A 200-year history of arctic and alpine fungi in North America: Early sailing expeditions to the molecular era

Chance Noftsinger\textsuperscript{a}, Cathy L. Cripps\textsuperscript{b}, and Egon Horak\textsuperscript{b}

\textsuperscript{a}Department of Plant Sciences and Plant Pathology, Montana State University, Bozeman, Montana, USA; \textsuperscript{b}Innbruck, Austria

**ABSTRACT**

Mushrooms and other fleshy fungi are important components of arctic and alpine habitats where they enhance nutrient uptake in plants and replenish poor soils through decomposition. Here we assemble the 200-year (1819–2019) record of their discovery in North America, beginning with early Arctic sailing expeditions, followed by intense taxonomic studies, and concluding with the molecular era, all of which highlight the difficulty of exhaustively revealing their biodiversity in these extreme, cold-dominated habitats. Compiled biogeographic data reveal that a majority of arctic fungi have large intercontinental distributions with disjunct alpine populations. A newly compiled checklist of 170 species of Basidiomycota in fifty-one genera and twenty families in the Rocky Mountain alpine zone provides current baseline data prior to expected environmental shifts.

**Introduction**

Alpine fungi exist at high elevations above treeline on mountaintops and plateaus, and their arctic counterparts occur beyond trees at high latitudes. In the Northern Hemisphere, fungi in these cold-dominated regions make up the ecologically important arcto-alpine mycota. These fungi exist as mutualists that enhance nutrient uptake in alpine plants; as decomposers that replenish nutrients in poor alpine soils; and as pathogens that affect alpine plant populations (Körner 1999; Haselwandter 2007). Those Basidiomycota that produce mushrooms or other kinds of visible fleshy fruiting bodies (i.e., basidiomes) are the focus of this review (Figure 1); the crust-like thelephoroids and Sebacinales are not covered. At treeline, all trees are associated with ectomycorrhizal fungi (Körner 2012), many of which produce basidiomes; above and beyond the trees, Salix, Betula, and Dryas are the primary ectomycorrhizal hosts (Cripps and Eddington 2005; Figure 2), although there are potential associations with Bistorta, Kobresia, and Helianthemum. In these habitats, cold-loving fungal decomposers fruit on bryophytes, willow branches, and soil; ascomycens attach themselves to rocks or soil; and basidiolichens exist on mud flats in association with algae (Dahlberg and Bültmann 2013). Without these fungi, plant life would be sparser in the cold-dominated arctic–alpine biome that covers 8 percent of the Earth (Körner 1995).

The story of the discovery of alpine mushrooms as scientific entities began in Europe, where significant knowledge has been amassed over decades. The father of alpine mycology, Jules Favre, spent twenty-one years examining the mushrooms above treeline in the Swiss National Park, hiking to higher elevations to collect specimens (Favre 1955; Horak 1993; reviewed in Brunner et al. 2017). Other mycologists soon followed his example in the high Alps, Pyrenees, and Carpathians, including Bon (1985, 1987, 1991, 1993), Kühner (1975), Lamoure (1982), Horak (1987a, 1987b), Senn-Irlet (1987), Graf (1994), Peintner and Moser (1996), Jamoni (1995, 2008), Bizio (1995, 1997), Ronikier (2008), and Corriol (2008). In North America, research has lagged behind, and no comprehensive review of the history and current knowledge of the diversity of alpine and arctic mushrooms has been compiled for this continent.

Greenland is considered part of North America, however, and arctic and alpine mushrooms in Greenland have been studied extensively (Lange 1957; Peterson 1977; Knudsen and Borgen 1982; Borgen 2006; Borgen, Elborne, and Knudsen 2006), and the data have been summarized in “Arctic and Alpine Mycology 6” (Boertmann and Knudsen...
Figure 1. Fleshy fruiting bodies of Rocky Mountain alpine fungi. (a) Arrhenia lobata, decomposer on Salix. (b) Rhizomarasmius epidryas, decomposer on Dryas octopetala. (c) Galerina, decomposer on moss. (d) Lichenomphalia basidiiomench. (e) Melampsora epitea, rust pathogen on Salix reticulata. (f) Lactarius lanceolatus, ectomycorrhizal with S. reticulata. (g) Russula nana, ectomycorrhizal with dwarf Salix. (h) Cortinarius absarokensis, a North American ectomycorrhizal endemic.
2006); these data are excluded from this work. Similarly, there has been significant research on the mushrooms inhabiting the arctic islands of Svalbard (Gulden, Jenssen, and Stordal 1985; Skifte 1989; Gulden and Torkelsen 1996) and Iceland (Christiansen 1941; Hallgrimsson 1998), and this information is similarly excluded.
Early expeditions to the Canadian Arctic (1819–1940)

Early exploration to discover fungi in cold climates in North America focused on Canada, where sailing ships provided access to remote Arctic lands to discover macrofungi (Linder 1947; Savile 1963; Estey 1994; Redhead and Baillargeon 1999; Väre 2017). During the nineteenth century, Arctic expeditions exploring the polar regions of North America were funded by wealthy businessmen or were supported by government agencies (Berkeley 1878; Rostrup and Simmons 1906; Lind 1910; Dearness 1923; Nares 2011). Botanical collections were of primary interest to scientifically minded individuals on these early expeditions. Nicholas Polunin summarizes the various accounts of these collectors in *Botany of the Canadian Eastern Arctic*, parts I and II (Polunin 1940, 1947). Historically, mycologists began investigating arctic fungi by examining the dried vascular plant material brought back by botanists for attached saprophytic or parasitic fungi (Linder 1947; Savile 1963). Occasionally, collectors brought back large, fleshy fungi from these expeditions; however, these were usually not identifiable due to improper handling and storage (Linder 1947; Savile 1963).

Starting in 1819, Captain William Edward Parry led two ships through the Canadian Archipelago on what would later be deemed the most successful attempt to find the Northwest Passage. The ships wintered at Melville Island, and in 1820 officers of the voyage collected *Cantharellus lobatus* (now called *Arrhenia lobata*) (Figure 1a), *Lycoperdon pratense* (a puffball), and fifteen species of lichens on the island (Brown 1823). According to Redhead and Baillargeon (1999), these two collections are the earliest published record of any agaric in Canada. Other Arctic expeditions followed, and their findings on the larger fleshy fungi are summarized in Table 1. Many of the taxa are known today under different names.

Captain Sir John Franklin’s second overland expedition (1825–1827) crossed through the Canadian Arctic via the Northwest Territories and reached the Arctic Ocean (Berkeley 1839; Väre 2017). John Richardson, a surgeon on board, made fungal collections that were eventually placed in the prestigious herbarium of Sir William Jackson Hooker, who became director of the Herbarium at Kew (Great Britain) in 1841 (Desmond 1995), and these are reported in Rev. Miles Joseph Berkeley’s (1839) paper on exotic fungi.

Franklin and 129 men were lost when two ships went down traversing the last unknown sections of the Northwest Passage around 1845 (Neatby and Mercer 2008); arctic fungi were collected on two expeditions funded by Lady Jane Franklin for the purpose of finding her husband’s lost remains. The search expedition led by Admiral Edward Belcher in 1852 set out with at least four ships, and only one returned. David Lyall, a physician and naturalist with the returning ship, again reported *Cantharellus lobatus* (now called *Arrhenia lobata*) in 1853 at Wellington Channel (Polunin 1940). This was the first confirmed collection (based on preserved material) of *A. lobata* from North America, and it was placed in the Herbarium at Kew (Redhead 1984b). The last expedition that set out to search for Franklin’s party in 1857 was led by Sir Francis Leopold M’Clintock; this was in the yacht Fox, a boat purchased by Lady Franklin (M’Clintock 1860).

David Walker, a surgeon and naturalist, collected five basidiomycetes and one ascomycete (Hooker 1860; Table 1). Walker’s collections were given to Sir Joseph Dalton Hooker, who passed them on to Berkeley (Hooker 1860). Berkeley subsequently published on twenty-six species (twenty-three species from Arctic Canada and three from Greenland) of Basidiomycota and Ascomycota collected during the Arctic Expedition from 1875 to 1876 (Berkeley 1878; Table 1).

In 1904, Pier A. Saccardo, Charles H. Peck, and William Trelease published a list of all known fungi in Alaska, including those collected by Trelease on the Harriman Alaska Expedition of 1899 (Trelease 1904). Three new species of arctic microfungi were described and four other arctic species were collected from Point Barrow (Saccardo, Peck, and Trelease 1904). In 1906, Emil Rostrup began careful examination of botanical collections made by Herman George Simmons during the second voyage of the Fram Expedition (1898–1902). These were collected on Ellesmere Island in Northern Canada, and eight new species of fungi were found on the dried plant specimens (Rostrup and Simmons 1906; Table 1). The Gjoa expedition under Captain Roald Amundsen from 1903 to 1906 visited King Point on the Yukon Coast and King William Island. Fungal collections were observed on leaves and stems by Jens Lind (1910), who noted the difficulty of identifying fungi that were deformed by the cold temperatures and exposed habitats of the Arctic, a problem still facing mycologists today. In 1909, the American agrostologist Albert S. Hitchcock traveled through the Alaskan interior looking at various grasses. He collected arctic uredineous rust fungi near Nome, which he shared with Joseph C. Arthur (Arthur 1911).

