita*** *fulva* (Karatygin et al. 1999).

21. ***Salix arbuscula*** L.; leg. S. J. Enander; Sweden, Härjedalen.
Eurasian. Arctic: northern Europe. Alpine: eastern Alps, Kazakhstan.

Example of ecto-mycorrhizal symbiont:

**Hebeloma alpinum* (Debaud 1983).

22. ***Salix barclayi*** Andersson; leg. G. Milke; Alaska, 63°05'N, 146°50'W.
North American arctic-alpine; **Eurasian arctic-alpine**. Arctic: Alaska, Canada (Yukon, Northwest Territories, Nunavut). Alpine: Alaska, Canada (British Columbia, Alberta), USA (Montana, Wyoming, Idaho, Oregon, Washington), Russia (Kamchatka).

We found no examples of ecto-mycorrhial symbionts.

23. ***Salix niphoclada*** Rydb.; leg. A.E. Porsild; Canada, Northwest Territories, Mackenzie River Delta; 68°40–55'N.

North American arctic-alpine; **Eurasian**. Arctic: Alaska, Canada (Yukon, Northwest Territories, Nunavut), Russia (Chukotka). Alpine: Canada (British Columbia).

We found no examples of ecto-mycorrhial symbionts.

24. ***Salix jenisseensis*** (F. Schmidt) Flod.; leg. M. Popov; Russia, Siberia, northwestern part of Lake Baikal, 54°20'N.

Eurasian arctic-alpine. Arctic-alpine: Russia except Kamchatka.

We found no examples of ecto-mycorrhial symbionts.

25. ***Salix arctophila*** Cockerell; H. Knudsen; central East Greenland, Constable Pynt; 70°75'N, 22°63'W.

North American arctic-alpine. Arctic: Alaska, Canada (except British Columbia and Alberta), Greenland.

Examples of ecto-mycorrhizal symbionts:

Amanita *groenlandica.*

Cortinarius *cinnamomeoluteus*, *huronensis*, *norvegicus.*

Hebeloma *arcticum*, *aurantioumbrinum*, *dunense*, *hiemale*, *marginatulum*, *mesophaeum*, *nigellum*, *oreophilum.*

Inocybe *lacera*, *mixtilis*, *praetervisa*, *rimosa*.

Laccaria *laccata.*

Lactarius *brunneoviolaceus*, *dryadophilus*, *nanus*, *pseudouvidus*, *salicis-herbaceae*, *tabidus*, *torminosulus.*

Leccinum *holopus.*

Mallocybe *dulcamara*, *fulvipes.*

Naucoria *amarescens.*

Russula *altaica*, *amoenoides*, *barlae*, *citrinochlora*, *gracillima*, *medullata*, *nana*, *nitida*, *norvegica*, *saliceticola.*

26. ***Salix planifolia*** Pursh; leg. M. J. Waterway; Canada, Labrador, 54°57'N, 67°10'W, 2300 feet.

North American arctic-alpine. Arctic: Alaska, Canada. Alpine: Canada, northern and northwestern USA.

Examples of ecto-mycorrhizal symbionts:

****Amanita*** *vaginata* (Cripps & Horak 2008). *Amanita* sp. (treated as *A. absarokensis* ad int., close to *A. groenlandica*, Cripps & Horak 2008).

****Cortinarius*** *absarokensis* (Moser & McKnight 1987).

****Inocybe*** *arthrocystis*, *dulcamara*, *leucoloma* (Cripps et al. 2010).

27. ***Salix calcicola*** Fernald & Wiegand; leg. A. E. Porsild; Canada, Manitoba, Churchill, 58°47'N, 94°14'W.

North American arctic-alpine. Arctic: Canada (Nunavut, Newfoundland). Alpine: Canada (Alberta, Manitoba, Labrador, Newfoundland), USA (Colorado).

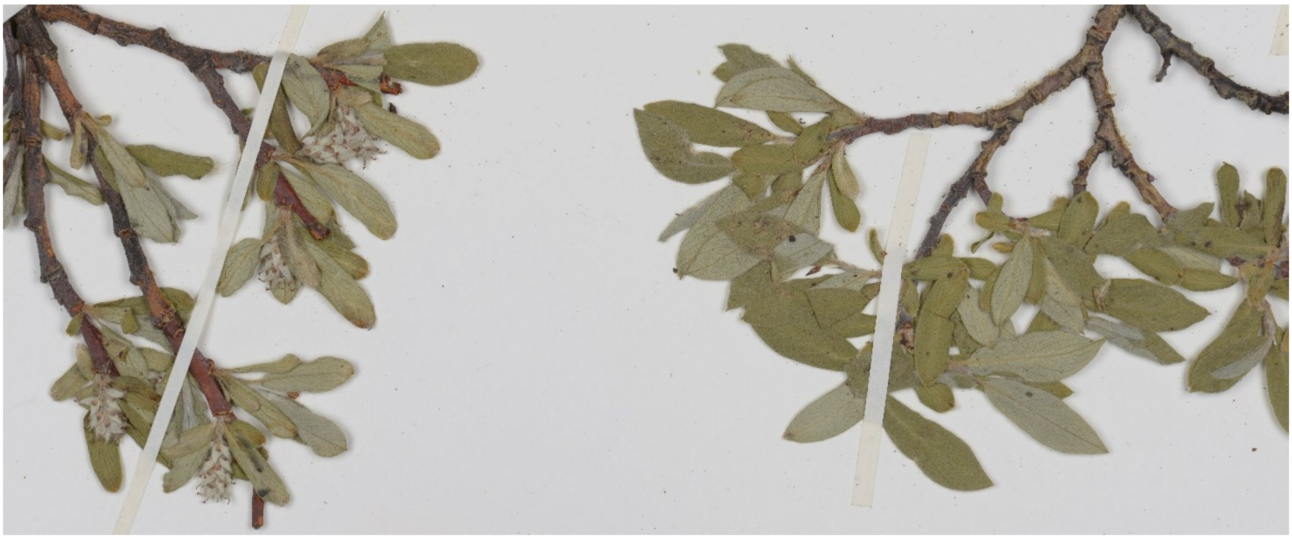
Example of ecto-mycorrhizal symbiont:

Lactarius salicis-herbaceae (Ohenoja & Ohenoja 1993).

28. ***Salix barrattiana*** Hook.; leg. R.T. Porsild; Canada, Yukon Territory.

North American arctic-alpine. Arctic: Alaska, Canada (Yukon, Northwest Territories). Alpine: Alaska, Canada (British Columbia, Alberta), USA (Montana, Wyoming).

We found no examples of ecto-mycorrhial symbionts.



29. ***Salix brachycarpa*** Nutt.; leg. G. N. Jones; USA, Colorado, 11000 feet.

North American arctic-alpine. Arctic: Canada (Northwest Territories, Nunavut). Alpine: in most of central Canada, and in the USA (Colorado, Montana, New Mexico, Wyoming, Oregon, Utah).

We found no examples of ecto-mycorrhial symbionts.

30. ***Salix commutata*** Bebb; leg. J. G. Jack; USA, Montana, 5300 feet.

North American arctic-alpine. Arctic: Alaska, Canada (Yukon). Alpine: western Canada, northwestern USA.

We found no examples of ecto-mycorrhial symbionts.

31. ***Salix farriae*** C.R. Ball; leg. M. R. Malte & W. O. Watson; Canada, Alberta.

North American arctic-alpine. Alpine: Canada (Yukon, Northwest Territories, British Columbia, Alberta), USA (Montana, Wyoming, Oregon, Idaho).

We found no examples of ecto-mycorrhial symbionts.

32. ***Salix stolonifera*** Coville; leg. P. Freuchen.

North American arctic-alpine. Arctic: Alaska. Alpine: Canada (British Columbia, Alberta).

We found no examples of ecto-mycorrhial symbionts.

33. ***Salix chamissonis*** Andersson; leg. A. W. Johnson, L. Viereck & H. Melchior; USA, Alaska, 68°05'N, 165°32'W.

North American arctic-alpine; **Eurasian arctic-alpine**. Arctic: Alaska, Canada, Russia (Chukotka).

We found no examples of ecto-mycorrhial symbionts.

34. ***Salix ovalifolia*** Trautv.; leg. W. C. Steere, O. W. Mårtensson & K. A. Holmen; USA, Alaska, Barrow, 71°20'N, 156°40'W.

North American arctic-alpine; **Eurasian arctic-alpine**. Arctic: Alaska, Canada, Russia (Chukotka).

We found no examples of ecto-mycorrhial symbionts.

35. ***Salix phlebophylla*** Andersson; leg. M. J. Waterway & M. J. Lechowicz; USA, Alaska, Barrow, 70°27'N, 157°25'W.

North American arctic-alpine; **Eurasian arctic-alpine**. Arctic: Alaska, Canada, Russia (Chukotka, Wrangel Island).

Ecto-mycorrhizal according to Laursen & Chmielewski (1982), but with no examples given.

36. ***Salix reptans*** Rupr.; leg. S. J. Enander; Russia, Siberia, Ananbiskiu near Jenissei, 69°45’N.
Eurasian arctic-alpine. Arctic: Russia.
We found no examples of ecto-mycorrhial symbionts.

37. ***Salix caesia*** Vill.; leg. N. Ambolt & S. Hedin; Kashmir, Karakorum, 4500 m.
Eurasian arctic-alpine. Europe: Austria, France, Italy, Switzerland. Asia: Kazakhstan.
We found no examples of ecto-mycorrhial symbionts.

38. ***Salix erythrocarpa*** Kom.; leg. V. Komarov; Kamchatka, Mt. Krasnij Gor., Lake Natchika.
Eurasian arctic-alpine. Alpine: Russia (Kamchatka, Magadan, Yakutskaya).
We found no examples of ecto-mycorrhial symbionts.

39. ***Salix krylovii*** E.L. Wolf; leg. I. V. Beljajeva; Russia, Yakutia (in herb. SVER).
Eurasian arctic-alpine. Arctic-alpine: Russia.
We found no examples of ecto-mycorrhial symbionts.

40. ***Salix nakamurana*** subsp. ***kurilensis*** (Koidz.) H. Ohashi; I. Savinov (CC); Russia, Sakhalin, North Kuril District.

Eurasian arctic-alpine. Arctic-alpine: Russia, Kamchatka, Kuril Islands.

We found no examples of ecto-mycorrhial symbionts.

41. ***Salix rectijulis*** Ledeb. ex Trautv.; leg. T. Derviz-Sokolova; Russia, Chukotka, Lavrentiya.

Eurasian arctic-alpine. Alpine: Russia (Central Siberia), Kazakhstan.

We found no examples of ecto-mycorrhial symbionts.

42. ***Salix turczaninowii*** Laksch. (= *S. herbacea* f. *altaica* Görz, = *S. liliputa* Nas.); leg. I. V. Kuznetsov; Russia, Yenisey, Kansk, 1300 m.

Eurasian arctic-alpine. Alpine: Russia (South-Central Siberia), Kazakhstan. A poorly known species.

We found no examples of ecto-mycorrhial symbionts.

43. ***Salix retusa*** L.; leg. B. Fredskild; Austria, Franz Josef Höhe.
Eurasian arctic-alpine. Alpine: Central, southern and eastern Europe.

Examples of ecto-mycorrhizal symbionts:

****Amanita*** *oreina* (Bresinsky & Schmid-Heckel 1983).

Cortinarius *alpinus*, *albonigrellus*, *anomalus*, *cedriolens*, *comatus*, *galerinoides*, *gausapatus*, *hinnuleus*, *inops*, *phaeopygmaeus*, *pulchripes*, *purpureoluteus*, *rusticellus*, *subtilior*, *subtorvus*, *tenebricus.* **Cortinarius tenebricus* (Bresinsky & Schmid-Heckel 1983). *Cortinarius alpinus* (Schmid-Heckel 1985, Kühner & Lamoure 1986). *Cortinarius alpinus* (Schmid-Heckel 1985, Moser & McKnight 1987, Peintner 2008). *Cortinarius alpicola* (Jamoni 2008).

