SYSTEMATIC ANALYSIS OF *RUSSULA* IN THE NORTH AMERICAN ROCKY
MOUNTAIN ALPINE ZONE

by

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ABSTRACT

Russula Pers. (Russulales) is an important ectomycorrhizal fungal genus in alpine and Arctic regions where it occurs in association with *Salix*, *Betula*, *Dryas*, and *Polygonum*. Despite *Russula*'s importance and abundance in Arctic and alpine systems there has been no in-depth systematic analysis of the genus in these habitats. This is also true for alpine areas of the Rocky Mountains where only four species of *Russula* have been casually reported above treeline. The genus *Russula* is large, diverse, and intraspecific morphological variation makes taxonomic classification difficult, which means verification using molecular techniques is necessary. This research compared Rocky Mountain alpine *Russula* collections to Arctic and alpine collections from Europe using an in-depth morphological study and a systematic molecular analysis of the nuc rDNA ITS1-5.8S-ITS2 region (ITS barcode) and the second largest subunit of the RNA polymerase II gene (*RPB2*). Over 130 *Russula* collections were sequenced including type material. This research confirmed eight species with intercontinental distributions in Arctic and alpine habitats, including *R. nana*, *R. laccata*, *R. subrubens*, *R. cf. pascua*, *R. heterochroa*, *R. saliceticola*, *R. purpureofusca*, and *R. laevis*. Two species are reported from subalpine habitats at treeline; *R. montana* with conifers and *R. altaica* with *Betula*. The *Russula* present in the Rocky Mountain alpine represent a subset of those known from other Arctic-alpine habitats and data show that multiple *Russula* species independently colonized alpine habitats. This is the first formal report of *R. altaica*, *R. saliceticola*, and *R. subrubens* in the Rocky Mountains and of *R. heterochroa* and *R. purpureofusca* in North America. Previous work matched sequences extracted from ectomycorrhiza in Canada to *R. laevis*, but this is the first work to collect this species and report it in North America. A key for the identification of alpine *Russula* in North America is provided. A history of Arctic and alpine mycology in North America is included and provides background material for the study. This work contributes to our knowledge of biodiversity in Arctic and alpine systems and will promote future ecological and taxonomic research on alpine *Russula* because little is known about these species or how to identify them.

Key words: Alpine, *Betula*, ITS, *RPB2*, *Salix*, taxonomy, Russulaceae

CHAPTER ONE

LITERATURE REVIEW: HISTORY OF ARCTIC AND ALPINE MYCOLOGY IN
NORTH AMERICA AND INTRODUCTION TO THE GENUS *RUSSULA*Arctic-Alpine Biome

The Arctic zone is defined as the vegetated areas between latitudes 66° and 70° N, which lies beyond the climatic limit of tree growth and south of the permanent ice sheets (Bliss 1988; Chapin & Körner 1995). The Arctic includes northern areas of Russia, Norway, Iceland, Greenland, Canada and the United States of America, which together comprise a circumpolar habitat (Callaghan et al. 2005). The alpine zone is defined as the open, vegetated areas above tree line in mountainous regions worldwide (Körner 2003). The lower limits of alpine regions can be as high as 3,500 m in equatorial regions or as low as 300 m in subpolar regions (Billings 1974). Alpine regions are disjunct habitats found at various latitudes. In North and South America, the alpine zone is a nearly contiguous system of island mountain tops stretching from the Arctic to the Subantarctic (Billings 1974; Körner 1995).

Distinguishing Arctic and alpine habitats from those of subarctic and subalpine habitats is often difficult because scattered and variable vegetation can obscure the boundaries between them. Arctic and alpine systems are responsible for retaining and regulating water resources for human use (Körner 2003) and also have the ability to store large amounts of carbon making them efficient carbon sinks (Tarnocai et al. 2009). Due to severe environmental filters, large coniferous and deciduous trees are unable to grow

and species richness declines with increasing latitude and altitude (Walker 1995; Billings 1974). Arctic and alpine habitats are similar in that they often experience cold temperatures, high winds, and a majority of their moisture as snow fall; these factors result in a short growing season and poorly developed soils (Billings 1973; Körner 1999, 2003). However, due to difference in geographic locations, there are daily and annual differences in temperature, and in the length of the growing season; there is also considerably more vertical relief in alpine zones (Billings 1973; Chapin & Körner 1995; Körner 1999). Together Arctic and alpine regions make up 5% and 3% of land on earth, respectively (Chapin & Körner 1995; Körner 1999, 2003), and because of their similarities, they are collectively referred to as the Arctic-alpine biome (Bliss 1962, 1988; Billings 1973; Löve & Löve 1974; Chapin & Körner 1995; Murray 1995).