In 1923, John Dearness of London, Ontario, examined over a hundred fungi collected by the naturalists of the Southern Party from the Canadian Arctic expeditions (Dearness 1923; Table 1). He noted the wide host range...
Table 1. Mushrooms and fleshy fungi collected during early North American Arctic expeditions, 1819–1931. Names and authorities as reported.

| Expedition | Species reported | Location | Citation |
|------------|------------------|----------|----------|
| Captain William Edward Parry’s expedition (1819–1820) Basidiomycota: *Cantharellus lobatus* Peck and *Lycoperdon pratense* Pers. | Melville Island, Canadian Arctic Archipelago | Brown (1823) |
| Captain Sir John Franklin’s second overland expedition (1825–1827) Basidiomycota: *Cantharellus canadensis* KL. MSS., *Favolus* (Pleurotus) *humboldtii* Berk., *Favolus* (Pleurotus) *hepaticus* KL., and *Favolus* (Pleurotus) *canadensis* KL. l. c. Basidiomycota: *Cantharellus lobatus* Peck | Northwest Territories and arctic regions in Canada | Berkeley (1839) |
| Arctic expedition led by Admiral Belcher in (1852–1854) Basidiomycota: *Agaricus aliosporus* Berk., *Agaricus cyathiformis* Bull., *Agaricus furfuraceus* P., *Agaricus vaginatus* Bull., and *Agaricus umbelligerus* L. | Wellington Channel, Nunavut, Canada | Polunin (1940) |
| Sir Francis Leopold McClintock’s expedition in the yacht Fox (1857–1859) Ascomycota: *Peziza stercorea* P. and *Urnula hartii* B., Basidiomycota: *Agaricus* (Citopilus) *undatus* Fr., *Agaricus* (Naucoria) *bellotianus* B., *Agaricus* (Omphalia) *umbiliferus* L., *Agaricus* (Omphalia) *umbilicatus* Schaeff., *Agaricus* (Stropharia) *feildeni* B., *Agaricus* (Tubaria) *fur furaceus* P., *Agaricus* (Tubaria) *pellucidas* Bull., *Cantharellus muscigenus* Fr., *Hygrophorus miniatus* Fr., *Hygrophorus virgineus* Fr., *Lycoperdon atrapipureum* Vitt., *Lycoperdon cretsasum* B., *Merulis aurantaciaca* Fr., and *Russula integra* Fr. | Boothia Peninsula, Nunavut, Canada | Hooker (1860) |
| Arctic expedition from 1875 to 1876 Basidiomycota: *Aurantia bunapius* Berk., *Aurantia gyniods* Bull., *Agaricus* (Berk.) *lloydii* Fr., and *Agaricus* (Berk.) *lloydii* Fr. | Northern Nunavut, Canada | Berkeley (1878) |
| Second voyage of the Fram Expedition (1898–1902) Ascomycota: *Mellisia grammis* (Desm.), *Niptera melaleuca* (Lasch.), and *Sclerotinia vahliana* Rostr. Basidiomycota: *Cantharellus lobatus* (Pers.), *Collybia dryophila* (Bull), *Galeria hymnorum* (Batsch), *Hebeloma fastibile* (Fr.), *Lycoperdon gemmatum* (Batsch), *Myecena pumila* (Bull), *Naucoria festiva* (Fr.), *Naucoria melinoides* (Fr.), *Naucoria nimosa* (Fr.), *Omphalia umbilicata* (L.), *Psalliota campestris* (L.), *Psalliota rodonia* (Peck), *Pseudephrylla polaris* n. sp., *Russula lutea* (Huds.), and *Tricholoma caesatum* (Fr.) | Ellesmere Island, Nunavut, Canada | Rostrup and Simmons (1906) |
| Canadian Arctic Expedition (1913–1918) Basidiomycota: *Pezza microspor* Pers. var. *flavidus* Phil., *Scleroderris fuliginosa* (Fr.) Karst., and *Sclerotinia scutellata* (L.) Basidiomycota: *Boletus scaber* Fr., *Cantharellus muscigenus* Fr., *Clavatia createa* (Berk.) Lloyd, *Galeria hymnorum* Batsch., *Hebeloma fastibile* Fr., *Hygrophorus cantharellus* Fr., *Hygrophorus sp., Inocybe floculosa* Berk., *Lycoperdon umbirum* Pers., *Naucoria sp., Omphalia umbilicata* Fr., and *Russula sp. | Northern regions of Nunavut, Northwest Territories, and the Yukon, Canada | Dearness (1923) |
| Oxford Exploration Club’s 1931 expedition to Akpatok Island Ascomycota: *Helvella lucuosa* Afs., *Pezza acutabulum* L., and *Sphaerospora asperina* (Nyl.) Sacc. Basidiomycota: *Boletus reticulatus* (Schaeff.) Boud., *Boletus sp., Cantharellus cibarius* Fr., *Cortinarius spp., Dictyolus muscigena* (Bull.) Quél., *Hygrophorus sp., Hypholoma sp., Inocybe-violacea Pat., Inocybe sp., *Laccaria lacca* (Scop.) B. & Br., *Lactarius Velleurus* Fr., *Lycoperdon perlatum* Pers., *Lycoperdon sp., Mycena polygramma* Quél., *Mycena spp., Omphalia sp., Psiocybe seminianatea* Fr., *Russula emetica* Fr., *Russula ochroleuca* Fr., and *Russula sp. | Akpatok Island, Nunavut, Canada | Polunin (1934) |

and relative lack of parasitic fungi, only recording three rusts (Pucciniales) and one smut (Ustilaginales). However, Savile (1963) explained these low numbers by pointing out that botanists avoid diseased plants in order to secure the best collections, leading early mycologists to underestimate parasitic fungal abundance in arctic environments. Dearness returned to the Basidiomycota after a half-century pause and focused on the fleshy fungi of southern Baffin Island (Dearness 1928). One of the last true Arctic expeditions was the Oxford Exploration Club’s 1931 excursion to Akpatok Island, after which Nicholas Polunin (1934) published a list of the twenty-four fungi he collected (Table 1). With a majority of Arctic North America mapped out and explored, expeditions began tapering off; however, detailed investigations of the fungi in these regions were just beginning. **Morphological studies of Arctic fleshy fungi**

Up until the 1950s, little detailed research had focused on the mushrooms and other fleshy fungi (Ascomycota and Basidiomycota) in the Arctic. In 1908, Elias J. Durand first confirmed Geoglossaceae (earth tongues) in arctic and subarctic regions of North America when he identified *Mitrula gracilis* in Labrador and Newfoundland (Durand 1908); others would also study Geoglossaceae in arctic regions (Mains 1955; Kankainen 1969). Durand noted that *M. gracilis* also had been collected in Greenland (Durand 1908) and appeared to have a wide distribution in arctic regions. Hugh S. Spence and Otto E. Jennings investigated the fleshy fungi of the Northwest Territories and on Southampton Island, respectively, and found species in the ectomycorrhizal genera *Boletus, Cortinarius, Hydnum, Hygrophorus, Lactarius,* and *Russula,* along
with the saprobic genera *Calvatia*, *Psathyrella*, and *Tubaria*, some of which were from arctic habitats (Spence 1932; Jennings 1936). David H. Linder (1947) summarized the current knowledge regarding fungi found in the Canadian eastern Arctic, coming to some conclusions that were ahead of his time. Linder recognized that fungi found in arctic habitats appeared to have circumpolar distributions and shared similarities with their alpine counterparts at lower latitudes. He also noted the parallels between distributions of arctic–alpine fungi and flowering plants, indicating that the study of fungi may substantiate theories concerning distributions of phanerogams.

During the 1950s several mycologists began focusing on fungi in Northern Canada and Alaska. Edith K. Cash compiled a list of all known fungi and Myxomycetes in Alaska, which consisted of 843 species names that included plant parasites, saprobic micromycetes, and basidymycetes collected in the northern arctic regions of the state (Cash 1953). Howard E. Bigelow studied collections secured by government biological survey parties that included Arctic collections in the Tricholomataceae (Bigelow 1959), and he contributed knowledge on arctic *Omphalina* in Alaska and Canada (Bigelow 1970). In the 1960s, research was also expanding to include ecological investigations in arctic regions. Sprague and Lawrence (1959, 1959–1960, 1960) published a three-part series with the goal of understanding the effects of deglaciation on pedological, botanical, and fungal development. Japanese mycologist Yosio Kobayasi and his team arrived in Point Barrow, Alaska, on 1 August 1965 and began three weeks of exploration in the region. They primarily isolated fungi from soil, dung, water (water molds), plant material, animal bones, and insects (in an unsuccessful search for Trichomycetes). However, they reported several species of larger fleshly fungi, including two Ascomycota (*Peziza* species) and forty-nine Basidymycota in Hygrophoraceae, Tricholomataceae, Amanitaceae, Agaricaceae, Coprinaceae, Strophariaceae, Cortinariaceae, Boletaceae, Russulaceae, and Lycoperdaceae (Kobayasi et al. 1967). Like Kobayasi, John A. Parmelee primarily studied micromycetes in the Canadian Arctic; however, his work also expanded our knowledge of larger mycorrhizal fungi on central Baffin Island (Parmelee 1969).

Toward the end of the 1960s, Orson K. Miller Jr., a mycologist trained under Alexander Smith, became interested in arctic fungi after visits to Alaska with Robert L. Gilbertson in 1967 and 1968 (Cripps 2010). Miller’s interest in arctic fungi would last for the next thirty years, and he inspired several students and colleagues to examine the understudied fungi in these remote regions. Miller published three papers on Gasteromycetes (puffballs) from the Yukon territory and adjacent Alaska; he was considered an expert on this group (Miller 1968, 1969; Miller et al. 1980). Miller then turned his attention to the arctic and subarctic agarics (gilled mushrooms) of Canada and Alaska, publishing on *Coprinus* with Roy Watling (Watling and Miller 1971); *Omphalina*, *Laccaria*, and *Coprinus* with David F. Farr (Farr and Miller 1972); and *Melanoleuca* with Linnea S. Gillman (Gillman and Miller 1977). Miller’s student, Gary Laursen, spent most of his career in Alaska, and he and Miller published on arctic and alpine agarics in Alaska and Canada (Miller, Laursen, and Murray 1973; Miller, Laursen, and Calhoun 1974; Laursen, Miller, and Bigelow 1976) and on the function, distribution, and known plant associates of mycorrhizal fungi of the Alaskan tundra (Miller and Laursen 1978; Miller 1982b). Laursen and Harold H. Burdsall Jr. reported the first hypogeous fungus from the Alaskan tundra, *Geopora cooperi*, in ectomycorrhizal association with *Salix alaxensis* (Laursen and Burdsall 1976). Rau (1977), another Miller student, studied fungi in decomposing litter from tundra plants near Barrow, Alaska, and student Robert Antibus reported on the ectomycorrhizal fungi with *Salix rotundifolia* (Antibus et al. 1981).