****Hebeloma*** *alpinum*, *minus* (Kühner & Lamoure 1986). *Hebeloma marginatulum* (Jamoni 2008). *Hebeloma alpinum*, *mesophaeum*, *minus*, *oreophilum* (Beker et al. 2016).

****Inocybe*** *canescens*, *decipiens* (Schmid-Heckel 1985). *Inocybe amoenolens*, *auricomella*, *canescens*, *concinnula*, *dulcamaroides*, *flocculosa*, *friesii*, *fuscomarginata*, *geraniodora*, *godfrinioides*, *guttuliferum*, *heterocystis*, *immaculipes*, *lutescens*, *melliolens*, *microfastigiata*, *oreina*, *paludosa*, *petiginosa*, *rimosa*, *squamosoannulata*, *subbrunnea*, *subfusca*, *tenerella* (Kühner & Lamoure 1986). *Inocybe mixtilis* (Senn-Irlet 1987a).

****Laccaria*** *altaica* (Schmid-Heckel 1985).

****Lactarius*** *salicis-reticulatae*, *uvidus* (Kühner & Lamoure 1986). *Lactarius salicis-herbaceae* (Jamoni 2008).

****Mallocybe*** *subannulata*, *M. umbrinofusca* (Kühner & Lamoure 1986, Bon 1991b).

Naucoria *chamiteae.*

****Russula*** *nana* (Kühner & Lamoure 1986).

****Tricholoma*** *hemisulphureum* (Bon 1989).

44. ***Salix serpillifolia*** Scop. ("*serpyllifolia*"); leg. W. Greuter; Switzerland, Valais, Valsorey, 2700 m.

Eurasian arctic-alpine. Alpine: Central Europe, western Balkans.

Examples of ecto-mycorrhizal symbionts:

****Cortinarius*** *pauperculus*, *phaeopygmaeus*, *pulchripes*, *scotoides* (Kühner & Lamoure 1986). *Cortinarius pauperculus* (Gumińska et al. 1991).

****Inocybe*** *canescens*, *concinnula*, *johannae*, *mundula*, *oreina*, *petiginosa*, *tenerella* (Kühner & Lamoure 1986).

****Mallocybe*** *fuscomarginata*, *M. squarrosoannulata* (Kühner & Lamoure 1986).

45. ***Salix foetida*** Schleich. ex DC.; A. Mihoric (CC); Italy, Piedmont, Turin.
Eurasian arctic-alpine. Alpine: Austria, France, Italy, Switzerland.

Examples of ecto-mycorrhizal symbionts:

****Cortinarius*** *albonigrellus*, *purpureoluteus*, *tenebricus* (Kühner & Lamoure 1986). *Cortinarius absarokensis* (Peintner 2008).

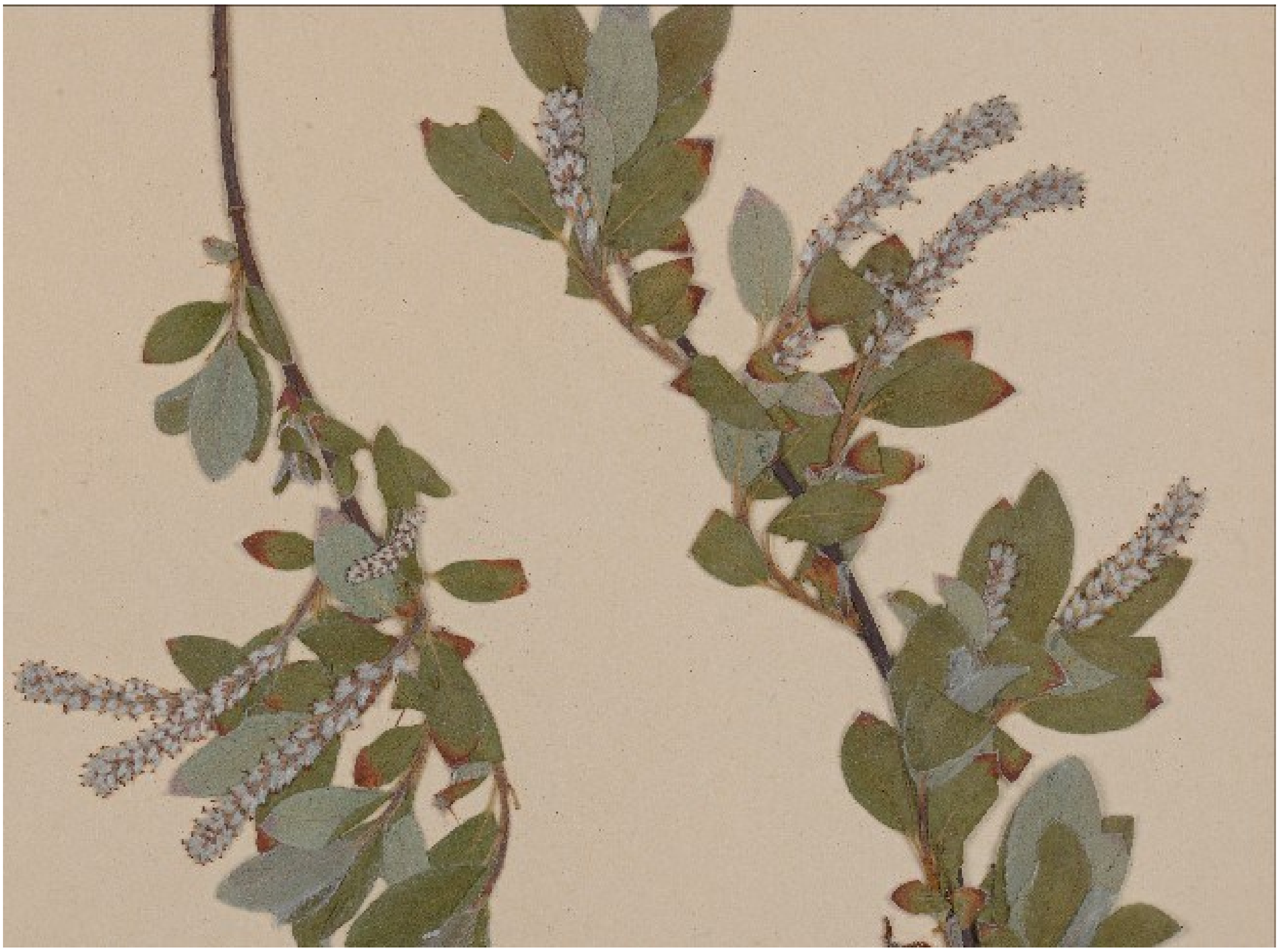
****Inocybe*** *geraniodora*, *godfrinioides*, *pelargoniodora*, *salicis-herbaceae*, *subbrunnea* (Kühner & Lamoure 1986).

****Naucoria*** *cholea* (Kühner & Lamoure 1986, Moreau et al. 2006a).

46. ***Salix helvetica*** Vill.; leg. W. Greuter; Switzerland, Valais, 2300 m.
Eurasian arctic-alpine. Alpine: eastern Alps, Pyrenees, western Carpathians.

Examples of ecto-mycorrhizal symbionts:

****Cortinarius*** *alpinus*, *cinnamomeolutea*, *pauperculus*, *rufostriatus* (Senn-Irlet 1993).
****Hebeloma*** *kuehneri*, *marginatulum* (Senn-Irlet 1993).
****Inocybe*** *lacera* var. *rhacodes* (Senn-Irlet 1993).
****Laccaria*** *montana* (Senn-Irlet 1993).
****Russula*** *norvegica* (Senn-Irlet 1993).
****Thelephora*** *caryophyllea* (Senn-Irlet 1993).



47. ***Salix pyrenaica*** Gouan; leg. S. J. Enander; Pyrenees.
Eurasian arctic-alpine. Alpine: France/Spain (Pyrenees).

Examples of ecto-mycorrhizal symbionts:

****Cortinarius*** *anomalus* var. *calcialpinus*, *hinnuleus* (Corriol 2008).
****Hebeloma*** *bruchetii*, *marginatulum* (Corriol 2008).
****Inocybe*** *subpiricystis* (Corriol 2008).
****Laccaria*** *pumila* (Corriol 2008).
****Mallocybe*** *leucoloma*, *squarrosoannulata* (Corriol 2008).

48. ***Salix alpina*** Scop.; leg. P. Sillinger; Slovakia, Lower Tatra.
Eurasian arctic-alpine. Alpine: Central and eastern Europe.

Examples of ecto-mycorrhizal symbionts:

**Inocybe dulcamara*, *geraniodora* (Kubička 1971).

49. ***Salix uva-ursi*** Pursh; leg. J. Feilberg; Greenland, Nuuk, 54°15’N, 50°12’W.
North American arctic-alpine. Arctic: Eastern Canada, Greenland.

Example of ecto-mycorrhizal symbiont:

Russula ochracea.

50. ***Salix tschuktschorum*** A.K. Skvortsov; D. Sergeyevich (CC); Russia, Kamchatka, Yelizovsky District.

Eurasian arctic-alpine. Alpine: Russia (Chukotka, Yakutskaya).

Example of ecto-mycorrhizal symbiont:

**Inocybe lacera* var. *rhacodes* (Peintner & Horak 2002).

51. ***Salix cascadensis*** Cockerell; leg. J. A. Calder & D. B. O. Savile; Canada, British Columbia, Mt. Apex.

North American arctic-alpine. Alpine: Canada (British Columbia), USA (Washington, Wyoming, Colorado, Utah).

We found no examples of ecto-mycorrhial symbionts.

52. ***Salix eastwoodiae*** Cockerell ex A. Heller (syn. *S. californica* Bebb); leg. L. O. Williams & R. P. Williams; USA, Wyoming, 10000 feet.

North America arctic-alpine. Alpine: northwestern USA.

We found no examples of ecto-mycorrhial symbionts.

53. ***Salix monticola*** Bebb; A. Boehm (CC); USA (Colorado).

North American arctic-alpine. Alpine: USA (Utah, Wyoming).

We found no examples of ecto-mycorrhial symbionts.

54. ***Salix nivalis*** Hooker; s. coll.; Alaska.

North American arctic-alpine. Alpine: Canada (British Columbia, Alberta), western USA (Wyoming, Montana, Utah).

We found no examples of ecto-mycorrhial symbionts.

55. ***Salix tweedyi*** (Bebb) C.R. Ball; B. Schwartz (CC); USA (Montana).

North American arctic-alpine. Alpine: Canada (British Columbia), USA (Idaho, Montana, Wyoming).

We found no examples of ecto-mycorrhial symbionts.

56. ***Salix myrsinites*** L.; H. H. Johnston 3482; Scotland, Orkney, 800 ft.
Eurasian. Arctic: northern Europe.

57. ***Salix breviserrata*** Flod.; leg. M. Thornberg; Austria, Kärnten.
Eurasian arctic-alpine. Alpine: Central and western Europe.
We found no examples of ecto-mycorrhial symbionts.

58. ***Salix glabra*** Scop.; leg. P. Lütken; Austria, Tirol, 2 km from Namlos, 1400 m.
Eurasian arctic-alpine. Alpine: Central Europe, Italy, Bosnia.
We found no examples of ecto-mycorrhial symbionts.

59. ***Salix hegetschweileri*** Heer; leg. O. Heer & C. Brugger; Austria, near St. Gotthard, 4500 m.
Eurasian arctic-alpine. Alpine: the Alps.
We found no examples of ecto-mycorrhial symbionts.

