



Arctic, Antarctic, and Alpine Research

An Interdisciplinary Journal

ISSN: (Print) (Online) Journal homepage: <https://www.tandfonline.com/loi/uaar20>

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To cite this article: Chance Noffsinger, Cathy L. Cripps & Egon Horak (2020) A 200-year history of arctic and alpine fungi in North America: Early sailing expeditions to the molecular era, Arctic, Antarctic, and Alpine Research, 52:1, 323-340, DOI: [10.1080/15230430.2020.1771869](https://doi.org/10.1080/15230430.2020.1771869)

To link to this article: <https://doi.org/10.1080/15230430.2020.1771869>



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Published online: 09 Jul 2020.



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

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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.

ARTICLE HISTORY

Received 2 March 2020
Revised 7 May 2020
Accepted 11 May 2020

KEYWORDS

Biodiversity; Basidiomycota; cold climate; past and present; species checklist

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 telephoroids and Sebaciales 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; ascolichens 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* basidiolichen. (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.

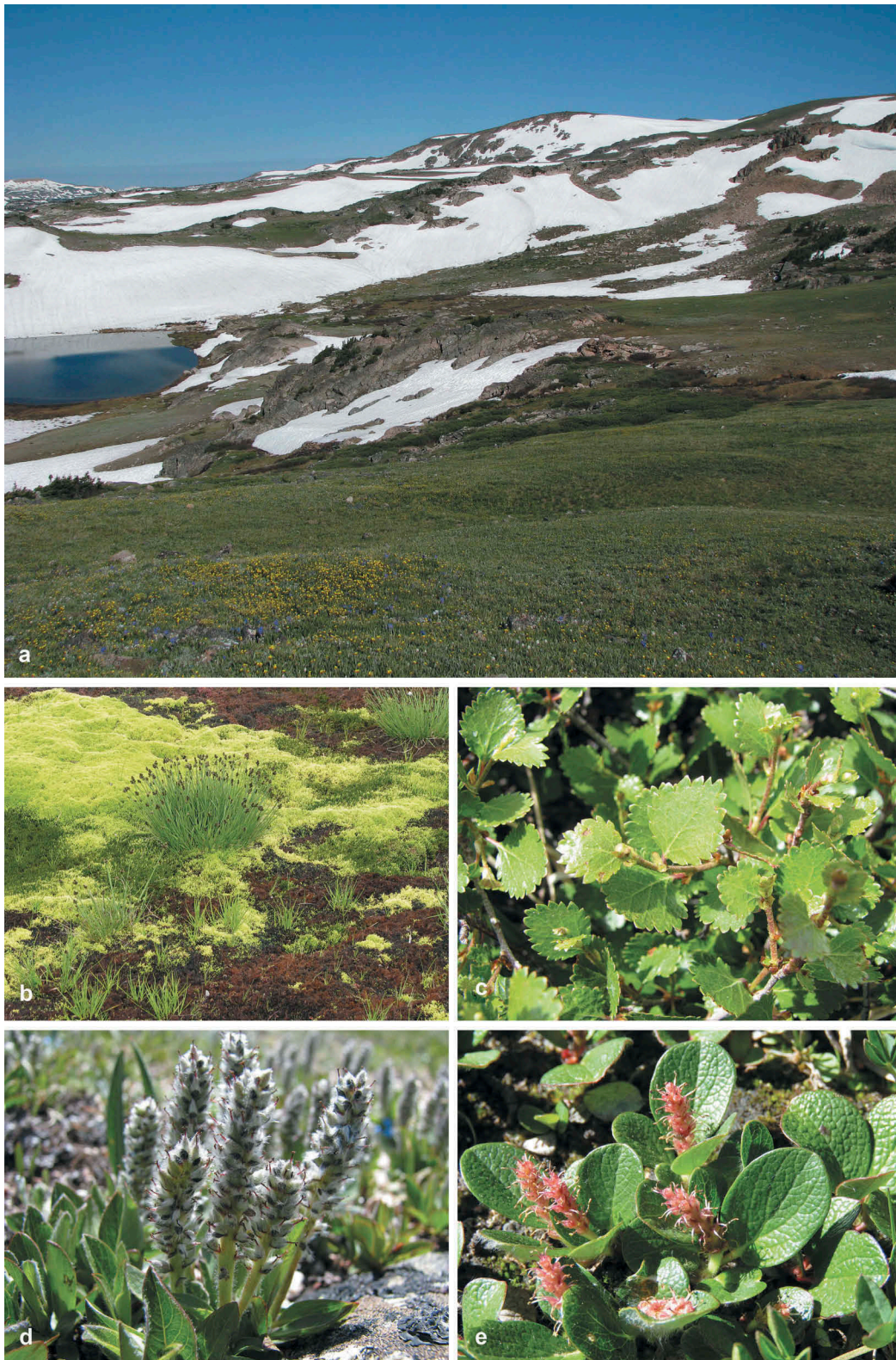


Figure 2. (a) Typical North American alpine habitat, Beartooth Plateau, Rocky Mountains. (b) Alpine bog. (c) *Betula nana*, ectomycorrhizal. (d) *Salix arctica*, ectomycorrhizal. (e) *Salix reticulata*, ectomycorrhizal.