Mounting evidence suggests that anthropogenic activity is drastically increasing the atmospheric concentration of carbon dioxide (CO₂) and other greenhouse gasses (H₂O, CH₄, N₂O, and O₃) leading to increased global warming and variable changes in precipitation (IPPC 2014; Semenova et al. 2016). Research suggests that Arctic and alpine environments are being disproportionately affected by global warming compared to other systems, this is referred to as Arctic amplification (Serreze and Barry 2011; IPPC 2014). The temperature in Arctic-alpine regions is increasing 0.1° C per year, which is among the highest temperature increases recorded (Anisimov et al. 2007; Comiso and Hall 2014). Recent work also suggests that higher elevations will see increased warming (Wang et al. 2016). Another factor that has been historically underestimated, is the thawing of permafrost in Arctic systems, which is releasing large amounts of greenhouse

gasses. As these gasses enter the atmosphere, it will create a positive feedback loop leading to increased rates of global warming (Tarnocia et al. 2009). As the climate warms, alpine communities will be restricted to ever-decreasing areas on mountain tops or will even disappear completely (Grabherr et al. 1995). Most alpine regions are highly fragmented, disconnected, and contained within small areas of land, and the species present are often adapted to the harsh conditions found at high elevations (Anthelme and Lavergne 2018). These unique characteristics of alpine habitats have important implications for conservation of biodiversity and ecosystem functioning. A changing climate along with increased warming has the potential to drastically increase extinction rates of Arctic and alpine species.

Arctic and Alpine Fungi

While much is known about the flora and fauna in Arctic and alpine habitats, less is known about the funga (Dahlberg and Bültmann 2013). Fungi play important roles in nutrient cycling in Arctic environments where they exist as symbionts, decomposers, and pathogens. Fungi are estimated to be one of the most species rich groups in the Arctic, yet most research has focused on lichenized fungi, which only represent a subset of fungal diversity. With climate inevitably changing, Arctic and alpine habitats are highly threatened, which could lead to the loss of understudied fungi that play important roles in the ecosystem. Therefore, it is important to monitor all Arctic and alpine fungi to gain a better understanding of fungal diversity and the role of fungi in ecosystem functioning (Dahlberg and Bültmann 2013).

Research on fungi in Arctic and alpine habitats, has been ongoing for the last two centuries, primarily in Europe. These studies have provided the basis for taxonomic classification of alpine fungi via morphological identification using macro and microscopic features derived from sporocarp surveys. Europe has a rich history of mycology that supports and encourages investigation by amateurs and professionals alike. Selected studies that provide information on fungi in Arctic and alpine habitats of Europe are outlined in TABLE 1.

Table 1. Selected surveys of Arctic and alpine fungi in Europe, Asia, and Arctic Islands.

Location	Reference(s)
Alps, Austrian	Peintner 1998
Alps, French	Kühner 1975; Lamoure 1982; Bon 1985; Kühner and Lamoure 1986; Bon and Cheype 1987; Bon 1991, 2000; Moreau 2002
Alps, German	Schmid-Heckel 1988; Bresinsky et al. 2000
Alps, Italian	Horak 1960; Bon 1987; Jamoni 1995, 2008
Alps, Swiss	Favre 1955; Irlet and Rieder 1985; Senn-Irlet 1987; Graf 1994
Bulgaria	Gyosheva and Dimitrova 2011
Faroe Islands	Vesterholt 1998
Finland	Ohenoja 2000
Iceland	Christiansen 1941; Hallgrimsson 1998
Norway	Lange and Skifte 1967; Gulden and Lange 1971; Gulden et al. 1985; Gulden 2005
Pyrenees	Bon and Noguera 1995; Bon and Ballarà 1996; Corriol 2008
Russia	Knudsen and Mukhin 1998; Niezdoiminogo 2003
Scotland	Watling 1987
Slovakia	Fellner and Landa 1993a, 1993b
Southern Carpathians	Ronikier 2008
Svalbard	Gulden et al. 1985; Skifte 1989; Gulden and Torkelsen 1996
Sweden	Kühner 1975