60. ***Salix laggeri*** Wimm.; A. Drobyazko (CC); Italy.
Eurasian arctic-alpine. Alpine: Austria, France, Italy, Switzerland.
We found no examples of ecto-mycorrhial symbionts.

61. ***Salix waldsteiniana*** Willd.; leg. Barina & Pifko; Albania, Shkodër, Mt. Buba, 1273 m.
Eurasian arctic-alpine. Alpine: Central and eastern Alps, northern Balkans.
We found no examples of ecto-mycorrhial symbionts.

62. ***Salix berberifolia*** Pall.; leg. Aljanskaja, Koschewnikova & Surova; Russia, Buryatia, Tunkinsky District.

Eurasian arctic-alpine. Alpine: Russia (Altai, Buryatia, Kamchatka, Sakhalin, Tuva, Yakutskaya), Kazakhstan.

We found no examples of ecto-mycorrhial symbionts.

63. ***Salix divaricata*** Pall.; A. P. Seregin (CC); Russia, Amur.

Eurasian arctic-alpine. Alpine: Russia (Altai).

We found no examples of ecto-mycorrhial symbionts.

64. ***Salix kochiana*** Trautv.; leg. H. Maltsev, 1902, Herb. Fl. Rossicae; Russia, Siberia, Irkutsk, Balagansky District.

Eurasian arctic-alpine.

We found no examples of ecto-mycorrhial symbionts.

65. ***Salix sajanensis*** Nasarow; leg. Aljanskaja, Koschewnikova & Surova; Russia, Buryatia, Tunkinsky District.

Eurasian arctic-alpine. Alpine: Russia (Sayan).

We found no examples of ecto-mycorrhial symbionts.

66. ***Salix tianschanica*** Regel; leg. A. K. Skvortsov; Kazakhstan, Almata, 2000–2400 m.
Eurasian arctic-alpine. Alpine: Kazakhstan.
We found no examples of ecto-mycorrhial symbionts.

BETULACEAE Gray

The birch family (Betulaceae) is the second most important symbiont family for ecto-mycorrhiza in arctic regions. The circumscription of species can be nebulous, some species are difficult to separate, and most of them have many synonyms. Two arctic-alpine genera, *Betula* L. and *Alnus* Mill., are included here.

Betula (birch) includes 59 species. Ecto-mycorrhization is suspected for all species, and has been observed in all of the arctic-alpine species we have seen. Two obvious groups exist: larger arboreal species such as *Betula pubescens*, *B. ermanii*, *B. alnoides* and *B. occidentalis*, and dwarf species like *Betula nana*, *B. glandulosa*, *B. fruticosa*, *B. exilis*, and *B. michauxii*. Their morphological distribution is straightforward: the higher the altitude, the shorter the (dwarf) plants. *Betula nana* grows north to Svalbard, where it becomes very short (knee height). Tree-sized birches occur in Greenland only north to 61°N, due to the cold sea current along the east coast. Zonation in northern areas from north to south normally goes from *Salix* through *Betula* to conifers. These zones are quite narrow in alpine areas, sometimes only a few hundred metres, but in flat regions the subarctic birch belt may be very broad, especially so in northern Finland and Russia, where these zones may reach hundreds of kilometres in width. All species of *Betula* have a large number of ecto-mycorrhizal symbionts.

Alnus is a small genus, and only one species (*A. alnobetula*, including four subspecies) is specially adapted to arctic-alpine areas. Previously, it was split into a handful of regional species, but now they are generally treated as subspecies of *A. alnobetula*. They most often occur in transitions from true alpine zones to the lower conifer belt. In flat arctic areas, they may fill larger areas between the arctic tundra and the conifer belt, especially in Siberia, but generally it is not a very important host for arctic and alpine fungi.

Table 7. Arctic-alpine species of *Betula* and their distribution in three geographical areas. One species is found in all six zones, one is found in five zones, one in four zones, one in three zones, three in two zones, and a single species is endemic to one zone.

	CONTINENT	North America		Europe		Asia	
	Betula species	Arctic	Alpine	Arctic	Alpine	Arctic	Alpine
1.	*B. pubescens*	X	X	X	X	X	X
2.	*B. nana*	X		X	X	X	X
3.	*B. glandulosa*	X	X			X	X
4.	*B. humilis*				X	X	X
5.	*B. ermanii*					X	X
6.	*B. fruticosa*					X	X
7.	*B. occidentalis*	X	X				
8.	*B. michauxii*	X					

1. *Betula pubescens* Ehrh. (including numerous synonyms); H. Knudsen; S-Greenland.

North American; **Eurasian**. Arctic: Greenland, Canada (Newfoundland), Eurasia except Russia (Chukotka). Alpine: Eurasia except Russia (Chukotka).

Examples of ecto-mycorrhizal symbionts:

Amanita *arctica*, *battarrae*, *fulva*, *groenlandica*, *mortenii*, *nivalis.*

Cortinarius *alboviolaceus*, *anomalus*, *armillatus*, *balaustinus*, *betulinus*, *brunneus*, *caninus*, *caperatus*, *casimiri*, *cinnamomeoluteus*, *cinnamomeus*, *croceus*, *decipiens*, *disjungendus*, *duracinus*, *durus*, *fennoscandicus*, *huronensis*, *imbutus*, *mucosus*, *obtusus*, *parvannulatus*, *porphyropus*, *raphanoides*, *salor*, *saniosus*, *saturninus*, *septentrionalis*, *talus*, *valgus*, *vibratilis*, *violaceus.*

Hebeloma *crustuliniforme*, *fragilipes*, *incarnatulum*, *leucosarx*, *vaccinum.*

Inocybe *albofibrillosa*, *assimilata*, *flocculosa.*

Laccaria *bicolor*, *proxima.*

Lactarius *duplicatus*, *glyciosmus*, *hysginoides*, *lapponicus*, *necator*, *pubescens*, *repraesentaneus*, *rufus*, *subcircellatus*, *theiogalus*, *torminosulus*, *torminosus*, *trivialis*, *utilis*, *uvidus*, *vietus.*

Leccinum *holopus*, *mortenii*, *rotundifoliae*, *variicolor*, *versipelle.*

Mallocybe *leucoblema*, *pygmaea.*

Paxillus *involutus.*

Russula *altaica*, *aurantiaca*, *citrinochlora*, *claroflava*, *delica*, *emetica*, *groenlandica*, *nana*, *nitida*, *saliceticola*, *versicolor*, *violaceoincarnata.*

Thelephora *terrestris*

Tricholoma *atrosquamosum.*

Xerocomus *subtomentosus.*

Fig. 101. *Russula emetica* is a well-known species from temperate and boreal coniferous forests, but also occurs in subarctic regions with *Betula pubescens*. This specimen is from southern Greenland.

Fig. 102. *Lactarius torminosulus* is a common associate of *Betula* species in moist habitats. This specimen is from southern Greenland.

2. *Betula nana* L.; H. Knudsen; Greenland

North American; **Eurasian**. Arctic: Canada (Northwest Territories), Greenland, Iceland, northern Europe, Russia (western Siberia). Alpine: many European countries, Russia (Altai, southern Siberia).

Examples of ecto-mycorrhizal symbionts:

Amanita *mortenii*. **Amanita battarrae* (Karatygin et al. 1999). *Amanita groenlandica*, *nivalis* (Knudsen & Mukhin 1998). *Amanita fulva*, *groenlandica*, *nivalis* (Ohenoja et al. 2018).

Chalciporus *piperatus*.

Cortinarius *absarokensis*, *agathosmus*, *alboviolaceus*, *caperatus*, *delibutus*, *hemitrichus*, *imbutus*, *mucosus*, *multiformis*, *norvegicus*, *porphyropus*, *raphanoides*, *saturninus*, *umbrinolens*. **Cortinarius armillatus*, *gausapatus* (Karatygin et al. 1999). *Cortinarius alboviolaceus*, *balteatus*, *caperatus*, *cinnamomeus*, *croceus*, *decipiens*, *delibutus*, *emunctus*, *fennoscandicus*, *obtusus*, *pholideus*, *raphanoides*, *talus* (Ohenoja et al. 2018).

Inocybe *albovelutipes*, *borealis*, *calamistrata*, *fuscidula*, *geophylla*, *giacomi*, *praetervisa*, *pruinosa*, *rennyi*, *rimosa*. **Inocybe assimilata*, *concinnula*, *fuscidula* (Karatygin et al. 1999). *Inocybe soluta* (Ohenoja et al. 2018).

Lactarius *aurantiacus*, *dryadophilus*, *glyciosmus*, *lanceolatus*, *musteus*, *nanus*, *pilatii*, *pubescens*, *repraesentaneus*, *rufus*, *subcircellatus*, *tabidus*, *theiogalus*, *torminosulus*, *vietus*. **Lactarius rufus*, *torminosus* (Lange & Skifte 1967). *Lactarius duplicatus*, *plumbeus*, *pubescens*, *repraesentaneus*, *rufus*, *scoticus*, *subcircellatus*, *tabidus*, *torminosus*, *trivialis* (Ohenoja et al. 2018).

Leccinum *rotundifoliae*, *scabrum*, *variicolor*, *versipelle.* **Leccinum rotundifoliae*, *variicolor*, *versipelle* (Karatygin et al. 1999). *Leccinum holopus*, *oxydabile*, *rotundifoliae*, *variicolor*, *versipelle* (Ohenoja et al. 2018).

Mallocybe *fulvipes*, *latispora.*

Russula *altaica*, *claroflava*, *consobrina*, *delica*, *depallens*, *groenlandica*, *maculata*, *nana*, *nitida*, *norvegica*, *oreina*, *persicina*, *saliceticola*, *versicolor*, *violaceoincarnata*, *xerampelina.* **Russula aeruginea*, *betularum*, *citrinochlora*, *claroflava*, *consobrina*, *decolorans*, *gracillima*, *nitida*, *renidens*, *pubescens*, *rivulicola*, *versicolor*, *vinosa*, *violaceoincarnata*, *xerampelina* (Ohenoja et al. 2018).

Tricholoma *virgatum.*

Xerocomus *subtomentosus* (Ohenoja et al. 2018).

Fig. 103. A species of *Russula* growing with *Betula nana*.

3. *Betula glandulosa* Michx. (incl. *B. exilis*, *B. rotundifolia*, etc.); H. Knudsen, Greenland.

North American; **Eurasian**. Arctic: Alaska, Canada, Greenland, Russia (Siberia). Alpine: northwestern USA.

Examples of ecto-mycorrhizal symbionts (**NB**: *Betula glandulosa* sometimes grows in boreal regions, where it may have ecto-mycorrhizal symbionts that do not occur in arctic-alpine regions):

Amanita *arctica*, *battarae*, *fulva*, *groenlandica*, *mortenii*, *nivalis*. **Amanita groenlandica* (Karatygin et al. 1999).

Boletus *edulis*.

Cortinarius *agathosmus*, *alboviolaceus*, *anomalus*, *betulinus*, *calopus*, *caperatus*, *cinnamomeus*, *croceoconus*, *croceus*, *decipiens*, *delibutus*, *diasemospermus*, *durus*, *erythrinus*, *imbutus*, *norvegicus*, *porphyropus*, *septentrionalis*, *subtorvus*, *uliginosus*.

Inocybe *lacera*, *rimosa*, *soluta*, *terrifera*.

Laccaria *bicolor*.

Lactarius *brunneohepticus*, *brunneoviolaceus*, *dryadophilus*, *duplicatus*, *fuscus*, *lanceolatus*, *mammosus*, *musteus*, *nanus*, *pilatii*, *pseudouvidus*, *pubescens*, *repraesentaneus*, *rufus*, *salicis-herbaceae*, *subcircellatus*, *tabidus*, *theiogalus*, *torminosulus*, *torminosus*, *trivialis*, *utilis*, *vietus*. **Lactarius rufus*, *trivialis* (Karatygin et al. 1999).