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; Hallgrímsson 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: <i>Cantharellus lobatus</i> Peck and <i>Lycoperdon pratense</i> Pers.	Melville Island, Canadian Arctic Archipelago	Brown (1823)
Captain Sir John Franklin's second overland expedition (1825–1827)	Basidiomycota: <i>Cantharellus canadensis</i> Kl. MSS., <i>Favolus (Pleuropus) humboldtii</i> Berk., <i>Favolus (Pleuropus) hepaticus</i> Kl., and <i>Favolus (Pleuropus) canadensis</i> Kl. l. c.	Northwest Territories and arctic regions in Canada	Berkeley (1839)
Arctic expedition led by Admiral Belcher in (1852–1854)	Basidiomycota: <i>Cantharellus lobatus</i> Peck	Wellington Channel, Nunavut, Canada	Polunin (1940)
Sir Francis Leopold M'Clintock's expedition in the yacht <i>Fox</i> (1857–1859)	Basidiomycota: <i>Agaricus allosporus</i> Berk., <i>Agaricus cyathiformis</i> Bull., <i>Agaricus furfuraceus</i> P., <i>Agaricus vaginatus</i> Bull., and <i>Agaricus umbelliferus</i> L.	Boothia Peninsula, Nunavut, Canada	Hooker (1860)
Arctic expedition from 1875 to 1876	Ascomycota: <i>Peziza stercorea</i> P. and <i>Urnula hartii</i> B. Basidiomycota: <i>Agaricus (Clitopilus) undatus</i> Fr., <i>Agaricus (Naucoria) bellotianus</i> B., <i>Agaricus (Omphalia) umbelliferus</i> L., <i>Agaricus (Omphalia) umbilicatus</i> Schaeff., <i>Agaricus (Stropharia) feildeni</i> B., <i>Agaricus (Tubaria) furfuraceus</i> P., <i>Agaricus (Tubaria) pellucidus</i> Bull., <i>Cantharellus muscigenus</i> Fr., <i>Hygrophorus miniatus</i> Fr., <i>Hygrophorus virgineus</i> Fr., <i>Lycoperdon atropurpureum</i> Vitt., <i>Lycoperdon cretaceum</i> B., <i>Merulius aurantiacus</i> Fr., and <i>Russula integra</i> Fr.	Northern Nunavut, Canada	Berkeley (1878)
Second voyage of the <i>Fram</i> Expedition (1898–1902)	Ascomycota: <i>Mollisia graminis</i> (Desm.), <i>Niptera melatephra</i> (Lasch.), and <i>Sclerotinia vahliana</i> Rostr. Basidiomycota: <i>Cantharellus lobatus</i> (Pers.), <i>Collybia dryophila</i> (Bull.), <i>Galera hypnorum</i> (Batsch), <i>Hebeloma fastibile</i> (Fr.), <i>Lycoperdon gemmatum</i> (Batsch), <i>Mycena pumila</i> (Bull.), <i>Naucoria festiva</i> (Fr.), <i>Naucoria melinoides</i> (Fr.), <i>Naucoria nimbosea</i> (Fr.), <i>Omphalia umbellifera</i> (L.), <i>Psalliota campestris</i> (L.), <i>Psalliota rodmani</i> (Peck), <i>Psathyrella polaris</i> n. sp., <i>Russulina lutea</i> (Huds.), and <i>Tricholoma caelatum</i> (Fr.)	Ellesmere Island, Nunavut, Canada	Rostrup and Simmons (1906)