In the 1980s, the agaric genera *Lactarius*, *Cortinarius*, and family Hygrophoraceae in the Alaskan Arctic tundra were studied by Laursen and Joseph Ammirati (Ammirati and Laursen 1982; Laursen and Ammirati 1982a; Laursen, Ammirati, and Farr 1987a). Miller contributed to a review of the current taxonomic understanding of arctic fungi at Point Barrow, Alaska (Bunnell et al. 1980); he then went on to study the fleshly fungi of the subarctic tundra of Alaska and the Yukon (Miller 1982b, 1987), *Marasmius epydryas* with Scott Redhead (Redhead et al. 1982), *Phaeogalera* and *Galerina* with European mycologist Egon Horak (Horak and Miller 1992), *Cystoderma* (Miller 1993), and *Hebeloma* (Miller 1998). Miller’s in-depth knowledge of arctic fungi provided him with the basis to recognize the large intercontinental distribution of some fungal species (Miller, Laursen, and Farr 1982). Later he focused on three *Hebeloma* species in the alpine tundra of Colorado, recognizing that these species were also present in the arctic tundra of Europe (Miller and Evenson 2001).

While Miller and colleagues were exploring the Alaskan tundra, Canadian mycologist Scott Redhead provided clarification for the arctic species *Gerronema pseudogrisella* (Redhead 1980), published a detailed overview of *Arrhenia* in arctic North America (Redhead 1984b), studied agarics in wetlands of Canada (Redhead 1984a), and briefly recounted early agaricology for each Canadian territory, which included information on early arctic fungal collections (Redhead and Baillargeon 1999). Redhead (1989) also focused on
the biogeographical patterns of Canadian fungi and noted that fungal species found in the high Arctic and in alpine habitats appeared to have intercontinental distributions that match arctic and alpine floristic patterns. Around the same time, Hutchinson, Summerbell, and Malloch (1988) noticed that a majority of the fungi they collected in Northern Quebec were also represented in arctic regions of Greenland and Northern Europe (Gulden, Jenssen, and Stordal 1985; Bresinsky 1987; Watling 1987). The observations of Durand (1908), Linder (1947), Miller, Laursen, and Farr (1982), Redhead (1984b), and Hutchinson, Summerbell, and Malloch (1988) supported the hypothesis that a majority of arctic fungi have large intercontinental distributions with disjunct distributions in the alpine, an idea that would continue to dominate arctic and alpine mycological and botanical research.

Several Finnish mycologists visited arctic habitats in North America. Heli Heikkila and Paavo Kallio from Finland showed Omphalina to be one of the most common agaric genera in the arctic habitats of Northern Canada (Heikkila and Kallio 1966, 1969), and Kallio (1980) surveyed the subarctic fungi of Schefferville, noting similarities to Finnish species. Seppo Huhtinen (1982, 1985) reported on the Pezizales and Helotiales in Northern Labrador and Quebec, finding sixteen new species of these Ascomycota in North America. Finnish mycologists Esteri Ohenoja and Martti Ohenoja made trips to the Canadian Arctic, more specifically to Hudson Bay in 1971 and 1974 (Northwest Territories and Manitoba). Working independently and in collaboration with various authors, they studied Lactarius (Ohenoja and Ohenoja 1993); Inocybe (Ohenoja, Vauras, and Ohenoja 1998); Marasmius epityrs (Redhead et al. 1982); Ascomycota in Finland, noting that some distributions extended into North America (Ohenoja 1975); and fungal diversity at Rankin Inlet (Ohenoja 1972). They subsequently summarized their findings, primarily of agars in the Canadian Arctic (Ohenoja and Ohenoja 2010), in Arctic and Alpine Mycology 8 (Cripps and Ammirati 2010). Norwegian mycologist Gro Gulden contributed knowledge on arctic and alpine species of Lepista from Alaska (Gulden 1983) and Galerina from Schefferville, Quebec (Noordeloos and Gulden 1992).

**International Symposia on Arctic and Alpine Mycology (1980–2020)**

On 16 August 1980, during the fruiting period for arctic and alpine fungi, an esteemed group of twenty-five mycologists from nine countries met at the Naval Arctic Research station in Point Barrow, Alaska. The First International Symposium on Arcto-Alpine Mycology (ISAM) was organized by acting president Gary Laursen. Many arctic and alpine mycologists were in attendance, including Savile, Miller, Kobayasi, Moser, Lamoure, Lange, Knudsen, and Horak. The symposium’s goal was to better understand fungi in arctic and alpine ecosystems, and the weeklong meeting produced valuable taxonomic information regarding the fungal community at Point Barrow (Laursen and Ammirati 1982a, 1982b). The format of the meeting consisted of several days of collecting fungi in the field followed by evening lectures to discuss proposed contributions to the proceedings. Because of the relative lack of knowledge on arctic–alpine fungi, the first ISAM focused on determining which fungi were present in these habitats. Fungal taxonomy would continue to dominate subsequent meetings.

After the first ISAM, it was decided that a select group of professional arctic and alpine mycologists would meet every four years in various countries to advance the knowledge of arctic and alpine fungi. At the end of each symposium, a representative would be selected to organize and act as sitting president for the next meeting. The format of the first ISAM has persisted through all ten symposia over thirty-six years, and more than one hundred different researchers have been involved in ISAM since its inception (Gulden and Høiland 2008; Cripps and Ammirati 2010). Each ISAM was held at an iconic arctic or alpine location, and all have improved our understanding of fungi in these environments. Table 2 summarizes the research published in each proceedings that contributes information on arctic and alpine mycology in North America. The eleventh symposium is scheduled to be held in the Altai Mountains of Russia in 2021, with hosts Victor Muhkin and Anton Shiryaev.

**Alpine mushrooms of the Rocky Mountains**

Many mycologists have focused their attention on arctic fungi in Alaska and Canada over the last century, but little attention was paid to the alpine fungi in the mountainous regions of the continent. At the beginning of the twentieth century, researchers began reporting fleshy fungi from the Rockies (Overholtz 1919; Kauffman 1921; Seaver and Shope 1930; Solheim 1949; Smith 1975); however, no substantial research on true alpine fungi above treeline took place until the 1980s. Meinhard Moser, an Austrian mycologist, made several collecting trips to North America and visited alpine habitats in Yellowstone National Park, the Beartooth Plateau in Montana and Wyoming, and the Windriver Mountains of Wyoming. Moser primarily described Cortinarius species from these regions, including the endemic C. absarokensis, but he also reported the iconic Russula nana (Figure 1g) for the first time from the...
Table 2. Research in the proceedings of the international symposia on arctic and alpine mycology focused on North American fungi.

| Symposium | Research |
|-----------|----------|
| 1st ISAM, August 1980. Barrow, Alaska | Basidiomycetes in subarctic Alaska (Miller 1982a; 1982b), Cortinarius in Alaska (Ammirati and Laursen 1982), Lactarius in Alaska (Laursen and Ammirati 1982), lower fungi in the Arctic (Kobayasi 1982), soil fungi in arctic tundra (Laursen and Chimelowski 1982), and mycorrhizal associations with Salix rutilidfolia (Linkins and Antibus 1982) |
| 2nd ISAM, August 1984. Swiss National Park, Switzerland | Basidiomycetes in the Rocky Mountain alpine (Moser and McKnight 1987), Cortinariaceae in the Yukon Territory of Alaska (Miller 1987), and Hygrophoraceae in the arctic–alpine tundra of Alaska (Laursen, Ammirati, and Farr 1987a) |
| 3rd ISAM, August 1988. Svalbard | The 3rd and 4th ISAM were combined into one proceeding and the following research related to arctic and alpine mycology in North America was included: Cystoderma in Alaska (Miller 1993), Lactarius in arctic Canada (Ohenoja and Ohenoja 1993), and Myxomycetes in the Alaskan tundra (Stephenson and Laursen 1993) |
| 4th ISAM, August 1992. Lanskebourg, France | Hebeloma from Alaska (Miller 1998), Inocybe species from arctic Canada (Ohenoja, Vauras, and Ohenoja 1998) |
| 5th ISAM, August 1996. Polar Utahs, Russia | Anthelia auriscalpium in Colorado (Cripps and Horak 2006) and Agrocybe praeclara in the Rocky Mountain alpine region (Moser and Horak 2006) |
| 6th ISAM, August 2000. Greenland | Cortinarius in the Rocky Mountain alpine (Peintner 2008) and a checklist of agarics from the Rocky Mountain alpine zone (Cripps and Horak 2008) |
| 7th ISAM, August 2005. Finse, Norway | Amarela found on the Beartooth Plateau (Cripps and Horak 2010), Marasmius epitys in the Rocky Mountain alpne (Roniker and Roniker 2010), Hebeloma hiemae in the Rocky Mountain alpine (Becker, Eberhardt, and Vesterholt 2010), larger fungi in arctic and subarctic Canada (Ohenoja and Ohenoja 2010), Inocybe (Mallophyte) in the Rocky Mountain alpine (Cripps, Larsson, and Horak 2010), Lycoperdaceae on the Beartooth Plateau (Kasuya 2010), Jalinik 2010, and Mollisio Ascomycetese on the Beartooth Plateau (Nauta 2010) |
| 8th ISAM, August 2008. Beartooth Plateau, Montana/Wyoming | Inocybe leiocephala, a species with an intercontinental distribution (Larsson, Vauras, and Cripps 2014), and Lactarius from the Rocky Mountain alpine zone (Cripps and Barge 2014) |
| 9th ISAM, August 2012. Utsjoki, Finland | Inocybe arctica and other species later reported in the North American alpine (Larsson, Vauras, and Cripps 2018) |
| 10th ISAM, August 2016. Kanazawa, Japan | Acting president: Gary Laursen, Publication Editor(s): Laursen and Ammirati (1982a) |

| Acting president | Publication Editor(s) |
|-----------------|------------------------|
| Gary Laursen | Laursen and Ammirati (1982a) |
| Egon Horak | Laursen, Ammirati, and Redhead (1997b) |
| Sigmund Sivertsen | Petrini and Laursen (1993) |
| Denise Lamoure | Petrini and Laursen (1993) |
| Viktork Mukhin | Mukhin and Knudsen (1998) |
| Torbjorn Borgen | Boetmman and Knudsen (2006) |
| Gro Gulden | Gulden and Hailand (2008) |
| Cathy Cripps | Cripps and Ammirati (2010) |
| Esteri Ohenoja | Ohenoja, Ruotsalaninen, and Vauras (2018) |
| Tamotsu Hoshino | Hoshino et al. (2018) |
Rocky Mountain alpine (Moser and McKnight 1987; Moser 1993; Moser, McKnight, and Sigl 1994; Moser, McKnight, and Ammirati 1995). Redhead (1984b) reported *Arrhenia lobata* from Colorado after examining several of Alexander H. Smith’s collections from the Rocky Mountain alpine; *A. lobata*, usually growing on moss, is a common arctic–alpine species known from the Alps, Greenland, and Iceland; this species was previously referred to as *Cantharellus lobatus* on early Arctic expeditions.