Leccinum *holopus*, *mortenii*, *oxydabile*, *rotundifoliae*, *variicolor*, *versipelle*. **Leccinum niveum*, *variicolor*, *versipelle* (Karatygin et al. 1999).

Paxillus *involutus*.

Russula *altaica*, *aeruginea*, *amoenipes*, *aquosa*, *aurantiaca*, *barlae*, *citrinochlora*, *claroflava*, *clavipes*, *consobrina*, *cremeoavellanea*, *delica*, *decolorans*, *depallens*, *emetica*, *favrei*, *fragilis*, *gracillima*, *graveolens*, *groenlandica*, *medullata*, *nana*, *nitida*, *norvegica*, *obscura*, *ochracea*, *pascua*, *pubescens*, *puellaris*, *saliceticola*, *vinosa*, *violaceoincarnata*. **Russula aeruginea* (Karatygin et al. 1999).

Xerocomus *subtomentosus*.

4. *Betula humilis* Schrank; H. Knudsen; Russia, Altai, Ukok Plateau, ca. 2000 m.

Eurasian. Alpine: central and eastern Europe, European part of Russia and western Siberia, Kazakstan, Mongolia.

We found no examples of ecto-mycorrhizal symbionts for this species.

5. *Betula ermanii* Cham.; H. Knudsen; Kamchatka.

Eurasian. Alpine: Russia (eastern Siberia).

Example of ecto-mycorrhizal symbionts:

Lactarius sp.

Russula *maculata*.

6. ***Betula fruticosa*** Pall. (syn. *B. middendorffii*); leg. N. Aljanskaja, B. Lvovoa, V. Makarov & G. Porubinskaja; Russia, Altai; 800 m.

Eurasian. Russia (NE Siberia, Altai).

Example of ecto-mycorrhizal symbiont:

Amanita *muscaria*.

7. ***Betula occidentalis*** Hook.; leg. F. E. Clements & E. S. Clements; USA, Colorado, Engelmann Canyon, 2700 m.

North American. Arctic: Alaska, Canada (except Nunavut and Labrador). Alpine: NW USA.

We found no examples of ecto-mycorrhizal symbionts for this species.

8. *Betula michauxii* Spach; leg. A. E. Porsild; Canada, Labrador, 53°27'N, 55°47'W.
North American. Southeastern Canada.
We found no examples of ecto-mycorrhizal symbionts with this species.

Alnus (alder) includes 41 species. Ecto-mycorrhization occurs in the only arctic-alpine species, and is suspected for all species. It has been proven for at least 31 arctic-alpine symbionts. The nitrogen-fixing bacterium *Frankia alni* also occurs in the roots of *Alnus*.

Alnus alnobetula sensu lato was previously divided into five distinct species, but is currently considered to be one species with five geographically separated subspecies; of which one, *A. suaveolens* (Req.) Lambinon & Kerguelen, is found in Corsica and is not considered here.

1a. *Alnus alnobetula* (Ehrh.) K. Koch subsp. ***alnobetula*** (*A. viridis*); H. Knudsen; Alps.
European. Central and southern Europe, and the northwestern part of Russia.

Examples of ecto-mycorrhizal symbionts: (merged for the four subspecies included here).

Alpova *diplophloeus.* **Alpova diplophloeus* (Schmid-Heckel 1985). **Alpova alpestris* (Moreau et al. 2011)

Amanita *friabilis.*

Cortinarius *alnetorum*, *alnobetulae*, *bibulus*, *helvelloides*.

Hebeloma *helodes*.

Inocybe *flocculosa* var. *croceifolia.*

Lactarius *alpinus*, *cyathuliformis*, *griseus*, *lanceolatus*, *lilacinus*, *necator*, *obscuratus*, *omphaliformis*, *pusillus*, *scoticus.***Lactarius alpigenes*, *lepidotus* (Kalamees & Vaasma 1993).

Mallocybe *agardhii.*

****Naucoria*** *cedriolens*, *escharoides*, *scolecina*, *subconspersa* (Schmid-Heckel 1985). **Naucoria striatula* (Karatygin et al. 1999, Peintner & Horak 2002). *Naucoria badia*, *cedriolens*, *luteolofibrillosa*, *submelinoides* (Moreau et al. 2006b). *Naucoria melinoides* (Jamoni 2008).

Paxillus *involutus.*

Russula *alnetorum*, *pumila.* **Russula alnetorum* (Jamoni 2008).

1b. ***Alnus alnobetula*** subsp. ***crispa*** (Aiton) Raus; H. Knudsen; Greenland, Kangilinnguit.

Distributed in SW Greenland and most part of Canada, except the treeless part of the Northwest Territories. These are the most developed scrubs of *Alnus* we have seen in Greenland, up to 3 m high, with a well-developed funga of *Alnus*-related species (see above under *A. alnobetula*).

1c. ***Alnus alnobetula*** subsp. ***fruticosa*** (Rupr.) Raus; A. Belov (creativecommons.org); Kamchatka.

North American; **Eurasian**. Alaska, western Canada and northwestern USA, and most of Russia except the eastern part.

1d. ***Alnus alnobetula*** subsp. ***sinuata*** (Regel) Raus; H. Knudsen; Russia, Altai.

North American; **Asian**. Russian Far East, northeastern China, Japan, northwestern North America, south to California and Wyoming.

ROSACEAE Juss.

Dryas L. (mountain avens) includes 11 species. Ecto-mycorrhization occurs in all of the arctic-alpine species we studied, and is suspected in all species except *D. drummondii*, which has nitrogen-fixing bacteria in its roots.

The genus has a stronghold in the amphiberingian area, but generally only a few species occur in any area. The genus has a strong preference for alkaline soils, and this seems to be more important for its distribution than climate. *Dryas* has a large number of ecto-mycorrhizal symbionts, although not so many obligate and specialized fungi as are associated with *Salix* and *Betula*. The 10 *Dryas* species included here are quite similar, and difficult to separate for non-specialists. Therefore, they are most often not identified to species level, and most hosts are only identified as "*Dryas* sp.".

1. *Dryas ajanensis* Juz.; R. Sealy (CC); Canada, Yukon.

North American; **Eurasian** (amphiberingian distribution). Arctic: Alaska, northwestern Canada, Russia (Sakha, Chukotka).

We found no examples of ecto-mycorrhial symbionts.

2. *Dryas alaskensis* Porsild; leg. A. E. & R. T. Porsild; Alaska, Castner Glacier, 2000-4000 feet, 63°25'N, 145°40'W (isotype).

North American; **Eurasian** (amphiberingian distribution). Arctic: Alaska, Canada (Yukon), Russia (Chukotka).

We found no examples of ecto-mycorrhial symbionts.

3. *Dryas drummondii* Hook.; SabineD (CC); Canada, Yukon.
North American. Alaska, Canada, northwestern USA (Montana, Washington).
We found no examples of ecto-mycorrhial symbionts. The roots include the actinorhizal *Frankia* sp.

4. *Dryas grandis* Juz.; I. Pospelov (CC); Russia, Putorana Plateau.
Eurasian arctic-alpine. Eastern Russia.
We found no examples of ecto-mycorrhizal symbionts.

5. ***Dryas hookeriana*** Juz.; leg. A.E. Porsild & W. A. Weber; USA, Colorado, 13000 feet.

North American. Arctic: Alaska, Canada (Northwest Territories). Alpine: Canada (British Columbia, Alberta), northwestern USA.

We found no examples of ecto-mycorrhial symbionts.

6. ***Dryas incisa*** (Malyschev) Juz. ex Jurtsev; leg. N. A. Sekretareva; Russia, Chukotka.

North American; **Eurasian**. Arctic: Alaska, Canada (Yukon, Northwest Territories), Russia (Siberia except Kamchatka).

We found no examples of ecto-mycorrhial symbionts.

7. ***Dryas integrifolia*** Vahl; J. de Lépinay (CC); Greenland, Qaanaaq.

North American arctic-alpine; **Eurasian arctic-alpine**. Alaska, Canada, Greenland, Russia (Siberia except Kamchatka).

Kohn & Stasovski (1994) found ecto-mycorrhizal hyphae in the root tips.

Examples of ecto-mycorrhizal symbionts:

Amanita *nivalis.* **Amanita* cf. *absarokensis* (Cripps & Horak 2008).

Cortinarius *anomalus*, *croceus*, *delibutus*, *durus*, *hinnuleus*, *norvegicus*, *polaris*, *saniosus*, *subtorvus.* **Cortinarius anomalus* (Lamoure et al. 1982).

Hebeloma *alpinum*, *dunense*, *hiemale*.

Inocybe *borealis*, *calamistrata*, *corydalina*, *decipiens*, *fuscomarginata*, *lacera*, *leiocephala*, *leptocystis*, *nematoloma*, *rimosa*, *soluta.*

Laccaria *laccata*, *pumila*.

Lactarius *brunneoviolaceus*, *dryadophilus*, *lanceolatus*, *pseudouvidus*, *salicis-reticulatae.*

Mallocybe *fulvipes*, *fuscomarginata*, *leucoblema*, *pygmaea.*

Naucaria *tantilla.*

Russula *altaica*, *delica*, *dryadicola*, *heterochroa*, *maculata*, *medullata.*

Tricholoma *scalpturatum*.

8. *Dryas octopetala* L. (including *D. punctata*); S.A. Elborne; West Greenland.

North American arctic-alpine; **Eurasian arctic-alpine**. Missing in Europe, USA and Kamchatka

Examples of ecto-mycorrhizal symbionts:

****Amanita*** *oreina* (Bresinsky & Schmid-Heckel 1983). *Amanita groenlandica*, *vaginata* (Karatygin et al. 1999).

****Boletus*** *edulis* (Miller 1982; considered an exception and not treated further in this work).

****Chalciporus*** *piperatus* (Pyrenees, 2350 m, considered an exception and not treated further in this work, Corriol 2008).

****Cortinarius*** *oreobius* (Lange & Skifte 1971). *Cortinarius anomalus*, *hinnuleus*, *illibatus*, *minutalis*. *Cortinarius cedriolens*, *hinnuleus*, *infractus*, *inops*, *levipileus*, *minutalis*, *minutulus*, *pauperculus*, *phaeochrous*, *pulchripes*, *stenospermus*, *subtorvus*, *violeovelatus* (Kühner & Lamoure 1986). *Cortinarius alpinus*, *anomalus*, *delibutus*, *polaris* (Gulden & Torkelsen 1996). *Cortinarius pauperculus* (Ohenoja et al. 2018). *Cortinarius alpinus*, *chamaesalicis* (Jamoni 2008).

****Hebeloma*** *alpinum* (Bresinsky & Schmid-Heckel 1983). *Hebeloma alpinum* (Ohenoja et al. 2018). *Hebeloma aanenii*, *alpinum*, *edurum*, *mesophaeum*, *minus*, *oreophilum*, *velutipes* (Beker et al. 2016). *Hebeloma velutipes* (Cripps et al. 2019).

Inocybe *albofibrillosa*, *calamistrata*, *fastigiata* var. *alpestris*, *frigidula*, *geraniodora*, *gymnocarpa*, *leucoblema*, *luteipes*, *nitidiuscula*, *praetervisa*. **Inocybe geophylla*, *pusio*, *pruinosa* (Lange & Skifte 1971). *Inocybe frigidula* (Bresinsky & Schmid-Heckel 1983). *Inocybe amoenolens*, *calamistrata*, *canescens*, *concinnula*, *eutheles*, *flocculosa*, *friesii*, *geraniodora*, *microfastigiata*, *mundula*, *oreina*, *rimosa*, *salicis-herbaceae*, *subacuta* (Kühner & Lamoure 1986). *Inocybe concinnula*, *curvipes* (*decipientoides* Peck sensu Favre), *egenula*, *favrei* (*decipiens* sensu Favre), *mundula*, *oreina*, *pseudohiulca* (Horak 1987b). *Inocybe melliolens* (Bon 1992). *Inocybe canescens*, *flavella*, *squamosoannulata* (Jamoni 2008).