Canadian Arctic Expedition (1913–1918)	Ascomycota: <i>Peziza micropus</i> Pers. var. <i>flavida</i> Phil., <i>Scleroderma fuliginosa</i> (Fr.) Karst., and <i>Scutellina scutellata</i> (L.) Basidiomycota: <i>Boletus scaber</i> Fr., <i>Cantharellus muscigenus</i> Fr., <i>Clavaria creatacea</i> (Berk.) Lloyd, <i>Galera hypnorum</i> Batsch., <i>Hebeloma fastibile</i> Fr., <i>Hygrophorus cantharellus</i> Fr., <i>Hygrophorus</i> sp., <i>Inocybe flocculosa</i> Berk., <i>Lycoperdon umbrinum</i> Pers., <i>Naucoria</i> sp., <i>Omphalia umbellifera</i> Fr., and <i>Russula</i> sp.	Northern regions of Nunavut, Northwest Territories, and the Yukon, Canada	Dearnness (1923)
Oxford Exploration Club's 1931 expedition to Akpatok Island	Ascomycota: <i>Helvella lacunosa</i> Afz., <i>Peziza acetabulum</i> L., and <i>Sphaerospora asperior</i> (Nyl.) Sacc. Basidiomycota: <i>Boletus reticulatus</i> (Schaeff.) Boud., <i>Boletus</i> sp., <i>Cantharellus cibarius</i> Fr., <i>Cortinarius</i> spp., <i>Dictyolus muscigena</i> (Bull.) Quél., <i>Hygrophorus</i> sp., <i>Hypholoma</i> sp., <i>Inocybe violacea</i> Pat., <i>Inocybe</i> spp., <i>Laccaria laccata</i> (Scop.) B. & Br., <i>Lactarius vellereus</i> Fr., <i>Lycoperdon perlatus</i> Pers., <i>Lycoperdon</i> sp., <i>Mycena polygramma</i> Quél., <i>Mycena</i> spp., <i>Omphalia</i> sp., <i>Psilocybe semilanceata</i> Fr., <i>Russula emetica</i> Fr., <i>Russula ochroleuca</i> Fr., and <i>Russula</i> 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. Dearnness returned to the Basidiomycota after a half-century pause and focused on the fleshy fungi of southern Baffin Island (Dearnness 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 basidiomycetes 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 fleshy fungi, including two Ascomycota (*Peziza* species) and forty-nine Basidiomycota 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 fleshy fungi of the subarctic tundra of Alaska and the Yukon (Miller 1982b, 1987), *Marasmius epidryas* 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 Heikkilä and Paavo Kallio from Finland showed *Omphalina* to be one of the most common agaric genera in the arctic habitats of Northern Canada (Heikkilä 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 epidryas* (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 agarics 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 arcto-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 Shiryayev.