Research into the fleshy fungi of alpine regions in North America, and especially the Rocky Mountains, was about to increase substantially. In 1996, Monique Gardes and Anders Dahlberg published a review on the diversity of mycorrhizal fungi in arctic and alpine regions. They observed the roots of mycorrhizal plant hosts and provided an overview of the mycorrhizal fungal genera present. Gardes and Dahlberg (1996) studied various mycorrhizal associations, including arbuscular mycorrhizae, dark septate fungi, ectomycorrhizae, and ericoid mycorrhizas. The occurrence of these mycorrhizal types is variable, and certain arctic–alpine plants lack mycorrhizal associations completely (Gardes and Dahlberg 1996). In general terms, Gardes and Dahlberg identified the known mycorrhizal associations in cold-dominated environments as a potential model for understanding the evolution of mycorrhizal symbioses. They outlined future research questions requiring investigation and focused on the potential use of molecular tools to answer questions about fungal diversity and on mycorrhizal community structure and dynamics. Their review set the stage for future research into mycorrhizal fungi in alpine areas, especially for the Rocky Mountains.

A National Science Foundation–funded survey of alpine fungi in the Rocky Mountains commenced in 1999, led by Cathy Cripps and Egon Horak. They were the first to survey alpine fungi in the Rocky Mountains on a large scale, and their work focused on the central and southern regions. That same year, they presented a preliminary report on mushrooms in the Rocky Mountain alpine zone at the International Botanical Congress (Cripps and Horak 1999) and later disseminated information on alpine ectomycorrhizal species of *Amanita*, *Inocybe*, *Russula*, *Lactarius*, and *Hebeloma* at subsequent conferences (Cripps and Horak 2002; Cripps 2003; Cripps and Horak 2005, 2007; Cripps, Horak, and Mohatt 2008). This led to a paper that explored the diversity of *Amanita* in the Rocky Mountain alpine (Cripps and Horak 2010). A review paper on the mycorrhizal status of alpine plants, including those of the Beartooth Plateau, reported that 68 percent of alpine vascular plant species form mycorrhizal associations; the paper covered ecto-, arbuscular, ericoid, and arbutoid mycorrhizae, with arbuscular associations being the most common (Cripps and Eddington 2005). For decomposers, the well-known arcto-alpine fungus *Arrhenia auriscalpium* was reported in Colorado at the highest elevation (3,650 m) and the furthest latitude (39° N) south recorded for the fungus (Cripps and Horak 2006).

A preliminary list of alpine fungi in the Rocky Mountains was published in the proceedings of the seventh ISAM (Cripps and Horak 2008). It was estimated that at least 75 percent of the mushroom-producing fungi in the Rocky Mountain alpine appeared to be known from other arctic–alpine environments and that 25 percent were potentially endemic. Based on these findings, the most diverse mycorrhizal families in the Rocky Mountain alpine zone were reported to be the Cortiniaceae, Inocybaceae, and Hymenogastraceae (*Hebeloma*). It was hypothesized that the diverse geology, habitat, and mesic conditions of the southern Rockies led to more variation in habitat and thus greater fungal diversity than observed further north in Wyoming and Montana (Cripps and Horak 2008). However, the diversity of fungi that do not fruit above-ground was not assessed. Studies have shown that some, such as the Sebacinales, *Cenococcum*, and thelephoroids, can be dominant on roots in the alpine Alps (Ryberg, Larsson, and Molau 2009) and in the Arctic (Timling et al. 2014).

**The molecular era**

Early in the twenty-first century, molecular DNA methods became cheaper and easier to use, providing researchers with a powerful and independent way to verify taxonomic determinations based on morphology and to confirm intercontinental distributions. The nuclear ribosomal internal transcribed spacer (ITS) region eventually became commonly used as a universal DNA barcode marker for fungi (Schoch et al. 2012). Several of Cripps’ students investigated the fungi in the Rocky Mountain alpine zone using this method, focusing primarily on ectomycorrhizal genera. The genus *Laccaria* was investigated in the Rockies by Todd Osmundson (Osmundson, Cripps, and Mueller 2005). Phylogenetic analysis of the ITS region of ribosomal DNA, along with morphological and cultural data, revealed five species in the Rocky Mountain alpine zone. *Laccaria laccata* var. *pallidofolia* and *L. nobilis* were confirmed for the first time in alpine habitats and *L. pseudomontana* was described as new to science. The distribution, morphology, and phylogenetics of the genus *Lactarius* in the Rocky Mountain alpine zone was tackled by Ed Barge. Six species were reported, one new to science (*Lactarius pallidomargina*), and all but the new endemic were molecularly confirmed using ITS/RPB2 sequence data to have intercontinental distributions in arctic–alpine regions (Barge and Cripps 2016; Barge, Cripps, and Osmundson...
2016). It was hypothesized that species distributions may have been shaped by glaciation during the various ice ages, joint migration with host plants, and long-distance dispersal. The diversity of Russula in the Rocky Mountain alpine zone was examined by Chance Noffsinger using molecular (ITS/RPB2), morphological, and ecological data. Ten species were determined to be present, including the well-known Russula nana, R. laccata, and R. subrubens; all but a species near R. pascua were confirmed to have intercontinental distributions in arctic–alpine habitats (Noffsinger 2020). Additional molecular and morphological analyses have investigated the ectomycorrhizal genera Hebeloma (Becker, Eberhardt, and Vesterholt 2010; Cripps et al. 2019), Cortinarius (Peintner 2008), and Inocybe (Cripps, Larsson, and Horak 2010; Larsson, Vauras, and Cripps 2014, 2018; Cripps, Larsson, and Vauras 2020) in the Rocky Mountain alpine zone. All of these molecular studies have confirmed intercontinental distributions and disjunct populations of numerous alpine species, with the exception of Osmundson, Cripps, and Mueller (2005), where only North American collections were examined.

Biogeography of Arctic and alpine fungi in North America

In the last decade, there has been a dramatic increase in the number of studies concerned with the biogeography and distribution of arctic fungi in North America. József Geml, a mycologist from Hungary, assessed the biodiversity of Lactarius in arctic tundra and boreal forests of Alaska using 95 and 97 percent ITS sequence similarity. He found strong habitat preference and a high diversity in the genus, noting that species richness appeared to decrease with increasing latitude (Geml et al. 2009). However, this study used operational taxonomic units as a proxy for species, which is common in ecological studies but does not clearly delimit species. A few studies have hypothesized that long-distance dispersal might play an important role in the distribution of arctic fungal genera (Geml et al. 2012; Timling et al. 2014). Others have assessed how mycorrhizal fungi are affected by climate change and a warming Arctic (Deslippe and Simard 2011; Deslippe et al. 2012; Geml et al. 2015, 2016; Morgado et al. 2015; Semenova et al. 2016). The current status of fungal diversity knowledge, especially lichens, was reviewed in Dahlberg and Bültmann (2013). More recently, the taxonomic and ecological structure of larger fleshy fungi in polar deserts of the Northern Hemisphere was addressed by Shiryaev, Zmitrovich, and Ezhev (2018), the cold adaptation strategies of fungi in polar regions was covered by Tsuji and Hoshino (2019), and the upward shifts in fungal frutiings at treeline was reported by Diez et al. (2020).

Biodiversity of alpine mushrooms in North America: Current knowledge

Approximately 170 species in fifty-one genera in twenty families of Basidiomycota are confirmed from alpine areas of North America, primarily from the Rocky Mountains, and data are newly compiled in Table 3. Fifty of these have been molecularly confirmed to have an intercontinental distribution in arctic–alpine habitats using ITS/RPB2 sequence data (Table 1), and more have been sequenced. Many of these species have also been reported from the North American Arctic, but most are not yet molecularly confirmed (Ozenoja and Ozenoja 2010). Of these, 104 are ectomycorrhizal species (61 percent) and 66 are saprophytic species (39 percent). The most species-diverse genera are Cortinarius (35), Inocybe including Mallophyte and Inosperma (27), Hebeloma (16), Russula (10), Lactarius (6), Laccaria (5), Entoloma (5+), and Galerina (8). All are potentially ectomycorrhizal genera except for Galerina and some species of Entoloma (Graf and Brunner 1996; Rinaldi, Comandini, and Kuyper 2008). Though these often appear to be the most diverse genera in arctic and alpine habitats, as indicated by aboveground structures, it is also possible that there has been collecting bias. Moser intensely collected Cortinarius in the Telamonia group, which was his specialty, and a majority of species listed are in this subgenus. Similarly, Cripps and Horak focused on Inocybe and Hebeloma with Beker and Eberhardt. Cripps’ students, as noted above, intensely searched for Laccaria, Lactarius, and Russula. In addition, eleven species of puffballs in genera Bovista, Bovistella, Calvatia, and Lycopodium are reported, mostly by Taiga Kasuya of Japan, who attended ISAM 8 on the Beartooth Plateau (Kasuya 2010). Also, belowground data were not collected and, as mentioned before, it is possible that Sebacinaceae, Centococcum, and thelephoroids could be dominant on roots as is found elsewhere (Ryberg, Larsson, and Molau 2009; Timling et al. 2014), but it remains to be seen whether this is also true for this part of the Rockies.

At the International Mycological Congress in 2002 in Oslo, Norway, Moser gave a talk titled “How Alpine Are ‘Alpine’ Fungi?,” a question that could be considered for arctic fungi as well (Moser 2002). Almost all of the arctic and alpine species in North American that have been sequenced are now confirmed to have intercontinental distributions; they also occur in Svalbard, Greenland, or arctic–alpine Europe. However, a majority of the Inocybe species, half of the Hebelomas, Lactarii, and Russulas listed (Table 3), are also reported from subarctic or boreal habitats, sometimes with Salix. Those that associate with dwarf Salix—for example, Lactarius
### Table 3. Current list of species of alpine Agaricales, Russulales, Boletales, and Ascomycota from the Rocky Mountains of Colorado, Montana, and Wyoming collected at elevations of ca. 3,000 to 4,200 m.