In contrast, there have been comparatively fewer studies of Arctic and alpine fungi in North America. This is likely due to that fact that there are fewer mycologists, Arctic and alpine habitats are remote, and a long mycological history is lacking. Arctic and alpine areas of North America are distributed across a large expansive landscape and many areas, particularly in the Canadian Arctic and the northern Rocky Mountains, are remote and inaccessible. Despite these limitations, there is some early information on the fungi present in Greenland (Borgen et al. 2006), Northern Canada (Ohenoja and Ohenoja 2010), Alaska (Laursen and Ammirati 1982a; Miller 1987, 1993, 1998), and the central and southern Rocky Mountains (Cripps and Horak 2008). In general, knowledge of fungal diversity in North America is much less complete than in Arctic-alpine Europe and particular Arctic islands.

The History of Arctic and Alpine Mycology in North America

Several papers have briefly summarized the history of Arctic mycology in North America (Kobayasi et al. 1967; Hutchison et al. 1988) and a few have provided detailed accounts of the mycological history of Canada, including Arctic regions (Savile 1963; Estey 1994; Redhead and Baillargeon 1999; Väre 2017). However, no historical review has focused on alpine fungi in North America and no comprehensive history of mycological studies in Arctic and alpine regions of North America has been compiled. As a contribution to the field, this section provides a historical overview of Arctic and alpine mycology in North America. Although Greenland is considered part of the North American continent, Arctic and alpine fungi on Greenland has been extensively studied (Lange 1957; Peterson 1977; Knudsen and Borgen 1982; Borgen 2006; Borgen et al.

2006) and summarized in *Arctic and Alpine Mycology 6* (Boertmann and Knudsen 2006) and therefore, this island is excluded from this work.

Early Expeditions to the Canadian Arctic (1819-1940)

During the nineteenth century, Arctic expeditions were exploring the northern polar regions of North America. These expeditions were funded by wealthy business men or supported by government agencies (Berkeley 1878; Rostrup and Simmons 1906; Lind 1910; Dearness 1923; Nares 2011) and included crew members with experience in sailing, Arctic travel, craftsmanship, engineering, and a variety of sciences. Arctic expeditions were often exciting, dangerous, and only for adventurous types as members often died during these expeditions, which could last for up to five years. 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 would bring back large fleshy fungi; 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* (*Arrhenia lobata*), *Lycoperdon pratense*, and

fifteen species of lichen on the island (Brown 1823). According to Redhead and Baillargeon (1999) these two collections are the earliest published record of any agaric in Canada. Dr. John Richardson, a surgeon on Captain Sir John Franklin's second overland expedition (1825–1827), was the next to collect Arctic fungi; this expedition through the Canadian Arctic crossed the Northwest Territories and reached the Arctic Ocean (Berkeley 1839; Väre 2017). Richardson's collections were placed in the prestigious herbarium of Sir William Jackson Hooker who was later appointed director of the Herbarium at Kew in 1841 (Desmond 1995). The names and descriptions of these fungi are found throughout Rev. Miles Joseph Berkeley's paper published on exotic fungi (Berkeley 1839). Berkeley, an English clergyman with a strong interest in cryptograms and mycology, is considered one of the founders of plant pathology (Massee 1913) and was one of the first mycologists to study fungal material from the Canadian Arctic.

Captain Franklin set out again in 1845 with two ships, the HMS Erebus and the HMS Terror, in an attempt to traverse some of the last unknown sections of the Northwest Passage. This final voyage would end tragically with the deaths of 129 men, including Franklin's, and the loss of both ships (Neatby and Mercer 2008). Franklin's widow, Lady Jane Franklin, would go on to finance five expeditions in search of her husband's lost remains. Interestingly, Arctic fungi were collected on two of these expeditions. The one led by Admiral Belcher in 1852 set out with at least four ships and only one returned; it is noteworthy that, Dr. David Lyall, a physician and naturalist who was with the returning expedition, collected *Arrhenia lobata* (again recorded as *Cantharellus lobatus*) in 1853 at Wellington Channel (Polunin 1940). Redhead (1984)