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 on arctic and alpine mycology in North America	Acting president	Publication Editor(s)
1st ISAM, August 1980. Barrow, Alaska	Basidiomycetes in subarctic Alaska (Miller 1982a; 1982b), <i>Cortinarius</i> in Alaska (Ammirati and Laursen 1982), <i>Lactarius</i> in Alaska (Laursen and Ammirati 1982b), lower fungi in the Arctic (Kobayasi 1982), soil fungi in arctic tundra (Laursen and Chimelewski 1982), and mycorrhizal associations with <i>Salix rotundifolia</i> (Linkins and Antibus 1982)	Gary Laursen	Laursen and Ammirati (1982a)
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)	Egon Horak	Laursen, Ammirati, and Redhead (1987b)
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: <i>Cystoderma</i> in Alaska (Miller 1993), <i>Lactarius</i> in arctic Canada (Ohenoja and Ohenoja 1993), and Myxomycetes in the Alaskan tundra (Stephenson and Laursen 1993)	Sigmund Sivertsen	Petrini and Laursen (1993)
4th ISAM, August 1992. Lanslebourg, France		Denise Lamoure	Petrini and Laursen (1993)
5th ISAM, August 1996. Polar Urals, Russia	<i>Hebeloma</i> from Alaska (Miller 1998), <i>Inocybe</i> species from arctic Canada (Ohenoja, Vauras, and Ohenoja 1998)	Viktor Mukhin	Mukhin and Knudsen (1998)
6th ISAM, August 2000. Greenland	<i>Arrhenia auriscalpium</i> in Colorado (Cripps and Horak 2006) and <i>Agrocybe praemagna</i> in the Rocky Mountain alpine region (Moser and Horak 2006)	Torbjorn Borgen	Boertmann and Knudsen (2006)
7th ISAM, August 2005. Finse, Norway	<i>Cortinarius</i> in the Rocky Mountain alpine (Peintner 2008) and a checklist of agarics from the Rocky Mountain alpine zone (Cripps and Horak 2008)	Gro Gulden	Gulden and Høiland (2008)
8th ISAM, August 2008. Beartooth Plateau, Montana/Wyoming	<i>Amanita</i> found on the Beartooth Plateau (Cripps and Horak 2010), <i>Marasmius epidryas</i> in the Rocky Mountain alpine (Ronikier and Ronikier 2010), <i>Hebeloma hiemale</i> in the Rocky Mountain alpine (Becker, Eberhardt, and Vesterholt 2010), larger fungi in arctic and subarctic Canada (Ohenoja and Ohenoja 2010), <i>Inocybe (Malloche)</i> in the Rocky Mountain alpine (Cripps, Larsson, and Horak 2010), Lycoperdaceae on the Beartooth Plateau (Kasuya 2010; Jalink 2010), and Mollisioid Ascomycetes on the Beartooth Plateau (Nauta 2010)	Cathy Cripps	Cripps and Ammirati (2010)
9th ISAM, August 2012. Utsjoki, Finland	<i>Inocybe leiocephala</i> , a species with an intercontinental distribution (Larsson, Vauras, and Cripps 2014), and <i>Lactarius</i> from the Rocky Mountain alpine zone (Cripps and Barge 2014)	Esteri Ohenoja	Ohenoja, Ruotsalainen, and Vauras (2018)
10th ISAM, August 2016. Kanazawa, Japan	<i>Inocybe arctica</i> and other species later reported in the North American alpine (Larsson, Vauras, and Cripps 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 Cortinariaceae, 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 Sebaciniales, *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. *pallidifolia* 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 pallidomarginata*), 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 Ezhov (2018), the cold adaptation strategies of fungi in polar regions was covered by Tsuji and Hoshino (2019), and the upward shifts in fungal fruitings 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 (Ohenoja and Ohenoja 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 *Mallochybe* 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 *Lycoperdon* 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 Sebaciniales, *Cenococcum*, 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 subalpine 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

AGARICACEAE

- Agaricus* cf. *aristocratus* Gulden¹
Agaricus campestris (L.) Fr.^{a,1}
Agaricus spp.
Bovista limosa Rostr.^{a,2}
Bovista nigrescens Pers.^{a,2}
Bovista pila Berk. & M.A. Curt.²
Bovista plumbea Pers.²
Bovistella utriformis (Bull.) Demoulin & Rebreiv²
Crucibulum laeve (Huds.) Kambly³
Cystoderma sp.¹
Lepiota alba (Bres.) Sacc.¹
Lepiota magnispora Murrill¹
Calvatia booniana A.H. Smith²
Calvatia cretacea (Berk.) Lloyd^{a,2}
Calvatia sculpta (Hark.) Lloyd²
Calvatia turneri (Ellis & Everh.) Demoulin & Lange^{a,2}
Lycoperdon frigidum Demoulin²
Lycoperdon norvegicum Demoulin²