#### BASIDIOMYCOTA

**AGARICALES**

| Taxon | Origin | Notes |
|-------|--------|-------|
| Agaricus | Fr. s.l. | \* |
| Agaricus campestris | Fr. | \* |

#### AGARICACEAE

| Taxon | Origin | Notes |
|-------|--------|-------|
| Arrhenia velutipes | Fr. | \* |
| Arrhenia auriscalpium | Fr. | \* |
| Laccaria pseudomontana | Fr. | \* |
| Laccaria pumila | Fr. | \* |
| Laccaria laccata | Fr. | \* |
| Laccaria nobilis | Fr. | \* |
| Malocybe substraminipes | Fr. | \* |
| Malocybe terrigena | Fr. | \* |
| Malocybe leucoloma | Fr. | \* |

#### HYMENOGASTRACEAE

| Taxon | Origin | Notes |
|-------|--------|-------|
| Inocybe alpinomarginata | C.L. | \* |
| Inocybe arctica | E. Larss. | \* |
| Inocybe balbissima | Kuehner | \* |
| Inocybe canescens | J. Favre | \* |
| Inocybe duclamara | (Pers.) | \* |
| Inocybe fraudans | (Bretzelm.) | \* |
| Inocybe giacomi | J. Favre | \* |
| Inocybe lacerca | (F. Kumm.) | \* |
| Inocybe leiocephala | D.E. | \* |
| Inocybe leonina | Estee-Rav. | \* |
| Inocybe leucodermata | Kuehner | \* |
| Inocybe melasmatipes | J. Favre | \* |
| Inocybe murina | E. Larss. | \* |
| Inocybe occulta | Estee-Rav., Bandini, B. Oertel & G. Moreno | \* |
| Inocybe paragiacomi | E. Larss., C.L. | \* |
| Inocybe phaeocystidiosa | Estee-Rav., G. Moreno & Bon & U. Eberh. | \* |
| Inocybe purpurpeoalba | Estee-Rav. & A. Caball. | \* |
| Inocybe rhacodes | J. Favre | \* |
| Inocybe subgigoci | C.L. | \* |
| Inocybe subgigoci | C.L. | \* |
| Inocybe subgigoci | C.L. | \* |
| Laccaria carniolica | F. | \* |
| Laccaria hygrophila | Peck & U. Eberh. | \* |
| Laccaria nigromontana | Kuehner | \* |
| Laccaria sublychna | Kuehner | \* |
| Laccaria subsimilis | Kuehner | \* |
| Laccaria substraminipes | Kuehner | \* |
| Laccaria tierannigra | (F. Kumm.) | \* |
| Laccaria vittata | (F. Kumm.) | \* |
| Malocybe hygropilosa | Estee-Rav. | \* |
| Malocybe montana | Estee-Rav. | \* |
| Malocybe pseudomontana | Osmundson, C.L. | \* |
| Malocybe velutipes | (P.D. Orton) | \* |

#### INOCYBACEAE

| Taxon | Origin | Notes |
|-------|--------|-------|
| Entoloma cetratum | M.M. | \* |
| Entoloma juncinum | Kuehner & Romagn. | \* |
| Entoloma sericeum | Quel. | \* |
| Rhodocybe cf. popinaulis | (Fr.) | \* |

#### HYGHROPHORACEAE

| Taxon | Origin | Notes |
|-------|--------|-------|
| Arthennia aceracea | Kuehner | \* |
| Arthennia auriscalpium | Fr. | \* |
| Arthennia lobata | Pers. | \* |
| Arthennia velutipes | (P.D. Orton) | \* |

(Continued)
Table 3. (Continued).

| Genus | Species | Author | Notes |
|-------|---------|--------|-------|
| **Gliophorus** | psittacinus | (Schaeff.) Herink | = Hygrocybe psittacina (Schaeff.) P. Kumm. |
| **Hygrocybe** | conica | (Schaeff.) P. Kumm. | |
| | marchii | (Bres.) F.H. Møller | |
| **Lichenomphalia** | sp. | | |
| **LYPHELLOLACEAE** | | | |
| **Calocybe** | chrysenteron | (Bull.) Singer | |
| | onychina | (Fr.) Donk | |
| **MARASMIACEAE** | | | |
| **Hydrelpus** | sp. | | |
| **Mycenaceae** | Hemimycena | sp. | |
| | Mycena pura | (Pers.) P. Kumm. | s.l. |
| **NIACEAE** | Flagellicyphus | sp. | |
| **PHYSALACEAE** | Flammulina | sp. | |
| **Rhizomarasmius** | epidiaphys | (Kühner ex A. Ronikier) A. Ronikier & Ronikier | |
| **STROPHARIACEAE** | Deconica | chionophila (Lamoure) Noordel. | |
| | elongatum | (Pers.) Ricken | |
| | Sterophoria | alpina | M. Lange |
| **TRICHOLOMATACEAE** | | | |
| **Clitocybe** | drydocola | (J. Favre) Harmaja | |
| | festivoides | Lamoure | |
| | Collybia | cookei | (Bres.) J.D. Arnold |
| | Dermaloma | sp. | |
| **Gamnindia** | leucophylla | (Gillet) H.E. Bigelow = Fayodia leucophylla (Gillet) M. Lange & Siwertzen | |
| | Lorelea | marchantiae | (Singer & Clémençon) Redhead, Moncalvo, Vilgalys & Lutzoni |
| | Melanoleuca | cognata | (Fr.) Konrad & Mouthbl. s.l. |
| | substrictipes | Kühner | |
| | Mycena | sp. | |
| | Omphalia | rivulicola | (J. Favre) Lamoure |
| **RUSSULALEAE** | | | |
| **Lactarius** | glycyronous | (Fr.) | |
| | lancerolatus | O.K. Miller & Laursen | |
| | nanus | J. Favre | |
| | pallidomarginatus | Barge & C. L. Cripps | |
| | represenentaenus | Britzelm. | |
| | salis-salicetorum | Kühner | |
| | altaica | (Singer) Singer | |
| | amoepoiesis | var. kutherriana | |
| | cf. heterochaeta | Kühner | |
| | intermedia | P. Kast | |
| | laevis | Käviäinen, Ruotsalainen & Taipale | |
| | laccata | Huijsmans | |
| | nana | Killerm. | |
| | purpureofusca | Kühner | |
| | salicetica | (Singer) Kühner ex Knudsen & T. Borgen | |
| **BOLETALES** | | | |
| **Boletaceae** | | | |
| **Leccinum** | rotundifolium | (Singer) A.H. Smith, Thiers & Watling | |
| **CANTHARELLES** | | | |
| **CANTHARELLACEAE** | | | |
| **Rickenella** | fhula | (Bull.) Raithelh. | |
| | swartzii | (Fr.) Kuyper | |
| **ASCOMYCOTA** | | | |
| **Bryoglossum** | gracile | (P. Kast.) Redhead | |
| | chioronia | (Vahl) T. Schumach. & L.M. Kohn | |
| | Marchella | sp. | |

Notes. 1Reported from Canadian Arctic, not molecularly confirmed (Ohoenoja and Ohoenoja 2010).  
2Genbank sequence available.  
3Interristeral distribution molecularly confirmed.  
4Cripps and Horak (2010).  
5Kasuya (2010).  
6Cripps, Unpublished. Representative specimens deposited in the fungal section of the MONT Herbarium, Bozeman, Montana.  
7Cripps and Horak (2010).  
8Mosler and Mcknight (1987).  
9Moser, Mcknight, and Ammariati (1995).  
10Cripps et al. (2019).  
11Cripps, Larsson, and Vauras (2010).  
12Larsson, Vauras, and Cripps (2014).  
13Osmundson, Cripps, and Mueller (2005).  
14Cripps and Horak (2006).  
15Barge, Cripps, and Osmundson (2016).  
16Barge and Cripps (2016).  
17Noftsinger (2020).
alpine areas of Europe, but progress is being made. Taxonomic baseline data are necessary for understanding evolutionary, physiological, biogeographical, and climate trends. Research has already shown that climate change is altering arctic and alpine habitats at alarming rates (Serreze and Barry 2011; IPCC 2014), which highlights the importance of understanding these communities prior to large environmental shifts.

Acknowledgments
We thank Almut Horak and Don Bachman, who have contributed to our alpine mycological endeavors in North America since 1999. We also thank Todd Osmundson, Leslie Eddington, Sara Klingsporn, Angela Imhof, Erin Lonergan, and Ed Barge, who contributed as students to this project.

Disclosure statement
No potential conflict of interest was reported by the authors.

Funding
We acknowledge the National Science Foundation for the original grant (9971210) that initiated the discipline of alpine mycology in the Rocky Mountains. Fieldwork was supported by the John W. Marr Fund provided by the University of Colorado Boulder.