***Lactarius** *dryadophilus* (Bresinsky & Schmid-Heckel 1983, Schmid-Heckel 1985, Kühner & Lamoure 1986). *Lactarius lanceolatus* (Gulden & Torkelsen 1996). *Lactarius repræsentaneus*, *uvidus* (Karatygin et al. 1999). *Lactarius nanus*, *salicis-reticulatae* (Jamoni 2008).

****Mallocybe*** *fuscomarginata*, *leucoblema* (Kühner & Lamoure 1986). *Mallocybe squarrosoannulata*, *substraminipes* (Bon 1989).

Russula *consobrina*, *delica*, *nana*. **Russula nana* (Gulden & Torkelsen 1996).

****Tricholoma*** *hemisulphureum* (Bon 1989, Jamoni 2008).

9. *Dryas oxyodonta* Juz.; leg. N. V. Gevjakina & N. Vorobeva; Russia, Altai, Katun-area.
Eurasian. Alpine: Russia (Western and Central Siberia), Kazakhstan.
We found no examples of ecto-mycorrhial symbionts.

10. *Dryas viscosa* Juz.; leg. L. Tjulina; Russia, southern Yakutia, at river Aldan.
Eurasian. Alpine: Russia (Sakha, Magadan).
We found no examples of ecto-mycorrhial symbionts.

Alchemilla L. (Lady's mantle) includes 743 species. Mycorrhization is suspected by some authors.

Harley & Harley (1987) tested 15 British species and found vesicular-arbuscular mycorrhiza, not ecto-mycorrhiza. Schmid-Heckel (1985: 9) presumed that *Alchemilla* in the German Alps formed ecto-mycorrhiza, but did not give examples. Jamoni (2008) mentioned nine species of *Cortinarius*, *Hebeloma*, *Inocybe*, *Laccaria*, and *Russula* "growing among" *Alchemilla pentaphyllea* and *Dryas* or *Salix*, but gave no records of fungi growing exclusively with *Alchemilla*. In Greenland, we have several times searched for ecto-mycorrhizal fungi around *Alchemilla*, but have not found any except when *Salix* or *Dryas* were also nearby.

1. *Alchemilla* sp.; H. Knudsen; S-Greenland; Qassiarsuk.

Not forming ecto-mycorrhiza according Wang & Qiu (2006). We have reached the same point of view from field observations.

CISTACEAE Juss.

At least two genera from this family form ecto-mycorrhiza, but one of them, *Cistus* L., does not occur in arctic-alpine regions and is not included here.

Helianthemum Mill. (rock-rose) includes 111 species. Ecto-mycorrhiza are found in some species, including the British representatives (Harley & Smith 1983), and the subtropical *H. lippii* with *Terfezia* truffles. However, the general situation in *Helianthemum* is complicated, with ecto-, ectendo- and vesicular-arbuscular mycorrhiza found in the species that have been studied.

The genus is large, but most species grow in warm and dry regions and therefore are not considered here. *Helianthemum nummularium* has a very scattered occurrence in alpine areas, and a few ecto-mycorrhizal symbionts have been recorded from the Alps (see below). In Denmark, we have e.g. recorded *Cortinarius anomalus* as a symbiont.

1. *Helianthemum nummularium* (L.) Mill.; H. Knudsen; Denmark, Røsnæs (with *Cortinarius anomalus*).

Eurasian. Widespread in Europe including temperate and alpine regions, also in Central Asia.

Examples of ecto-mycorrhizal symbionts:

Amanita sp.

****Cortinarius*** *phaeochrous* (Kühner & Lamoure 1986, with *Helianthemum grandiflorum*), *violaceovelatus* (with *H. vulgare*).

****Hebeloma*** *aanenii*, *griseopruinatum*, *laterinum*, *mesophaeum*, *velutipes* (Beker et al. 2016).

****Tricholoma*** *hemisulphureum* (Jamoni 2008).

POLYGONACEAE Juss.

In this family the ability of the individual species to form ecto-mycorrhiza is not well known. Harley & Harley (1987) listed *Bistorta vivipara* (*Polygonum viviparum*) as the only ecto-mycorrhizal member of the family in the UK. Wang & Qiu (2006) summarized the knowledge of the family, including three species in three different genera: *Bistorta vivipara* (see below), *Persicaria capitatum* (Koske et al. 1992), and *Koenigia weyrichii* (Titus & Tsuyuzaki 2002).

Koenigia islandica L. is widespread in arctic-alpine areas, but has not been reported as ecto-mycorrhizal, and we have no observations to the contrary.

Bistorta (L.) Scop. (bistort) includes 43 species. Ecto-mycorrhization is only known for one species, but the genus is poorly investigated for this symbiosis. Most species occur in the Himalayas.

Fig. 104. *Bistorta vivipara* forming ecto-mycorrhiza with a small *Laccaria* in Greenland.

1. *Bistorta vivipara* (L.) Delarbre; H. Knudsen; Greenland, Constable Pynt.

North American; **Eurasian**. Found in all countries with mountains; missing only in Hungary, Belarus, Portugal, and a few lowland countries in northwestern Europe.

Examples of ecto-mycorrhizal symbionts:

Amanita *nivalis.*

Cortinarius *acutus*, *anomalus.* **Cortinarius hinnuleus*, *inops* (Kühner & Lamoure 1986).

Hebeloma *hiemale.*

Inocybe *alpigenes*, *borealis*, *calamistrata*, *favrei*, *lacera*, *leiocephala*, *mixtilis*, *praetervisa*, *rimosa.*

Laccaria *laccata*, *pumila*.

Lactarius *brunneoviolaceus*, *dryadophilus*, *lanceolatus*, *nanus*, *pseudouvidus*.

Mallocybe *abruptibulbosa*, *agardhii*, *dulcamara*, *fulvipes*, *pygmaea*, *squamosoannulata.*

Naucoria *amarescens*, *bohemica*, *cholea.* **Naucoria cholea* (Moreau et al. 2006a).

Russula *medullata*, *nana*, *pascua*, *saliceticola*, *subrubens.* **Russula nana*, *pascua* (Schmid-Heckel 1985).

Thelephora *caryophyllea.*

CYPERACEAE Juss.

Carex L. (Sedge) includes 2002 species. Ecto-mycorrhization has only been proven for one species (*Carex myosuroides*, cf. Kohn & Stasovski 1994, Mühlmann & Peintner 2008). Schmid-Heckel (1985: 9) suspected ecto-mycorrhization to occur in *Carex firma* in the German Alps. However, the majority of *Carex* species are devoid of mycorrhiza, even in a broad sense.

1. *Carex myosuroides* Vill. (*Kobresia myosuroides*); leg. B. Fredskild; Greenland, Qaanaaq.

North American; **Eurasian**. Circumpolar-circumboreal, missing only in the northwestern European lowlands, Hungary, and Portugal.

Examples of ecto-mycorrhizal symbionts (identified from DNA sequences from roots, cf. Mühlmann & Peintner 2008):

Cortinarius cf. *inops* (record from northern Greenland, Zackenberg, by TB) *Cortinarius* spp.

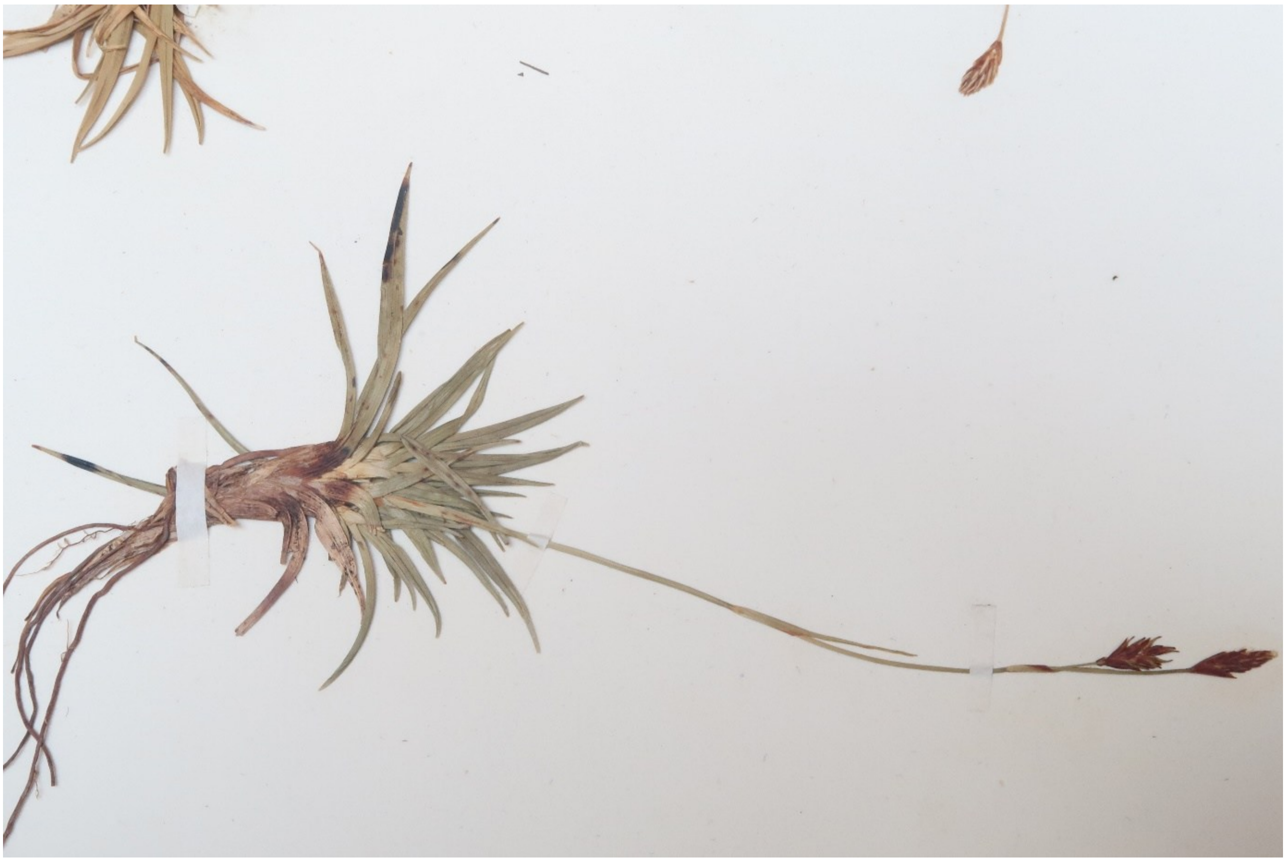
Hebeloma sp.

Inocybe spp.

Sebacina *incrustans*, *Sebacina* sp.

Tomentella spp. (incl. *Thelephora*).

Kohn & Stasovski (1994) found ecto-mycorrhizal hyphae in the root tips of *Carex myosuroides*, but did not identify any of the symbionts. So far no records of basidiomata from the field have been recorded. We have searched populations of this plant, and have never found basidiomata of any kind. We assume that formation of basidiomata only takes place under very favourable conditions, and that in a normal situation there is too little energy/exchange of nutrients between the symbiont and the host plant for the fungus to make basidiomata.



2. ***Carex firma*** Mygind ex Host; G. van Buggenhout; Italy, Tirol, Bolzano, Pordoi Pass.
Eurasian. Alpine: central European mountains.

Examples of ecto-mycorrhizal symbionts:

****Hebeloma*** *alpinum* (Schmid-Heckel 1985).
****Inocybe*** *oreina* (Schmid-Heckel 1985).

Schmid-Heckel (1985) stated that "surprisingly few fungi are characteristic for the Caricetum firmae", and only one of the three species he mentioned are known to form ecto-mycorrhiza.