AMANITACEAE

- Amanita groenlandica* f. *montana* Cripps & Horak^{a,1}
Amanita nivalis Grev.^{a,1,4}
Amanita vaginata (Bull.) Lam.^{1,4}

BOLBITACEAE

- Agrocybe praecox* (Pers.) Fayod¹
Agrocybe cf. *praemagna* M.M. Moser & E. Horak¹
Conocybe sp.

CORTINARIACEAE

- Cortinarius absarokensis* M.M. Moser & McKnight^{1,5}
Cortinarius adelbertii J. Favre^{1,6}
Cortinarius albonigrellus J. Favre^{1,5}
Cortinarius alpinus Boud. = *Cortinarius favrei* D.M. Henderson^{a,b,c,1,5}
Cortinarius anomalus (Fr.) Fr.^{a,b,c,1}
Cortinarius atroalbus M.M. Moser^{1,6}
Cortinarius caninus Fr.^{b,c,1}
Cortinarius chrysomallus Lamoure^{1,5}
Cortinarius cinnamomeolutes P.D. Orton^{a,1}
Cortinarius expallens M.M. Moser^{1,6}
Cortinarius ferrugineifolius M.M. Moser^{1,6}
Cortinarius fuscoflexipes M.M. Moser & McKnight^{1,5}
Cortinarius galerinoides Lamoure^{1,6}
Cortinarius hemitrichus (Pers.) Fr.³
Cortinarius hinnuleus Fr. s.l.^{1,6}
Cortinarius hinnuleus var. *favreanus* Bon^{c,3}
Cortinarius hybospermus M.M. Moser^{1,6}
Cortinarius inops J. Favre^{1,6}
Cortinarius laetus M.M. Moser^{1,6}
Cortinarius minutalis Lamoure^{a,1,6}
Cortinarius mucronatus M.M. Moser & McKnight^{1,5}
Cortinarius paraphaeochrous M.M. Moser^{1,6}
Cortinarius parvannulatus Kühner^{a,3}
Cortinarius pauperculus J. Favre^{1,5}
Cortinarius phaeochrous J. Favre^{1,6}
Cortinarius phaeopygmaeus J. Favre^{1,6}
Cortinarius polaris Høiland^{a,b,c,1}
Cortinarius pusillus M.M. Moser, McKnight & Sigl¹
Cortinarius rufoanuliferus M.M. Moser & McKnight^{1,5,6}
Cortinarius stenospermus Lamoure^{1,5,6}
Cortinarius subrigidipes M.M. Moser^{1,6}
Cortinarius subtorvus Lamoure^{a,b,c,1,6}
Cortinarius tenebricus J. Favre^{1,5}
Cortinarius cf. *umbilicatus* P. Karsten³
Cortinarius vibratilis (Fr.) Fr.¹
Cortinarius vulpicolor M.M. Moser & McKnight^{1,5,6}

ENTOLOMATACEAE

- Entoloma alpicola* (Favre) Bon and Jamoni^{a,1}
Entoloma cf. *atrosericeum* (Kühner) Noordel.³

Table 3. (Continued).

- Entoloma cetratum* (Fr.) M.M. Moser¹
Entoloma juncinum (Kühner & Romagn.) Noordel.¹
Entoloma sericeum Quél.^{a,1}
Rhodocybe cf. *popinalis* (Fr.) Singer^{a,1}