ORCID
Cathy L. Cripps http://orcid.org/0000-0002-3402-2422

References
Ammirati, J. F., and G. A. Laursen. 1982. Cortinarii in Alaskan Arctic tundra. In Arctic and Alpine Mycology, The First International Symposium on Arcto-Alpine Mycology, ed. G. A. Laursen and J. F. Ammirati, 282–315. Seattle: University of Washington Press.
Antibus, R. K., J. G. Croxdale, O. K. Miller Jr., and A. E. Linkins. 1981. Ectomycorrhizal fungi of Salix rotundifolia. 3. Canadian Journal of Botany 59:2458–65. doi:10.1139/b81-297.
Arthur, J. C. 1911. Some Alaskan and Yukon rusts. The Plant World 14 (10):233–36.
Barge, E. G., and C. L. Cripps. 2016. New reports, phylogenetic analysis, and a key to Lactarius Pers. in the Greater Yellowstone Ecosystem informed by molecular data. MycoKeys 15:1–58. doi:10.3897/mycokeys.15.9587.
Barge, E. G., C. L. Cripps, and T. W. Osmundson. 2016. Systematics of the ectomycorrhizal genus Lactarius in the Rocky Mountain alpine zone. Mycologia 108 (2):414–40. doi:10.3852/15-177.
Becker, H. J., U. Eberhardt, and J. Vesterholt. 2010. Hebeloma hiemale Bres. in Arctic/Alpine Habitats. North American Fungi 5:51–65.
Berkeley, M. J. 1839. XLII. Descriptions of exotic fungi in the collection of Sir W. J. Hooker, from memoirs and notes of J. F. Klotzsch, with additions and corrections. Journal of Natural History 3 (19):375–401.
Berkeley, M. J. 1878. Enumeration of the fungi collected during the Arctic expedition, 1875–76. Journal of the Linnaean Society, Botany 17:13–17. doi:10.1111/j.1095-8339.1878.tb00453.x.
Bigelow, H. E. 1959. Notes of fungi from northern Canada IV. Tricholomataceae. Canadian Journal of Botany 37 (5):769–79. doi:10.1139/b59-062.
Bigelow, H. E. 1970. Omphalina in North America. Mycologia 62 (1):1–32. doi:10.1080/00275514.1970.12018941.
Bizio, E. 1995. Alcune Inocybe più frequenti della zona alpina delle Dolomiti. Rivista di Micologia 38 (2suppl.):1–60.
Bizio, E. 1997. Alcune Inocybe più frequenti della zona alpina delle Dolomiti: 2nd contribution. Rivista di Micologia 40 (4):339–62.
Boertmann, D., and H. Knudsen. 2006. Arcto and arctic mycology 6. Meddelelser om Grønland, Bioscience 56:1–161.
Bon, M. 1985. Stage Mycologie Alpine Lanslebourg (Savoie) du 1 au 3 septembre 1984. Bulletin trimestriel de la fédération mycologique dauphiné-savoie 96:19–25.
Bon, M. 1987. Quelques recoltes mycologiques de la zone alpine au 7ème convegno di micologia. Fiera di Primiero (Italie). Micologia Italiana 17 (3):267–70.
Bon, M. 1991. Inventaires des espèces récoltes au stage de mycologie alpine. Bulletin trimestriel de la fédération mycologique dauphiné-savoie 122:25–28.
Bon, M. 1993. Russules alpine nouvelles ou interessantes. Bulletin trimestriel de la fédération mycologique dauphiné-savoie 128:20–24.
Borgen, T. 2006. Distribution of selected basidiomycetes in oceanic dwarf-scrub heaths in the Paamiut area, low arctic South Greenland. Meddelelser om Grønland, Bioscience 56:25–36.
Borgen, T., S. A. Elborne, and H. Knudsen. 2006. A checklist of the Greenland basidiomycetes. Meddelelser om Grønland, Bioscience 56:37–59.
Bresinsky, A. 1987. Bemerkenswerte Grosspilzfunde in der Bundersrepublik Deutschland. Zeitschrift für Mykologie 53:289–302.
Brown, R. 1823. A list of plants collected in Melville Island in the year 1820; by the officers of the voyage of Discovery under the orders of Captain Parry. Chloris Melvilliana, 49. London: Printed by W. Clowes, Northumberland-Court, Strand.
Brunner, I., B. Frey, M. Hartmann, S. Zimmermann, F. Graf, L. M. Suz, T. Niskanen, M. I. Bidartondo, and B. Senn-Irlet. 2017. Ecology of alpine macrofungi-combining historical with recent data. Frontiers in Microbiology 8:e2066. doi:10.3389/fmicb.2017.02066.
Bunnell, F. L., O. K. Miller Jr., P. W. Flanagan, and R. E. Benoit. 1980. The microflora: Composition, biomass, and environmental relations. In An Arctic ecosystem. The coastal tundra at Barrow, Alaska. US/IBP synthesis series 120, ed. J. Brown, P. Miller, L. Tieszen, and F. L. Bunnell, 255–90. Stroudsburg, PA: Dowden, Hutchinson and Ross, Inc.
Cash, E. K. 1953. A checklist of Alaskan fungi. The Plant Disease Reporter 21:93–70.
Christiansen, M. P. 1941. Studies in the larger fungi of Iceland. The Botany of Iceland 3 (2):187–227.
Corriol, G. 2008. Checklist of Pyrenean alpine-stage macrofungi. Sommerrfelta 31:29–99. doi:10.2478/v10208-011-0004-6.

Cripps, C. and E. Barge. 2014. Notes on the genus Lactarius from the Rocky Mountain alpine zone in regard to Finnish arctic alpine species. Karstenia 53:29–37.

Cripps, C. L. 2003. Interesting distributions of ectomycorrhizal alpine fungi along the Rocky Mountain cordillera. Pacific Grove, CA: Mycological Society of America. July 27–31.

Cripps, C. L. 2010. Orson K. Miller Jr., 1930–2006. Mycologia 102 (5):1216–20. doi:10.3852/10-042.

Cripps, C. L., and E. Horak. 1999. Alpine Mycota (Agaricales) Rocky Mountain Tundra, USA: A preliminary report. St. Louis, MO: International Botanical Congress. August 6.

Cripps, C. L., and E. Horak. 2000. Alpine species of Lactarius in the Rocky Mountains. Corvallis, OR: Mycological Society of America. June 24–26.

Cripps, C. L., and E. Horak. 2005. Amanita in the Rocky Mountain Alpine Zone: Where mycorrhizal mushrooms tower over miniature forests. Hilo, HI: Joint meeting of Japanese Mycological Society and Mycological Society of America. July 30–August 5.

Cripps, C. L., and E. Horak. 2006. Arrhenia auriscalpium in arctic-alpine habitats: World distribution, ecology, new reports from the southern Rocky Mountains, USA. In Arctic and alpine mycology 6. Meddelelser om Grønland, Bioscience 56, ed. D. Boertmann and H. Knudsen, 17–24.

Cripps, C. L., and E. Horak. 2007. Alpine agarics with Dryas octopetala (Rosaceae) in arctic-alpine habitats of the Rocky Mountains (USA). Baton Rouge, LA: Mycological Society of American meeting. August 6–9.

Cripps, C. L., and E. Horak. 2008. Checklist and ecology of the Agaricales, Russulales and Boletales in the alpine zone of the Rocky Mountains (Colorado, Montana, Wyoming) at 3000–4000 m asl. Sommerrfelta 31:101–23. doi:10.2478/v10208-011-0005-5.

Cripps, C. L., and E. Horak. 2010. Amanita in the Rocky Mountain alpine zone, USA: New records for A. nivalis and A. groenlandica. North American Fungi 5:9–21.

Cripps, C. L., E. Horak, and K. Mohatt. 2008. Ectomycorrhizal fungi at alpine treeline in the Rocky Mountains: Baseline data and a review in the context of climate change. MTNCLIME. June 9–12. Consortium for Integrated Climate Change Research in Western Mountains, Silverton, CO.

Cripps, C. L., E. Larsson, and E. Horak. 2010. Subgenus Malloocybe (Inocybe) in the Rocky Mountain alpine zone with molecular reference to European arctic-alpine material. North American Fungi 5:97–126.

Cripps, C. L., E. Larsson, and J. Vaaras. 2020. Nodulate-spored Inocybe from the Rocky Mountain alpine zone molecularly linked to European and type specimens. Mycologia 121 (1):1–21.

Cripps, C. L., and J. Ammirati. 2010. Eighth International Symposium on Arctic-Alpine Mycology (ISAM 8), Beartooth Plateau, Rocky Mountains, USA 2008. North American Fungi 5:232.

Cripps, C. L., and L. H. Eddington. 2005. Distribution of mycorrhizal types among alpine vascular plant families on the Beartooth Plateau, Rocky Mountains, USA, in reference to large-scale patterns in arctic-alpine habitats. Arctic, Antarctic, and Alpine Research 37 (2):177–88. doi:10.1657/1523-0430(2005)037[0177:DOMTAA]2.0.CO;2.

Cripps, C. L., U. Eberhardt, N. Schütz, H. J. Beker, V. S. Ensonov, and E. Horak. 2019. The genus Hebeloma in the Rocky Mountain Alpine Zone. MycoKeys 46:1–54. doi:10.3897/mycokeys.46.32823.

Dahlberg, A., and H. Bülmann. 2013. Fungi. Chapter 10. In Arctic Biodiversity Assessment. Status and Trends in Arctic Biodiversity. Conservation of Arctic Flora and Fauna (CAFF), ed. H. Meltofte, 354–71. Denmark: Narayana Press.

Dearness, J. 1923. The fungi of the Arctic Coast of America West of the 100th meridian. Report of the Canadian Arctic Expedition 1913–1918. Volume IV: Botany. Part C. Fungi, 1–24. Ottawa: F. A. Acland.

Dearness, J. 1928. Report on fleshy fungi collected in August 1926. In A faunal investigation of southern Baffin Land. National Museum of Canada Bulletin no. 53 Biological Series, ed. J. D. Soper, 120–23. Ottawa: Dept. of Mines and Resources, National Museum of Canada.

Deslippe, J. R., M. Hartmann, S. W. Simard, and W. W. Mohn. 2012. Long-term warming alters the composition of Arctic soil microbial communities. FEMS Microbiology Ecology 82 (2):303–15. doi:10.1111/j.1574-6941.2012.01350.x.

Deslippe, J. R., and S. W. Simard. 2011. Below-ground carbon transfer among Betula nana may increase with warming in Arctic tundra. New Phytologist 192 (3):689–98. doi:10.1111/j.1469-8137.2011.03835.x.

Desmond, R. 1995. Kew: The history of the Royal Botanic Gardens, 150–238. London: The Harvill Press.

Diez, J., H. Kauserud, C. Andrew, E. Heegaard, I. Krisai-Greilhuber, B. Senn-Irlet, K. Høiland, S. Egli, and U. Büngetn. 2020. Alitudinal upwards shifts in fungal funneling in the Alps. Proceedings of the Royal Society B: Biological Sciences 287:20192348. doi:10.1098/rspb.2019.2348.

Durand, E. J. 1908. The Geoglossaceae of North America. Annales Mycologici 6:387–477.

Estey, R. H. 1994. Essays on the early history of plant pathology and mycology in Canada, 383. Montreal, QC: McGill-Queen’s University Press.

Farr, D. F., and O. K. Miller Jr. 1972. Notes on arctic and subarctic Basidiomycetes. Virginia Journal of Science 23:120.

Favre, J. 1955. Les champignons supérieurs de la zone alpine du Parc National Suisse. Resultats des recherches scientifiques entreprises au Parc National Suisse. Ergebnisse der wissenschaftlichen Untersuchungen des schweizerischen National Parks 5:212.

Gardes, M., and A. Dahlberg. 1996. Mycorrhizal diversity in Arctic and alpine tundra: An open question. New Phytologist 133 (1):147–57. doi:10.1111/j.1469-8137.1996.tb04350.x.

Geml, J., G. A. Laursen, I. Timling, J. M. McFarland, M. G. Booth, N. Lennon, C. Nusbaum, and D. L. Taylor. 2009. Molecular phylogenetic biodiversity assessment of arctic and boreal ectomycorrhizal Lactarius Pers. (Russulales; Basidiomycota) in Alaska, based on soil and sporocarp DNA. Molecular Ecology 18 (10):2213–27. doi:10.1111/j.1365-294X.2009.04192.x.