Harley & Harley (1987) reported no British species of *Carex* to form ecto-mycorrhiza, but Mühlmann & Peintner (2009) showed that the roots of *Carex* (*Kobresia*) *myosuroides* contain hyphae from a number of classical ecto-mycorrhizal genera of basidiomycetes (see above).

The roots of *Carex firma* have not yet been studied, but Bresinsky & Schmid-Heckel (1983) believed that it is ecto-mycorrhizal.

PRIMULACEAE Batsch ex Borkh.

Primula L. (primrose) includes 532 species. Vesicular-arbuscular mycorrhiza are found in all British species, but ecto-mycorrhiza have not been confirmed. Schmid-Heckel (1985: 9) suspected that *Primula minima* has the ability to form ecto-mycorrhiza. Harley & Harley (1987) opposed this view, as did Wang & Qiu (2006).

1. *Primula minima* L.; P. Lütken; Austria, Salzburg, near Ferleiten, 2100 m.
Eurasian. Alpine: central European mountains.

Examples of ecto-mycorrhizal symbionts:

****Cortinarius*** *scotoides* (Schmid-Heckel 1985).

****Inocybe*** *praetervisa* (Schmid-Heckel 1985).

Schmid-Heckel (1985) found *Cortinarius scotoides* growing in the middle of *Primula minima*; Favre (1955) found it growing with dwarf willows. Schmid-Heckel (1985) found *Inocybe praetervisa* growing in many plant societies, including with *Primula minima.*

ERICACEAE Durande

Arctous Nied. (bearberry p.p.) includes three species. Harley & Harley (1987) reported only ericoid mycorrhiza in this family, but Kohn & Stasovski (1994) reported ecto-mycorrhiza in the roots. Species of Ericaceae do not normally form ecto-mycorrhiza.

1. *Arctous alpina* (L.) Sied. (syn. *Arctostaphylos alpina*). W. Rose (CC); northern Norway.
North America; **Eurasia.** Circumpolar, missing only in the lowlands in northern Europe.

Example of mycorrhizal symbiont:

****Amanita*** *regalis* (Karatygin 1999).
****Lactarius*** *bresadolianus*, *L. deterrimus* (Schmid-Heckel 1985).
****Leccinum*** *arctoi* (Vassilkov 1978).

Arctous alpina was not mentioned by Harley & Harley (1987) or Wang & Qiu (2006). The species is poorly known. The related *Arbutus menziesii* forms ecto-mycorrhiza, but is not arctic-alpine. We found *Russula medullata* in the middle of a population of *Arctous alpina*, but with dwarf shrubs nearby.

Cassiope D. Don (mountain-heather or bell-heather) includes18 species.

In arctic regions *Cassiope tetragona* forms arctic heaths. As a heather plant, it does not normally form ecto-mycorrhiza. However, in the northern part of Greenland, we have found it with typical ecto-mycorrhizal symbionts, and in fact with symbionts not found with other hosts in Greenland.

1. *Cassiope tetragona*; H. Knudsen; East Greenland, Constable Pynt, 2017.
North American; **Eurasian**. Circumpolar, but missing in central and southern Europe.

Examples of ecto-mycorrhizal symbionts:

Tricholoma *hemisulphureum*, *scalpturatum*.

Kohn & Stasovski (1994) found ecto-mycorrhizal hyphae in the root tips of *Cassiope.* We found *Tricholoma scalpturatum* in a High Arctic locality with *Cassiope*.

Rhodothamnus Rchb. (dwarf alpenrose) includes two species.

1. *Rhodothamnus chamaecistus* (L.) Rchb. (syn. *Rhododendron chamaecistus*);
M. Weber (CC); Germany, Bayern.

Example of ecto-mycorrhizal symbiont:

**Inocybe oreina* (Schmid-Heckel 1985).

SAXIFRAGACEAE Juss.

Saxifraga Tourn. ex L. includes 477 species.

1. *Saxifraga oppositifolia* L.; G. van Vliet (CC); Alaska, Juneau, Mendenhall Glacier.

Example of ecto-mycorrhizal symbiont:

****Naucoria* chamiteae*** (Kühner & Lamoure 1986: 107).

Kohn & Stasovski (1994) found evidence of ecto-mycorrhizal anatomy in the root tips of *Saxifraga oppositifolia*, but did not list any symbionts. We have not found basidiomata associated with *Saxifraga.*

Cortinarius *paleifer* (syn. *C. flexipes*) has also been reported to form ecto-mycorrhiza with an unidentified species of *Saxifraga*.

SCROPHULARIACEAE Juss.

Pedicularis L. (lousewort) includes 680 species.

1. *Pedicularis capitata* Adams; T. Bradley (creativecommons.org); Alaska, Denali.

Kohn & Stasovski (1994) identified mycorrhizal root tips in *Pedicularis capitata*, but did not list any symbiont. We have not found basidiomata associated with *Pedicularis*.

10. Gasteromycetation

The gasteromycetes are a group of basidiomycetes united by an inability to actively spread their spores. The largest group is adapted to dry localities, spreading their spores only when rain falls on their "skin", or when an animal steps on them. Another group is spread by animals like flies, which pick up the spores on their feet and then fly to another site where they are deposited. Finally some are adapted to spread by peridioles (small packets of spores) that are dispersed by raindrops. These adaptations are present in many climates, from the tropics to the Arctic, but it may be that the highest relative number of gasteromycete species occurs in open arctic areas. In the widespread dry arctic deserts or semideserts, members of Agaricaceae such as *Apioperdon*, *Bovista*, *Bovistella*, *Calvatia*, *Disciseda*, *Fuscospina*, *Lycoperdon*, and *Utraria* are well represented, and they are often easily seen even at a distance among the low green or greyish vegetation.

Examples of gasteromycetes in open dry land:

Apioperdon pyriforme.

Bovista aestivalis, *limosa*, *nigrescens*, *pusilla*, *tomentosa*.

Bovistella utriformis.

Calvatia arctica, *bellii*, *connivens*, *excipuliforme*, *horrida*, *septentrionalis*, *tatrensis*.

Disciseda calva.

Fuscospina nigrescens.

Geastrum minimum.

Lycoperdiscus lividus.

Lycoperdon echinella, *norvegicum*, *perlatum*, *radicata*, *spadiceum*.

Utraria cretacea, *frigida*, *lambinonii*, *mollis*, *nivea*, *turneri*, *umbrina*.

Examples of gasteromycetes on wood or woody substrates:

Crucibulum laeve.

Mycocalia denudata, *duriaeana*.

Sphaerobolus stellatus.

Fig. 105. The bird's nest fungus *Crucibulum laeve* is common in southern Greenland.

11. Lichenization

The symbiosis between a fungus and an alga is called lichenization and the result is a lichen. This mode of life is very common among ascomycetes in arctic and alpine regions. In Greenland, the number of known lichenized ascomycetes is comparable to that of the non-lichenized ascomycetes, about 1050 species according to Eric Steen Hansen (C).

For basidiomycetes, the situation is the opposite. The number of lichenized basidiomycetes is low everywhere. From temperate and arctic areas only two genera are known, *Lichenomphalia* and *Multiclavula.* Both are small genera with small species, and it is evident that this way of life has not been very successful among the basidiomycetes. They have a clear preference for cold climates, where most of the known species occur. *Multiclavula mucida* is an exception, growing on old fallen tree trunks in moist temperate climates, but the others occur in arctic-alpine areas, where symbiotic lichenization seems to be a successful strategy. Growth is extremely slow, and algae enclosed by fungal hyphae may better survive the severe cold and drought of the winter. Even if lichenization does not particularly favour the two symbiont partners, it may be an adaptation to survive the harsh arctic-alpine climate.

Figure 106. *Lichenomphalia hudsoniana* with basidiomata. The grey-green scales at the base (*Coriscium*-state) are the vegetative part of this lichen, and the yellow omphalinoid basidiomata carry the basidia. When the spores have spread by wind, the basidiomata die away, but the green scales containing unicellular algae will continue to photosynthesize.

Examples of lichenized basidiomycetes:

Lichenomphalia alpina, *ericetorum*, *luteovitellina*, *pararustica*, *umbellifera*, *velutina*.

Multiclavula corynoides, *vernalis*.

12. Preliminary conclusions

The preliminary conclusions below will be confirmed or removed in the second edition of volume 1. This will hopefully be issued together with the last of volumes 4-7.

It should be stressed that there are at this point no references for the conclusions below, whether they are our own or taken from other mycologists. This will be remedied in the second version.

FN = Funga Nordica, second edition (Knudsen & Vesterholt 2012).

The conclusions below contrast the situation in arctic-alpine regions with that of temperate-boreal regions of the Northern Hemisphere.

From volume 1: General patterns

§ 1. In general the arctic-alpine funga is a depauperate version of the boreal-temperate funga. Many genera are found in both regions, but most often in different numbers.

§ 2. Most species of rusts and smut fungi, ca. 63%, occur in both North America and Eurasia.

§ 3. The relative number of mycorrhiza-forming species is greater than in warmer regions, presumably as an adaptation to the harsher climate.

§ 4. Most trees and shrubs occurring in arctic and alpine regions are ecto-mycorrhizal, with the exception of *Sorbus*, *Juniperus*, and *Rhododendron*. In temperate and boreal regions there are many more non-mycorrhizal woody genera, e.g. *Acer*, *Fraxinus*, *Crataegus*, *Ulmus*, *Juniperus*, *Sorbus*, *Cornus*, etc.

§ 5. All arctic-alpine organisms must be conditioned to abrupt freezing, even in the middle of their growing season. One of the adaptations to this is the evolution of antifreeze proteins (AFPs). Hoshino et al. (1998, 2001) and others have shown that this character has evolved multiple times across the fungal kingdom. In basidiomycetes, it has been demonstrated in basidiomycetous yeasts (*Cryptococcus*, *Dioszegia*, *Leucosporidium*, *Mrakia*, *Rhodotorula*), and also in agarics like *Coprinopsis psychromorbida* and in the snow mold club fungi *Typhula ishikariensis*, *T. phacorrhiza*, *T. incarnata* and *T. variabilis*. Duman & Olsen (1993) identified the presence of thermal hysteresis AFP in basidiomycetes like *Flammulina velutipes* s.l., *Pleurotus* sp., *Trametes versicolor* and *Stereum* sp.

§ 6. Mycelia in arctic and alpine regions are generally darker than in temperate and boreal regions, and the cell walls are often thicker and darkly pigmented. This important character is interpreted as a protection against desiccation in open landscapes with strong arctic winds, and also as a protection against strong ultraviolet radiation. This feature is most strongly developed in the Arctic, due to the long – even continuous – days of midnight sun, but also in alpine regions due to the strong radiation at high altitudes. The dark colour also helps to absorb more sunlight and thus warm up the mycelia.

§ 7. The number of plant species in the Arctic is only about half of that in the Alps.

§ 8. Favre (1955: 172-181) introduced the term "nanisme" (dwarfism) for fungi in alpine regions, in reference to the fact that the basidiomata of alpine fungi are smaller than those of their counterparts in warmer areas. We can not confirm this.

§ 9. Peyronel (1930: 661) reasoned that dwarf shrubs do not have a sufficient "mass" to allow their ecto-mycorrhizal symbionts to develop to normal size. It should however be possible for alpine saprotrophic species. Heim (1922: 469) was of the opinion that the same species did not change size with increasing altitude, and we agree.

§ 10. Favre (1955: 172-181) mentioned examples of species, which have smaller basidiomata in alpine regions than in temperate regions (e.g. *Clavulina cinerea* or *Melanoleuca grammopodia*). According to our experience this is not generally correct, but it is true that small specimens of a particular species may be found more often in colder regions. We think this is a response to temporarily cold conditions, rather than a heritable feature.