HYMENOGASTRACEAE

- Alnicola* sp.¹
Galerina annulata (J. Favre) Singer¹
Galerina arctica (Singer) Nezdolj.¹
Galerina atkinsoniana A.H. Smith¹
Galerina clavata (Velen.) Kühner¹
Galerina subclavata Kühner³
Galerina cf. *pseudomycenopsis* Pilát^{a,1}
Galerina unicolor (Vahl.) Singer = *Galerina marginata* (Batsch) Kühner¹
Galerina spp.
Hebeloma alpinicola A.H. Sm., Evenson & Mitchel^{b,7}
Hebeloma alpinum (J. Favre) Bruchet^{a,b,c,1,7}
Hebeloma aurantiumbrinum Beker, Vesterh. & U. Eberh.^{b,c,7}
Hebeloma avellaneum Kauffman^{b,7}
Hebeloma excedens (Peck) Sacc.^{b,7}
Hebeloma dunense L. Corb. & R. Heim^{b,c,7}
Hebeloma hiemale Bres.^{b,c,7}
Hebeloma hygrophilum Poumarat & Corriol^{b,c,7}
Hebeloma marginatulum (J. Favre) Bruchet^{b,c,7}
Hebeloma mesophaeum (Pers.) Quél.^{a,b,c,1,7}
Hebeloma nigellum Bruchet^{a,c,7}
Hebeloma oreophilum Beker & U. Eberh.^{b,c,7}
Hebeloma spetsbergense Beker & U. Eberh.^{b,c,7}
Hebeloma subconcolor Bruchet^{b,c,7}
Hebeloma vaccinum Romagn.^{b,c,7}
Hebeloma velutipes Bruchet^{b,c,7}
Phaeogalera stagnina (Fr.) Kühner³

INOCYBACEAE

- Inocybe alpinomarginata* C.L. Cripps, E. Larss. & Vauras^{b,c,8}
Inocybe arctica E. Larss., Vauras & C.L. Cripps^{b,c,8}
Inocybe cf. *bulbosissima* (Kühner) Bon¹
Inocybe canescens J. Favre¹
Inocybe dulcamara (Pers.) P. Kumm.^{a,b,c,1,9}
Inocybe fraudans (Britzelm.) Sacc.¹
Inocybe giacomini J. Favre^{b,c,1,7}
Inocybe lacera (Fr.) P. Kumm.^{a,1}
Inocybe leioccephala D.E. Stuntz^{a,b,c,1,10}
Inocybe leonina Esteve-Rav. & A. Caball.^{b,c,7}
Inocybe leucoblema Kühner^{b,c,9}
Inocybe cf. *maculipes* J. Favre¹
Inocybe murina E. Larss., Cripps, & Vauras^{b,c,8}
Inocybe occulta Esteve-Rav., Bandini, B. Oertel & G. Moreno^{a,b,c,8}
Inocybe paragiacomini E. Larss., C.L. Cripps & Vauras^{b,c,8}
Inocybe phaeocystidiosa Esteve-Rav., G. Moreno & Bon^{b,c,8}
Inocybe purpurpeobadia Esteve-Rav. & A. Caball.^{b,c,8}
Inocybe cf. *rhacodes* J. Favre¹
Inocybe subgiacomini C.L. Cripps, Vauras & E. Larss.^{b,c,8}
Inosperma calamistratum (Fr.) Matheny & Esteve-Rav.^{a,1}
Inosperma cf. *subhirsutum* (Kühner) Matheny & Esteve-Rav.¹
Mallocybe arthrocytis (Kühner) Matheny & Esteve-Rav.^{b,c,9}
Mallocybe fulvipes (Kühner) Matheny & Esteve-Rav.^{b,c,9}
Mallocybe fuscomarginata (Kühner) Matheny & Esteve-Rav.^{b,c,1,9}
Mallocybe leucoloma (Kühner) Matheny & Esteve-Rav.^{b,c,9}
Mallocybe terrigena (Fr.) Matheny, Vizzini & Esteve-Rav.^{a,b,c,9}
Mallocybe substraminipes (Kühner) Matheny & Esteve-Rav.^{b,c,9}
Pseudosperma cf. *rimosum* (Bull.) Matheny & Esteve-Rav.¹

HYDNANGIACEAE

- Laccaria nobilis* A.H. Sm. In G.M. Mueller^{b,1,11}
Laccaria laccata var. *pallidifolia* (Peck) Peck = *L. tetraspora*
 Singer = *L. laccata* (Scop.) Cooke^{a,b,1,11}
Laccaria montana Singer^{a,b,1,11}
Laccaria pumila Fayod^{a,b,1,11}
Laccaria pseudomontana Osmundson, C.L. Cripps & G.M. Mueller^{b,1,11}