Geml, J., I. Timling, C. H. Robinson, N. Lennon, H. C. Nusbaum, C. Brochmann, M. E. Noordeloos, and D. L. Taylor. 2012. An arctic community of symbiotic fungi
assembled by long-distance dispersers: Phylogenetic diversity of ectomycorrhizal basidiomycetes in Svalbard based on soil and sporocarp DNA. *Journal of Biogeography* 39 (1):74–88. doi:10.1111/j.1365-2699.2011.02588.x.

Gemm, J., L. N. Morgado, T. A. Semenova, J. M. Welker, M. D. Walker, and E. Smets. 2015. Long-term warming alters richness and composition of taxonomic and functional groups of arctic fungi. *FEMS Microbiology Ecology* 91 (8):fi095. doi:10.1139/femsec/fi095.

Gemm, J., T. A. Semenova, L. N. Morgado, and J. M. Welker. 2016. Changes in composition and abundance of functional groups of arctic fungi in response to long-term summer warming. *Biology Letters* 12 (11):20160503. doi:10.1098/rsbl.2016.0503.

Gillman, L. S., and O. K. Miller Jr. 1977. A study of the boreal, alpine, and arctic species of *Melandoleucia. Mycologia* 69 (5):927–51. doi:10.2307/3745514.1977.12020146.

Gra, F. 1994. Ecology and sociology of macromycetes in snow-beds with *Salix herbacea* L. in the alpine valley of Radönt (Grisons, Switzerland). *Dissertationes Botanicae* 235:242.

Gra, F., and I. Brunner. 1996. Natural and synthesized ectomycorrhizas of the alpine dwarf willow *Salix herbacea*. *Mycorrhiza* 6:227–35. doi:10.1007/s005720050130.

Gulden, G. 1983. Studies in *Lepista* (Fr.) W.G. Smith. Section *Lepista* (Basidiomycotina, Agaricales). *Sydowia*: *Annales mycologici* 36:59–73.

Gulden, G., and A. E. Torkelsen. 1996. Fungi I. Basidiomycota: Agaricales, Gasteromycetales, Aphyllorhosphorales, Exobasidiales and Tremellales. *Skrifter-Norsk Polarinsttitut* 198:173–206.

Gulden, G., and K. Hialand. 2008. ISAM VII at Finse, Norway, 2005. *Sommerfeltia* 31:7–16. doi:10.2478/v10208-011-0002-8.

Gulden, G., K. M. Jenssen, and J. Stordal. 1985. *Arctic and alpine fungi*, Vol. 1. 61. Oslo, Norway: Lubrecht & Cramer Ltd. Soppkonsulenten.

Hallgrimsson, H. 1998. Checklist of *Icelandic fungi V: Agarics*. Naturufraedistornun Islands. Akureyri, Iceland: Akureyri Museum of Natural History.

Haselwandter, K. 2007. Mycorrhiza in the alpine timberline ecotone: Nutritional implications. In *Trees at their upper limit*, ed. G. Wieser and M. Tausz, 57–66. The Netherlands: Springer.

Heikkila, H., and P. Kallio. 1966. On the problem of subarctic basidiolichens I. *Reports from the Kevo Subarctic Research* 3:48–74.

Heikkila, H., and P. Kallio. 1969. On the problem of subarctic basidiolichens II. *Reports from the Kevo Subarctic Research* 4:90–97.

Hooker, J. D. 1860. An account of the plants collected by Dr. Walker in Greenland and Arctic America during the expedition of Sir Francis M’Clintock, RN, in the Yacht ‘Foxy’. *Botanical Journal of the Linnaean Society* 5 (18):79–89.

Horak, E. 1987a. *Astrosporina* in the alpine zone of the Swiss National Park (SNP) and adjacent regions. In *Arctic and alpine mycology*, ed. G. Laursen, J. Ammirati, and S. A. Redhead, 205–34. ISAM II.

Horak, E. 1987b. Revision der von J. Favre aus der Region des Schweizer Nationalparks beschriebenen alpinen Arten von *Cortinarius* subgen. *Telamonia* (Agaricales). *Candollea* 42:771–803.

Horak, E. 1993. *Entoloma* in the alpine zone of the Alps: 1. Revision of the taxa described by J. Favre (1955). - 2. New records from the Swiss National Park and other locations in the Alps. *Bibliotheca Mycologica* 150:63–91.

Horak, E., and O. K. Miller Jr. 1992. *Phaeogalera* and *Galerina* in arctic-subarctic Alaska (USA) and the Yukon Territory (Canada). *Canadian Journal of Botany* 70 (2):414–33. doi:10.1139/b92-055.

Hoshino, T., N. Tuno, Y. Degawa, T. Kasuya, Y. Yamada, E. Kawahara, and I. Nose. 2018. The 10th International Symposium on Arctic and Alpine Mycology. *Mycoscience* 30:1–2.

Huhtinen, S. 1982. Ascomycetes from central and northern Labrador. *Karstenia* 22:1–8. doi:10.29203/ka.1982.206.

Huhtinen, S. 1985. Mycoflora of Poste-de-la-Baleine, northern Quebec: Ascomycetes. *Le Naturaliste Canadien* 112 (4):735–542.

Hutchinson, L. J., R. C. Summerbell, and D. W. Malloch. 1988. Additions to the mycota of North America and Quebec: Arctic and boreal species from Schefferville, northern Quebec. *Le Naturaliste Canadien* 115:39–56.

IPCC. 2014. *Climate Change 2014: Synthesis Report*. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R. K. Pachauri and L. A. Meyer, eds.]. IPCC, Geneva, Switzerland, 151 pp.

Jalink, L. 2010. Additional notes on the *Lycoperdaceae* of the Beartooth Plateau. *North American Fungi* 5:173–180.

Jamoni, P. G. 1995. Russulaceae della zona alpine. Proposta di chiavi di determinazione per le specie crescenti nella zona alpina delle Alpi. *Rivista di Micologia* 2:75–80.

Jamoni, P. G. 2008. *Funghi alpini, delle zone alpine superiori e inferiori*, 543. Trento: Associazione Micologica Bresadola, Fondazione centro Studi Micologici.

Jennings, O. E. 1936. The exploration of Southampton Island, Hudson Bay. 3. Botany. 1. Algae and fungi. *Memoirs of the Carnegie Museum* 12 (3):1–4.

Kallio, P. 1980. Some observations on the fungi of the central Quebec-Labrador peninsula. *McGill Subarctic Research Report* 30:1–16.

Kankainen, E. 1969. On the structure, ecology, and distribution of the species of *Mittrula* s. lat. *Karstenia* 9:23–34. doi:10.29203/ka.1969.56.

Kasuya, T. 2010. *Lycoperdaceae* (Agaricales) on the Beartooth Plateau, Rocky Mountains, USA. *North American Fungi* 5:159–71.

Kauffman, C. H. 1921. The mycological flora of the higher Rockies of Colorado. *Papers of the Michigan Academy of Science, Arts and Letters* 1:101–50.

Knudsen, H., and T. Borgen. 1982. Russulaceae in Greenland. In *Arctic and alpine mycology I*, ed. G. A. Laursen and J. F. Ammirati, 216–41. Seattle: University of Washington Press.

Kobayasi, Y. 1982. Ecology and distribution of Arctic lower fungi. In *Arctic and Alpine Mycology I*, ed. G. A. Laursen and F. J. Ammirati, 16–26. Seattle: University of Washington Press.

Kobayasi, Y., H. Hiratsuka, K. Aoshima, R. Korf, M. Soneda, K. Tubaki, and J. Sugiyama. 1967. *Mycological studies of the Alaskan Arctic*, 138. Osaka: Annual Report of the Institute for Fermentation.
Morgado, L. N., T. A. Semenova, J. M. Welker, M. D. Walker, E. Smet, and J. Geml. 2015. Summer temperature increase has distinct effects on the ectomycorrhizal fungal communities of moist tussock and dry tundra in Arctic Alaska. *Global Change Biology* 21 (2):959–72. doi:10.1111/gcb.12716.

Moser, M. and E. Horak. 2006. Agrocybe praemagna; a new alpine species from Colorado, Idaho and Wyoming, Rocky Mountains, USA. In *Arctic and alpine mycology* 6, ed. D. Boertmann and H. Knudsen, *Meddelelser om Grønland, Bioscience* 56:133–138.

Moser, M. M. 1993. Studies on North American Cortinarii. III. The *Cortinarius* flora of dwarf and shrubby Salix associations in the alpine zone of the Wind River Mountains, Wyoming, USA. *Sydowia* 45:275–306.

Moser, M. M. 2002. How alpine are “alpine” fungi? Paper presented at International Mycological Congress (IMC7), August 11–17, Oslo, Norway. http://plantsciences.montana.edu/alpinemushrooms/imc7.html.

Moser, M. M., K. H. McKnight, and J. F. Ammirati. 1995. *Moser, M. M. 1993. Studies on North American Cortinarii. I. New and interesting taxa from the greater Yellowstone area.* *Mycotaxon* 60:301–46.

Moser, M. M., K. H. McKnight, and M. Sigl. 1994. The genus *Cortinarius* (Agaricales) in the Greater Yellowstone Area: Mycorrhizal host associations and taxonomic considerations. In *Plants and their environments, Proceedings of the First Biennial Scientific Conference on the Greater Yellowstone Ecosystem*, ed. D. G. Despain, 239–46. Denver, CO: US Department of the Interior National Park Service, Natural Resources Publications Office.

Mukhin, V. A., and H. Knudsen. 1998. *Arctic and alpine mycology* 5. *Russian Academy of Sciences: Ural Division*, 172. Yekaterinburg: Yekaterinburg Publishers.

Nares, G. 2011. *Narrative of a voyage to the Polar Sea during 1875–6 in HM ships alert and discovery: With notes on the natural history*, Vol. 1. Cambridge, UK: Cambridge University Press.

Nauta, M. 2010. Notes on Mollisiosid Ascomycetes from the Beartooth Plateau, Rocky Mountains, USA. *North American Fungi* 5:181–186.

Nealby, L. H., and K. Mercer. 2008. Sir John Franklin. The Canadian encyclopedia. Historica Canada. Accessed April 9, 2019. https://www.thecanadianencyclopedia.ca/en/article/sir-john-franklin.