§ 11. Favre (1955: 178-180) emphasized the number of lamellae as an important feature of alpine fungi. He hypothesized that the higher the altitude, the fewer lamellae. There are only a few monographs where the number of lamellae has consistently been reported, but Beker et al. (2016) did use lamella numbers to separate some of species of *Hebeloma*. This would be an unfortunate diagnostic character if lamella numbers were to vary with temperature instead of being genetically fixed, but we have no evidence that this is the case.

§ 12. Lange in Savile (1982) expressed the view that spores become larger with increasing altitude, but he did not provide specific examples.

§ 13. Lange in Savile (1982: 364, 366) indicated that it is difficult to get a spore-print from an agaric in arctic areas, since he assumed that they make fewer spores than in temperate regions. We can not confirm this.

§ 14. Gulden in Savile (1982: 367) disagreed, at least for open areas where spore deposits are often observed in the vegetation around an agaric. We agree with Gulden, but suggest that spore development in arctic and alpine areas may sometimes be aborted by frost during the short growing season.

§ 15. Favre (1955: 169) believed that from a mycological point of view, dwarf shrubs and *Dryas* constitute an alpine floor above the forest floor, a new kind of forest floor with microscopic leaves.

§ 16. It is possible that low temperatures and a very short growing season correspond with fewer spores per basidioma than in warmer areas, but this has not been closely investigated. It is also possible, as suggested by Laursen (in Savile 1982: 367), that fewer of the spores are actually viable, but this is again an assumption that has not been checked.

§ 17. Savile (1972) suggested that species found in both arctic regions and warmer temperate regions would be smaller in the arctic region. We are not able to confirm this.

§ 18. Savile (1982) stated that "although we have many species that are at least largely confined to the arctic, few if any genera or higher taxa are fully arctic." We agree.

§ 19. A cold climate and the resulting slow biological processes, in conjunction with the small size of available substrates, results in selection for small basidiomata.

§ 20. The overall mass of organic debris in arctic and alpine regions is less then in warmer climates, resulting in many genera with small basidiomata, such as *Calathella*, *Crepidotus*, *Flagelloscypha*, *Glabrocyphella*, *Gloiocephala*, *Hemimycena*, *Hohenbuehelia*, *Merismodes*, *Mucronella*, *Pellidiscus*, *Pterula*, *Rectipilus*, *Resupinatus*, *Stromatocyphella*, *Tectella*, and *Typhula.*

§ 21. The number of two-spored taxa is relatively higher in arctic and alpine regions than it is in temperate and boreal regions. Many species also have a mixture of 2-and 4-spored basidia. Some examples are: *Arrhenia acerosa* var. *phaeotellus* (2), *Entoloma infula* var. *chlorinosum* (2-4), *Entoloma longistriatum* var. *sarcitulum* (2-4), *Galerina atkinsoniana* var. *atkinsoniana* (2), *Galerina jaapii* (2), *Galerina lubrica* (2), *Galerina lubrica* (2), *Galerina subannulata* (2), *Galerina subclavata* (2), *Galerina vittiformis* f. *vittiformis* (2), *Hebeloma grandisporum* (2), *Hygrocybe laeta* (2-4), *Hygrocybe virginea* var. *fuscescens* (2-4), *Hydropus dryadicola* (2), *Laccaria pumila* (2), *Lepiota favrei* (2-4), *Lichenomphalia velutina* (2-4), *Mycena adonis* (2), *Mycena cinerella* (2), *Mycena citrinomarginata* (2-4), *Mycena galericulata* (2-4), *Mycena metata* (2-4), *Omphalia grisella* ss. Favre (2), *Rickenella marchantiae* (2-4), and *Rickenella pseudogrisella* (2-4).

We think we will be able to expand this list when the species in vols. 4-7 have been investigated for this character.

§ 22. The order Agaricales is by far the largest order in arctic-alpine climates, as it is in warmer climates.

From volume 2: Rusts

Fig. 107. *Salix* infected by *Melampsora*. When the infected buds burst open, the plant becomes completely covered with yellow aeciospores.

§ 23. The most conspicuous feature of rust fungi in cold regions is the predominance of microcyclic species that complete their life cycle in one stage (teleuto), as opposed to macrocyclic species with different types of spores. The advantage, or perhaps more correctly, the necessity of the microcyclic lifestyle lies in the short time needed to complete the cycle. In areas with a short growing season, and a constant threat of freezing even in the middle of the season, this is a necessity or at least an advantage. The complex life cycle of heteroecious species involving a host change naturally takes longer than completing the cycle on the same plant (autoecy).

§ 24. All species of rusts are self-fertilising. This naturally is a faster process than waiting to be fertilised by another individual.

§ 25. In the rusts, with the single order Pucciniales, the families Raveneliaceae and Pyxidaceae are absent from arctic and alpine regions. In Cronartiaceae, *Endocronartium* and *Endophyllum* are absent. In Phragmidiaceae, *Frommeella* and *Kuehneola* are absent. In Pucciniaceae, *Cumminsiella* and *Miyagia* are absent. In Pucciniastraceae, *Milesia* and *Milesina* are absent.

§ 26. Rust fungi exhibit a greater frequency of dark-coloured, thick-walled spores in arctic and alpine regions, and among closely related species, the darker-spored ones are found in the cold regions. This serves to protect them from dessication in strong winds and from strong solar radiation (midnight sun).

§ 27. Durrieu & Adhikari (1993) showed that the numbers of Erysiphaceae and Peronosporaceae decrease with higher altitude, whereas the relative numbers of Uredinales and Ustilaginales increase with altitude.

§ 28. According to Savile (1972), some species of *Chrysomyxa* may survive up to hundreds of kilometres above the treeline. They alternate between conifers and heath plants, but only because they live on evergreen hosts where their uredinia may overwinter and start again.

§ 29. The figure below is a comparison of lowland (colline) and alpine rusts. Macrocyclic species are more than twice as common in the lowlands than in the Alps, and the reverse is true for microcyclic species. In Norway, 23% of all rusts are microcyclic, and in the mountains it is 43%. This agrees well with Parmelee (1989), who stated that approximately half of the species in the Canadian Arctic are microcyclic. Arthur (1929) was the first to note the prevalence of microcyclic species in cold regions, followed by Jørstad (1964).

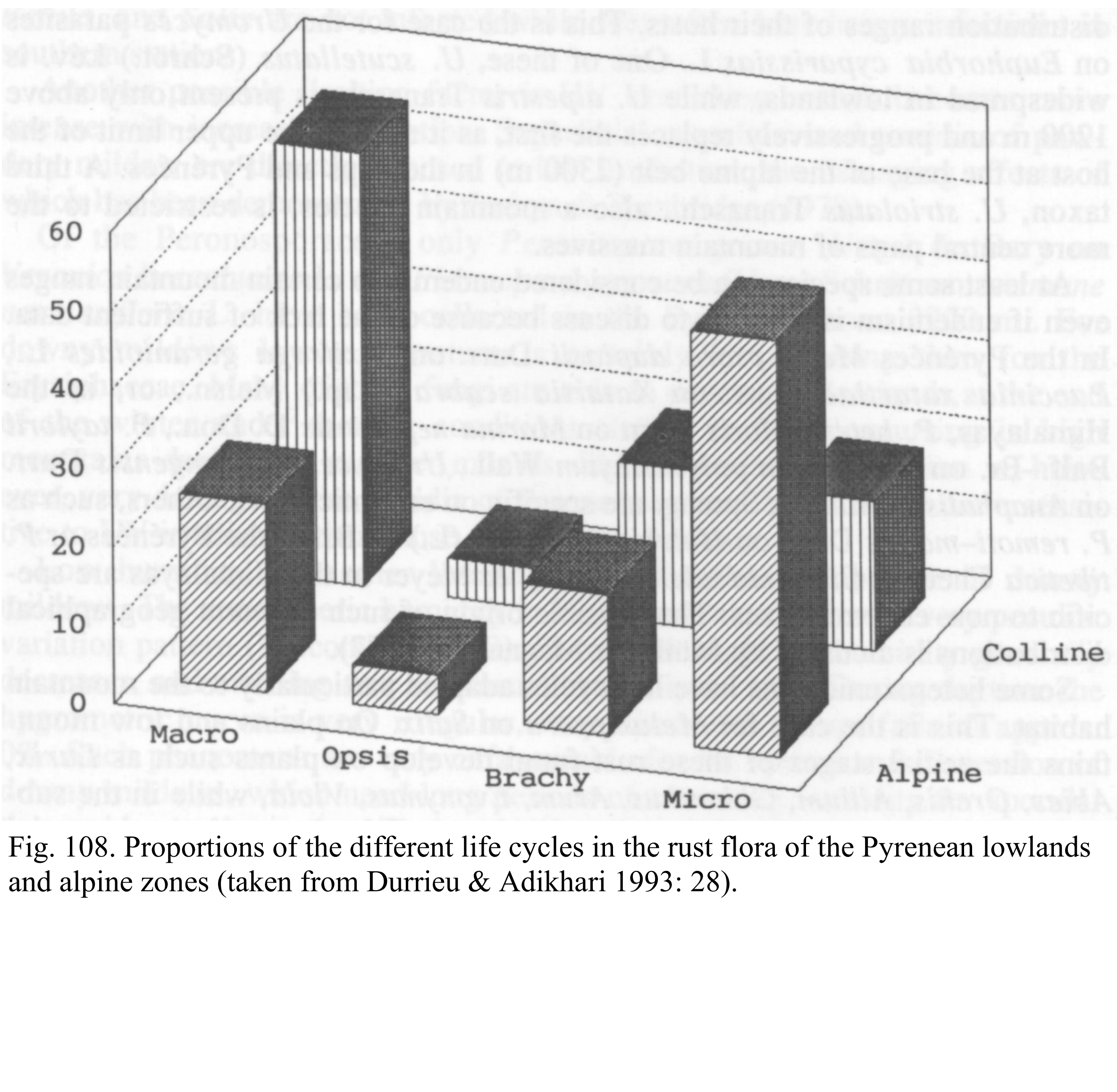


Fig. 108. Proportions of the different life cycles in the rust flora of the Pyrenean lowlands and alpine zones (taken from Durrieu & Adikhari 1993: 28).

From volume 3: Smut fungi and tremelloids

§ 30. In Doassansiaceae (Doassansiales), *Nannfeldtiomyces*, *Pseudoassansia*, *Tracya*, and *Ustacystis* are absent.

§ 31. In Rhamphosporaceae (Doassansiales), *Rhamphospora* is absent.

§ 32. In Entorrhizaceae (Entorrhizales), *Entorrhiza* is absent.

§ 33. In Microbotryaceae (Microbotryales), *Zundeliomyces* is absent from arctic and alpine regions.

§ 34. In Tilletiaceae (Tilletiales), *Neovossia* is absent.

§ 35. In Anthracoidaceae (Ustilaginales), *Farysia* is absent, whereas *Anthracoidea* seems to be “overrepresented”.

§ 36. In Melanotaeniaceae (Ustilaginales), *Melanotaenium* is absent.

§ 37. In Ustilaginaceae (Ustilaginales), *Moesziomyces* and *Sporisorium* are absent.

From volume 4: Phallales, Geastrales, Cantharellales, Sistotrematales, Trechisporales, Corticiales, Hymenochaetales, Thelephorales, Polyporales, Russulales

§ 38. Phallales, Hysterangiales, and Gloeophyllales are completely absent from the arctic-alpine funga. Cantharellales is included in Funga Arctica &Alpina, but was not included in FN.

§ 39. In Hymenochaetales most of the poroid genera are absent, but *Coltricia*, *Inonotus, Mensularia*, *Phellinus*, and *Xanthoporus* are present with one or a few species. Among the genera with small fleshy basidiomata in this order, *Alloclavaria*, *Atheloderma*, *Contumyces*, and *Repetobasidium* are absent.