HYGROPHORACEAE

- Arrhenia acerosa* (Fr.) Kühner¹
Arrhenia auriscalpium (Fr.) Fr.^{a,1,12}
Arrhenia lobata (Pers.) Kühner & Lamoure ex Redhead^{a,1}
Arrhenia velutipes (P.D. Orton) Redhead, Lutzoni, Moncalvo & Vilgalys^{a,1}

(Continued)

(Continued)

Table 3. (Continued).

<i>Gliophorus psittacinus</i> (Schaeff.) Herink = <i>Hygrocybe psittacina</i> (Schaeff.) P. Kumm. ¹
<i>Hygrocybe conica</i> (Schaeff.) P. Kumm. ^{a,1}
<i>Hygrocybe marchii</i> (Bres.) F.H. Möller ¹
<i>Lichenomphalia</i> sp. ^{a,1}
LYOPHYLLACEAE
<i>Calocybe chrysenteron</i> (Bull.) Singer ¹
<i>Calocybe onychina</i> (Fr.) Donk ¹
MARASMIACEAE
<i>Hydropus</i> sp. ¹
MYCENACEAE
<i>Hemimycena</i> sp. ¹
<i>Mycena pura</i> (Pers.) P. Kumm. s.l. ¹
NIACEAE
<i>Flagelloscypha</i> sp. ¹
PHYSALACRIACEAE
<i>Flammulina</i> sp. ¹
<i>Rhizomarasmius epidryas</i> (Kühner ex A. Ronikier) A. Ronikier & Ronikier ^{a,1}
STROPHARIACEAE
<i>Deconica chionophila</i> (Lamoure) Noordel. ¹
<i>Hypholoma elongatum</i> (Pers.) Ricken ³
<i>Stropharia alpina</i> M. Lange ¹
TRICHOLOMATACEAE
<i>Clitocybe dryadicola</i> (J. Favre) Harmaja ¹
<i>Clitocybe festivoidea</i> Lamoure ³
<i>Collybia cookei</i> (Bres.) J.D. Arnold ¹
<i>Dermoloma</i> sp. ¹
<i>Gamundia leucophylla</i> (Gillet) H.E. Bigelow = <i>Fayodia leucophylla</i> (Gillet) M. Lange & Sivertsen ¹
<i>Gymnopus alpicola</i> (Bon & Ballarà) Esteve-Rav., V. González, Arenal & E. Horak ³
<i>Lorelia marchantiae</i> (Singer & Cléménçon) Redhead, Moncalvo, Vilgalys & Lutzoni ¹
<i>Lepista</i> cf. <i>ricekii</i> Bon ³
<i>Melanoleuca cognata</i> (Fr.) Konrad & Moutbl. s.l. ^{a,b,c,1}
<i>Melanoleuca strictipes</i> Kühner ³
<i>Mycenella</i> sp. ¹
<i>Omphalina rivulicola</i> (J. Favre) Lamoure ¹
RUSSULALES
RUSSULACEAE
<i>Lactarius glycosmus</i> (Fr.) Fr. ^{a,c,1,13,14}
<i>Lactarius lanceolatus</i> O.K. Miller & Laursen ^{a,b,c,13,14}
<i>Lactarius nanus</i> J. Favre ^{a,b,c,1,5,13,14}
<i>Lactarius pallidomarginatus</i> Barge & C.L. Cripps ^{b,13,14}
<i>Lactarius repraesentaneus</i> Britzelm. ^{b,c,1,13,14}
<i>Lactarius salicis-reticulatae</i> Kühner ^{b,c,1,13,14}
<i>Russula altaica</i> (Singer) Singer ^{a,b,c,15} similar to <i>Russula gracillima</i> Jul. Schff.
<i>Russula amoenipes</i> var. <i>kuehneriana</i> ¹⁵
<i>Russula</i> cf. <i>heterochroa</i> Kühner ^{c,15}
<i>Russula intermedia</i> P. Karst. ^{b,c,15}
<i>Russula laevis</i> Kälviäinen, Ruotsalainen & Taipale ^{a,b,c,15}
<i>Russula laccata</i> Huijsman ^{a,b,c,1,15}
<i>Russula nana</i> Killerm. ^{a,b,c,1,5,15}
<i>Russula purpureofusca</i> Kühner ^{b,c,15}
<i>Russula salicicola</i> (Singer) Kühner ex Knudsen & T. Borgen ^{b,c,15}
<i>Russula subrubens</i> (J.E. Lange) Bon ^{b,c,1,15}
BOLETALES
BOLETACEAE
<i>Leccinum</i> cf. <i>rotundifoliae</i> (Singer) A.H. Smith, Thiers & Watling ^{b,c,1}
CANTHARELALES
CANTHARELLACEAE
<i>Rickenella fibula</i> (Bull.) Raithehl. ^{a,1}
<i>Rickenella swartzii</i> (Fr.) Kuyper ¹
ASCOMYCOTA
<i>Bryoglossum gracile</i> (P. Karst.) Redhead ^{a,3}
<i>Ciborinia ciborium</i> (Vahl) T. Schumach. & L.M. Kohn ³
<i>Morchella</i> sp. ^{b,3}