Noffsinger, C. R. 2020. Systematics of *Russula* in the Rocky Mountain alpine zone. Ms. Thesis, Montana State University.

Noordeloos, M. and G. Gulden. 1992. Studies in the genus *Leotia, Cudonia, Spathularia* and *Neolecta* (Ascomycetes) in Finland. *Annals Botanici Fennici* 12:123–30.

Odenhoj, E., A. L. Ruotsalainen, and J. Vauras. 2018. Mycological records from ISAM 9, Kevo, Finland. *Mycoscience* 59 (4):263–67. doi:10.1016/j.myc.2017.12.003.

Odenhoj, E., J. Vauras, and M. Odenhoj. 1998. The *Inocybe* species found in the Canadian Arctic and west Siberian sub-arctic, with ecological notes. In *Arctic and alpine mycology* 5. *Russian Academy of Sciences: Ural Division*, ed. V. A. Mukhin and H. Knudsen, 106–21. Yekaterinburg: Yekaterinburg Publishers.

Odenhoj, E., and M. Odenhoj. 1993. Lectarii of the Franklin and Keewatin districts of the Northwest Territories, Arctic Canada. In *Arctic and Alpine mycology* 3–4, ed. O. Petruni and G. A. Laursen, 179–92. Stuttgart, Berlin: J Cramer.

Odenhoj, E., and M. Odenhoj. 2010. Larger fungi of the Canadian arctic. *North American Fungi* 5:85–96.

Osmundson, T. W., C. L. Cripps, and G. M. Mueller. 2005. Morphological and molecular systematics of Rocky Mountain alpine *Laccaria*. *Mycologia* 97 (5):949–72. doi:10.1080/00275514.2006.11832746.

Overholtz, L. 1919. Some Colorado fungi. *Mycologia* 11 (5):245–58. doi:10.1080/00275514.1919.12016799.

Pammelee, J. A. 1969. Fungi of Central Baffin Island. *Canadian Field Naturalist* 83:48–53.

Peintner, U. 2008. *Cortinarius alpinus* as an example for morphological and phylogenetic species concepts in ectomycorrhizal fungi. *Sommerfeldia* 31:161–77. doi:10.2478/v10208-011-0009-1.

Peintner, U., and M. Moser. 1996. The mycobiota (Basidiomycetes) of an Alpine Tyrolean Valley. *Phyton (Horn Austria)* 36 (4):65–82.

Peterson, P. M. 1977. Investigations on the ecology and pheno-logy of the macromycetes in the Arctic. *Meddelelser om Grønland, Bioscience* 199:2–72.

Petruni, O., and G. A. Laursen. 1993. Arctic and alpine mycology 3–4. *Bibliotheca Mycologica* 150:269.

Polunin, N. 1934. The Flora of Akpatok Island, Hudson Strait. *Journal of Botany* 72:197–204.

Polunin, N. 1940. Botany of the Canadian eastern Arctic. Part I. *Pteridophyta and Spermatophyta. National Museum of Canada Bulletin No. 92 Biological Series no. 24*, 395. Ottawa: Dept. of Mines and Resources, National Museum of Canada.

Polunin, N. 1947. Botany of the Canadian Eastern Arctic. Part II: *Thallophyta and bryophyta. National Museum of Canada Bulletin No. 97 Biological Series No. 26*. Ottawa: Dept. of Mines and Resources, National Museum of Canada.

Rau, T. G. 1977. Fungi in decomposing litter from tundra plants near Barrow, Alaska, 53.Ms. Thesis, Virginia Polytechnic Institute and State University.

Redhead, S. A. 1980. *Gerronema pseudogrisella. Fungi Canadenses no. 170*. Ottawa: Agriculture Canada.

Redhead, S. A. 1984a. Additional Agaricales on wetland Monocotyledoneae in Canada. *Canadian Journal of Botany* 62:1844–51. doi:10.1139/b84-251.

Redhead, S. A. 1984b. *Arrhenia and Rimbachia*, expanded generic concepts, and a reevaluation of *Leptoglossum* with emphasis on musicolous North American taxa. *Canadian Journal of Botany* 62 (5):865–92. doi:10.1139/b84-126.

Redhead, S. A. 1989. A biogeographical overview of the Canadian mushroom flora. *Canadian Journal of Botany* 67 (10):3003–62. doi:10.1139/b89-384.

Redhead, S. A., and G. Baillargeon. 1999. Fungal database development and early historical records of mushrooms from Canada. *Mycologia* 14 (1):73–82.
Redhead, S. A., O. K. Miller Jr., R. Watling, and E. Ohenoja. 1982. *Marasmius epidryas*. Fungi Canadensis No. 213. Ottawa: Agriculture Canada.

Rinaldi, A. C., O. Comandini, and T. W. Kuyper. 2008. Ectomycorrhizal fungal diversity: Separating the wheat from the chaff. *Fungal Diversity* 33:1–45.

Ronikier, A. 2008. Contribution to the biogeography of arctic-alpine fungi: First records in the Southern Carpathians (Romania). *Sommerfeltia* 31:191–211. doi:10.2478/v10208-011-0011-7.

Ronikier, A. and M. Ronikier. 2010. Biogeographical patterns of arctic-alpine fungi: distribution analysis of *Marasmius epidryas*, a typical circumpolar species of cold environments. *North American Fungi* 5: 23–50.

Rostrup, E., and H. G. Simmons. 1906. Fungi collected by HG Simmons on the 2nd Norwegian Polar expedition, 1898–1902. In *Report of the second Norwegian Arctic Expedition in the "Fram"*, 1898–1902 2 (9), 1–10. Oslo: Videnskabs-Selskabet I Kristiania.

Ryberg, M., E. Larsson, and U. Molau. 2009. Ectomycorrhizal diversity on *Drys octopetala* and *Salix reticulata* in an alpine cliff ecosystem. *Arctic, Antarctic, and Alpine Research* 41:506–14. doi:10.1657/1938-4246-41.4.506.

Saccardo, P. A., C. H. Peck, and W. Trelease. 1904. The fungi of Alaska. Harriman Alaska expedition. *Cryptogamic Botany* 5:44–49.

Savile, D. B. O. 1963. Mycology in the Canadian arctic. *Arctic* 16 (1):17–25. doi:10.14430/arctic3518.

Schöch, C. L., K. A. Seifert, S. Huhndorf, V. Robert, J. L. Spouge, C. A. Levesque, and W. Chen. 2012. Nuclear ribosomal internal transcribed spacer (ITS) region as a universal DNA barcode marker for Fungi. *Proceedings of the National Academy of Science, USA* 109:6241. doi:10.1073/pnas.1117018109.

Seaver, R., and P. F. Shope. 1930. A mycological foray through the mountains of Colorado, Wyoming, and South Dakota. *Mycologia* 22 (1):1–8. doi:10.1080/00275514.1930.12016975.

Semenova, T. A., L. N. Morgado, J. M. Welker, M. D. Walker, E. Smets, and J. Geml. 2016. Compositional and functional shifts in arctic fungal communities in response to experimentally increased snow depth. *Soil Biology & Biochemistry* 100:201–09. doi:10.1016/j.soilbio.2016.06.001.

Senn-Inlet, B. I. 1987. Pilze aus der alpinen stufe des Val d’Anniviers (Wallis). *Bulletin de la Murithienne* 105:87–106.

Serrez, M. C., and R. G. Barry. 2011. Processes and impacts of Arctic amplification: A research synthesis. *Global and Planetary Change* 77 (1–2):85–96. doi:10.1016/j.gloplacha.2011.03.004.

Shiryaev, A. G., I. V. Zmitrovich, and O. N. Ezhev. 2018. Taxonomic and ecological structure of basidial macromycetes biota in polar deserts of the Northern Hemisphere. *Contemporary Problems of Ecology* 11 (5):458–71. doi:10.1134/S1995425518050086.

Skjøte, O. 1989. *Russula* of the island Bjornoya (Bear Island), Svalbard. *Opera Botanica* 100:233–39.

Smith, A. H. 1975. *A field guide to western mushrooms*, 280. Ann Arbor: The University of Michigan Press.

Solheim, W. 1949. Studies on Rocky Mountain fungi: I. *Mycologia* 41 (6):623–31.

Spence, H. S. 1932. Sub-arctic mushrooms. *Canadian Field Naturalist* 46:53–54.

Sprague, R., and D. B. Lawrence. 1959. The fungi on deglaciated Alaskan terrain of known age. 1. *Research Studies Washington State University* 27 (3):110–28.

Sprague, R., and D. B. Lawrence. 1959–1960. The fungi on deglaciated Alaskan terrain of known age. 2. *Research Studies Washington State University* 27 (4):214–29.

Sprague, R., and D. B. Lawrence. 1960. The fungi of deglaciated Alaskan terrain of known age. 3. *Research Studies Washington State University* 28 (1):1–20.

Stephenson, S. and G. Laursen. 1993. A preliminary report on the distribution and ecology of Myxomycetes in Alaskan tundra. In *Arctic and Alpine mycology 3–4*, ed. O. Petrini and G. A. Laursen, 251–257, Berlin: J Cramer.

Timling, I., D. A. Walker, C. Nusbaum, N. J. Lennon, and D. L. Taylor. 2014. Rich and cold: Diversity, distribution and drivers of fungal communities in patterned-ground ecosystems of the North American Arctic. *Molecular Ecology* 23:3258–72. doi:10.1111/mec.12743.

Trelease, W. 1904. Vol. V. 13. In: *Harriman Alaska expedition, 1899, vol. V. containing cryptogamic Botany of Alaska, by William Trelease*. New York: Doubleday, Page & Company.

Tsutui, M., and T. Hoshino. 2019. *Fungi in polar regions*, 146. Florida: CRC Press Taylor and Francis Group.

Väre, H. 2017. Finnish botanists and mycologists in the Arctic. *Arctic Science* 3 (3):525–52. doi:10.1139/as-2016-0051.

Watling, R. 1987. Larger arctic-alpine fungi in Scotland. In *Arctic and alpine mycology 2*, ed. G. Laursen, J. F. Ammirati, and S. A. Redhead, 17–45. New York, NY: Plenum Press.

Watling, R., and O. K. Miller Jr. 1971. Notes on eight species of *Coprinus* of the Yukon Territory and adjacent Alaska. *Canadian Journal of Botany* 49 (9):1687–90. doi:10.1139/b71-237.