§ 40. In Geastraceae (Geastrales), *Myriostoma* and *Radiigera* are absent.

§ 41. In Sclerogastraceae (Geastrales), *Sclerogaster* is absent.

§ 42. In Geastraceae (Geastrales), *Geastrum minimum* has been recorded once from Greenland, and this species is also the northernmost *Geastrum* in mainland Europe. FN records 21 species of the genus.

§ 43. In Auriscalpiaceae (Russulales), *Artomyces*, *Auriscalpium*, and *Gloiodon* are absent. Elsewhere in Russulaceae, the gastroid genera *Gymnomyces*, *Macowanites*, and *Zelleromyces* are also absent.

§ 44. Only a few genera of polypores s.l. are present: *Bjerkandera*, *Ceriporia*, *Cystidiopostia*, *Fomes*, *Fomitopsis*, *Hapalopilus*, *Picipes*, *Postia*, *Resiniporia*, *Trechispora*, and *Tyromyces*; and each of them is represented by only a few species. This is only a fraction of the polypores found in any country with a temperate-boreal climate.

From volume 5: Boletales, Agaricales p.p.

§ 45. In Boletales, Tapinellaceae, Serpulaceae, Gastrosporiaceae, Hygrophoropsidaceae, Gomphidiaceae, Suillaceae, Sclerodermataceae, Gyroporaceae, Pisolithaceae, Diplocystidiaceae, and Octavianinaceae are absent.

§ 46. In Paxillaceae (Boletales), *Gyrodon*, *Hydnomerulius*, and *Melanogaster* are absent.

§ 47. In Boletaceae (Boletales), all genera except *Leccinum* and *Xerocomus* are absent.

§ 48. Species of *Leccinum* (Boletales) are common in arctic-alpine areas as long as *Betula* is nearby. We are currently working on a phylogeny of *Leccinum* based on DNA evidence. The results will appear in volume 5.

§ 49. *Boletus* sensu lato (Boletales) is practically absent from arctic and alpine regions. A specimen of *Xerocomus* has been tentatively identified as *X. subtomentosus*, but it might be another species.

§ 50. In Agaricales, Stephanosporaceae, Schizophyllaceae, Cystostereaceae, Fistulinaceae, and Macrocystidiaceae are absent.

§ 51. In Clavariaceae (Agaricales), *Hyphodontiella* is absent.

§ 52. In Hygrophoraceae (Agaricales), *Chrysomphalina*, *Eonema*, *Hygroaster*, and *Hygrophorus* are absent. *Hygrophorus melizeus* occurs in subarctic regions, forming ecto-mycorrhiza with *Picea*, *Pinus*, and *Betula pubescens.* FN lists 39 species of *Hygrophorus*. *Arrhenia* and *Lichenomphalia* seem to be "overrepresented".

§ 53. Lange in Savile (1982: 364) suggested that the few lichenized basidiomycetes in the Arctic have the same strategy for dispersal as many ascolichens, i.e. they spread through propagules composed of a small amount of mycelium surrounding a few algal cells. *Lichenomphalia hudsoniana* has a scaly *Coriscium*-state (Fig. 106) at the bases of the basidiomata, and in *L. alpina* there is a *Botrydina*-state of algae surrounded by mycelia.

It is well-known that in higher latitudes, where plants and animals are close to the northern limit of their range, reproduction may fail in certain years due to the extra-harsh climate. According to Lange in Savile (1982: 365), it is difficult to find populations of *Sphagnum* with sporophytes at the northern limit of its range. In his words, in arctic-alpine areas "we are in the propagule area of the world." This is also the case for many other plants, and possibly to a lesser extent for fungi.

§ 54. In Cyphellopsidaceae (Agaricales), *Nia* and *Woldmaria* are absent.

§ 55. In Cyphellaceae (Agaricales), *Baeospora*, *Cheimonophyllum*, *Cyphella*, and *Granulobasidium* are absent.

§ 56. In Pterulaceae (Agaricales), *Aphanobasidium*, *Coronicium*, *Merulicium*, and *Phyllotopsis* are absent.

§ 57. In Physalacriaceae (Agaricales), naturally occurring *Armillaria*, as well as *Cylindrobasidium*, *Dactylosporina*, *Hymenopellis*, *Mucidula*, *Mycaureola*, *Paraxerula*, *Physalacria*, *Rhizomarasmius*, *Rhodotus*, *Strobilurus*, and *Xerula* are absent.

§ 58. In Marasmiaceae (Agaricales), *Calyptella*, *Campanella*, *Chaetocalathus*, *Clitocybula*, *Crinipellis*, *Gerronema*, *Lentinula*, *Marasmiellus*, *Omphalotus* and *Pleurocybella* are absent.

§ 59. In Amanitaceae (Agaricales), *Limacella* is absent.

§ 60. In Pluteaceae (Agaricales), *Volvariella* is absent.

§ 61. In Mycenaceae (Agaricales), *Resinomycena*, *Roridomyces*, and *Sarcomyxa* are absent, while *Hemimycena* seems to be "overrepresented".

§ 62. In Tricholomataceae (Agaricales), *Callistosporium*, *Catathelasma*, *Cellypha*, *Delicatula*, *Dendrocollybia*, *Dermoloma*, *Haasiella*, *Leucocortinarius*, *Leucopaxillus*, *Leucopholiota*, *Melanomphalia*, *Porpoloma*, *Pseudoclitocybe*, *Pseudoomphalina*, *Resupinatus*, and *Tricholomopsis* are absent.

§ 63. Also in Tricholomataceae (Agaricales), *Tricholoma* is practically absent. We have recorded two rarely occurring species in Arctic regions, *T. scalpturatum* and *T. hemisulphureum*, with *Dryas* and *Salix*. Most records are with the heath plant *Cassiope tetragona*, on calcareous ground in central East Greenland. FN lists 60 species.

From volume 6: Agaricales p.p.

§ 64. In Lyophyllaceae, *Asterophora*, *Calocybe*, *Gerhardtia*, *Hypsizygus*, *Ossicaulis*, and *Tricholomella* are absent.

§ 65. In Agaricaceae, *Battarraea*, *Chamaemyces*, *Chlorophyllum*, *Cystolepiota*, *Disciseda*, *Echinoderma*, *Floccularia*, *Leucogaricus*, *Leucocoprinus*, *Macrolepiota*, *Melanophyllum*, *Montagnea*, *Mycenastrum*, *Nidularia*, *Phaeolepiota*, *Phellorinia*, *Queletia*, *Squamanita*, and *Tulostoma* are absent.

§ 66. In Lycoperdaceae, *Langermannia* is absent. *Calvatia* seems to be "overrepresented".

§ 67. Leathery and woody basidiomata in arctic regions may take two seasons to complete development of their basidiomata. It is a regular phenomenon to find specimens of *Calvatia* in very different stages, suggesting that the oldest are from last year and the youngest from the current season. Again, we know of no specific studies, but we have seen the phenomenon many times ourselves, and we can confirm the observations of Savile (1972). We have not seen this apparent biennial habit among the agarics, whereas it is common among the polypores.

§ 68. In Psathyrellaceae, *Stagnicola* is absent.

§ 69. In Hydnangiaceae, *Hydnangium* is absent. *Laccaria* seems to be "overrepresented".

§ 70. In Bolbitiaceae, *Descolea* and *Gymnoglossum* are absent.

§ 73. In Agaricacae, *Lepiota* is poorly presented by three species, two of which occur widely in Europe. The third, *Lepiota favrei*, is typically arctic-alpine. It is known from the Alps, Greenland, and northern Norway. FN lists 33 species of *Lepiota*.

§ 74. In Amanitaceae, *Amanita* is present with a number of species, but they all belong to *Amanita* sect. *Amanita* (ringless species), except for a recent record of *A. muscaria* from Kangilinnguit in Greenland.

§ 75. In Cortinariaceae, *Cortinarius* sensu lato is the most diverse genus, with more than 100 species and all segregate genera/subgenera represented. The subgenus *Telamonia* sensu stricto seems to be "overrepresented".

From volume 7: Hymenogastraceae (Agaricales).

§ 76. From our expeditions to many Arctic regions, we believe that *Hebeloma* may be the best-represented genus overall, although not the one with the most basidiomata.

§ 77. In Strophariaceae, *Flammula*, *Hemipholiota*, *Hemistropharia*, and *Meottomyces* are absent.

§ 78. In Crepidotaceae including Chromocyphellaceae, *Episphaeria* and *Pseudoflammula* are absent.

§ 79. *Inocybe* sensu lato is the second most numerous genus in arctic and alpine regions, with >100 species known, including *Inocybe* sensu stricto, *Inosperma*, *Mallocybe*, and *Pseudosperma*. At least *Mallocybe* seems to be "overrepresented".

§ 80. In Hymenogastraceae, *Phaeocollybia* is absent.

13. Alphabetical list of genera included in volumes 2-7.

Below is a list of basidiomycete genera currently known from arctic-alpine regions (November 2025), and the volumes in which they appear. New genera may later be found in the fungarium, and some names may be dropped due to misidentification. Names are also prone to change following new DNA evidence.

Inonotus	4
Jamesdicksonia	3
Kneiffiella	4
Kuehneromyces	7
Laccaria	6
Lacrymaria	6
Lactarius	4
Leccinum	5
Lentinellus	4
Lepidomyces	5
Lepiota	6
Lepista	5
Leptosporomyces	5
Leratiomyces	7
Lichenomphalia	5
Loreleia	4
Lycoperdon	6
Lyophyllum	5
Macrotyphula	5
Mallocybe	7
Marasmius	5
Melanoleuca	5
Merismodes	5
Microbotryum	3
Mucronella	5
Multiclavula	4
Muscinupta	4
Mycena	5
Mycenella	5
Mycocalia	5
Mythicomyces	6
Myxarium	5
Myxomphalia	5
Naucoria	7
Omphalina	5
Orphanomyces	3
Panaeolus	7
Panellus	5
Parasola	6
Paullicorticium	4
Paxillus	5
Pellidiscus	7
Peniophora	4
Phaeogalera	7
Phaeomarasmius	7
Phaeonematoloma	7
Phaeotremella	5
Phanerochaete	4
Phellinus	4
Phlebia	4
Pholiota	7
Pholiotina	6
Planetella	3
Pleurotus	5
Plicatura	5
Pluteus	6
Polyporus	4
Postia	4
Psathyrella	6
Pseudobaeospora	5
Pseudochaete	4
Pseudosperma	7
Pseudotomentella	4
Psilocybe	7
Pterula	5
Puccinia	2
Radulomyces	5
Ramaria	5
Ramariopsis	5
Rectipilus	5
Resupinatus	5
Rhizoctonia	5
Rhodocollybia	5
Rhodocybe	6
Rickenella	4
Rimbachia	5
Ripartites	5
Rugosomyces	5
Russula	4
Saccosoma	3
Sarcomyxa	5
Schizonella	3
Scopuloides	4
Scytinostroma	4
Sebacina	3
Simocybe	7
Sistotrema	4
Sistotremastrum	4
Sphaerobolus	5
Steccherinum	4
Stegocintractia	3
Stereum	4
Stromatocyphella	5
Stropharia	7
Stypella	5
Subulicystidium	4
Tectella	5
Thelephora	4
Tilletia	3
Tomentella	4
Trametes	4
Tranzschelia	2
Tranzscheliella	3
Trechispora	4
Tremella	5
Tricholoma	5
Tubaria	7
Tubulicrinis	4
Tulasnella	5
Typhula	5
Tyromyces	4
Urocystis	3
Uromyces	3
Ustilago	3
Ustilentyloma	3
Vararia	4
Xerocomus	5
Xeromphalina	5
Xylodon	4

14. Literature

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