Notes. ^aReported from Canadian Arctic, not molecularly confirmed (Ohenoja and Ohenoja 2010).

^bGenbank sequence available.

^cIntercontinental distribution molecularly confirmed.

¹Cripps and Horak (2008).

²Kasuya (2010).

³Cripps, Unpublished. Representative specimens deposited in the fungal section of the MONT Herbarium, Bozeman, Montana.

⁴Cripps and Horak (2010).

⁵Moser and McKnight (1987).

⁶Moser, McKnight, and Ammirati (1995).

⁷Cripps et al. (2019).

⁸Cripps, Larsson, and Vauras (2020).

⁹Cripps, Larsson, and Horak (2010).

¹⁰Larsson, Vauras, and Cripps (2014).

¹¹Osmundson, Cripps, and Mueller (2005).

¹²Cripps and Horak (2006).

¹³Barge, Cripps, and Osmundson (2016).

¹⁴Barge and Cripps (2016).

¹⁵Noffsinger (2020).

nanus, *Russula nana*, and some *Hebelomas*—are more likely to be restricted to arctic and alpine habitats like their hosts. Even the so-called true alpine decomposer *Arrhenia auriscalpium* has been found below treeline, although it is rare (Cripps and Horak 2006). However, ecotypes and populations have not been studied in arctic and alpine fungi using new molecular techniques. Further, because many of the Rocky Mountain collections are not yet sequenced, Table 3 is likely an underestimate of the diversity.

Although new molecular techniques hold the promise of analyzing an entire fungal community in alpine or arctic soils in a timely manner, caution is advised when interpreting the results. Brunner et al. (2017) compared historical morphological data generated by Favre (1955) to data produced using novel high-throughput DNA sequencing techniques on soil cores. He concluded that these new techniques using 97 percent sequence similarity were effective at genus-level identification but often failed to effectively delineate species. The molecular analysis of soil found many species not known from alpine habitats and produced molecular errors that complicated the analyses (chimeric sequence formation, primer bias, etc.). These molecular techniques also have the potential to amplify DNA that may not represent metabolically active members of the soil community. A problem inherent to next-generation sequencing techniques or high-throughput sequencing data is that the length of the DNA fragments that can be sequenced (ca. 300 bp) is small and often not informative enough to delimit species. Further, they do not produce vouchers of fungal collections. Brunner et al. (2017) stressed the importance of improving fungal DNA databases that will make high-throughput DNA sequencing techniques more effective in the future. The best way to improve fungal databases is through detailed taxonomic studies that combine morphological and molecular data, including the sequencing of type material when possible. The taxonomy of arctic and alpine fungi in North America is still poorly understood compared to that in arctic and

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.

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