noted that Lyall's collection of *A. lobata* would be the first confirmed collection (based on preserved material) of the fungus from North America and it was placed in the Herbarium at Kew. The fifth and final expedition that set out to search for Franklin's party, in 1857, was led by Sir Francis Leopold M'Clintock in the Yacht 'Fox', a boat purchased by Lady Franklin (M'Clintock 1860). M'Clintock's expedition included Dr. David Walker, surgeon and naturalist, who was the next documented explorer to collect Arctic fungi. Walker focused primarily on botanical collections; however, he also collected five basidiomycete fungi in the genus *Agaricus* (agarics) and one ascomycete (Hooker 1860). Walker was not well versed in botany; therefore, all 170 collections were given to Sir Joseph Dalton Hooker, William Hooker's son who succeeded him as director at Kew (Desmond 1995), for determination. Hooker then passed all of the fungi to Berkeley for review (Hooker 1860). Berkeley continued to contribute to Arctic mycological investigations when he published on 26 species (23 species from Arctic Canada and three from Greenland) of Basidiomycota and Ascomycota collected during the Arctic Expedition from 1875–1876 (Berkeley 1878).

The study of Arctic fungi continued with the Harriman Alaska Expedition of 1899 when William Trelease and other botanists collected Arctic fungi from Alaska (Trelease 1904). In 1904 Pier A. Saccardo, Charles H. Peck, and W. Trelease published a list of all known fungi in Alaska. Their list contained the names of fungi collected from the Harriman Alaska Expedition, from which, Saccardo and Scalia describe three new species of Arctic micromycetes. The list also includes four other Arctic species, all of which were collected from Point Barrow (Saccardo et al. 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 fungi were collected from Ellesmere Island in Northern Canada and included macromycetes and micromycetes, although most were saprotrophs associated with phanerogamous vegetation; eight new species were described (Rostrup and Simmons 1906). The Gjoa expedition under Captain Ronold Amvindsen from 1904–1906 visited King Point on the Yukon Coast and King William Island. Fungal collections extracted from plants were observed 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. Lind would continue researching Arctic micromycetes throughout the early 20th century. He examined herbarium material of Arctic vascular plants and produced detailed publications focused on the parasitic and saprophytic fungi present; including their ecology, hosts, dispersal, geographic distribution and diversity (Lind 1927, 1934). In 1909, agrostologist A. S. Hitchcock traveled through the Alaskan interior looking at various grasses. He collected Arctic uredineous rust fungi Near Nome, which he shared with J. 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). He noted the wide host range and relative lack of parasitic fungi, only recording three rusts and one smut. 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 later returned to the Basidiomycota after more than a half century focusing on the fleshy fungi of southern Baffin Island (Dearness 1928). One of the last true Arctic Expeditions was the Oxford Exploration Club's 1931 expedition to Akpatok Island, after which Nicholas Polunin (1934) published a list of the 24 fungi he collected. The macromycetes collected during the eight major arctic expeditions outlined above are listed in TABLE 2. Overall, research from these early expeditions found relatively few fungi in multiple genera and with a variety of ecological roles. Most if not all of these fungi were originally described from Europe and were similar to the fungi found in previously studied Arctic regions. These studies provide a base for future mycologist to begin exploring fungal diversity in Arctic regions of North America. 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.

Table 2. Macromycetes collected during early Arctic expeditions from 1819 though 1931. Names and authorities as reported.

Expedition	Species Reported	Location	Citation
Captain William Edward Parry's Expedition (1819-1820)	<u>Basidiomycota</u> : <i>Cantharellus lobatus</i> Peck and <i>Lycoperdon pratense</i> Pers.	Melville Island, Canada Arctic Archipelago	Brown 1823
Captain Sir John Franklin's Second overland expedition (1825-1827)	<u>Basidiomycota</u> : <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)	<u>Basidiomycota</u> : <i>Cantharellus lobatus</i> Peck	Wellington Channel, Nunavut, Canada	Polunin 1940
Sir Francis Leopold M'Clintock's Expedition in the Yacht 'Fox' (1857-1859)	<u>Basidiomycota</u> : <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 1875-1876	<u>Ascomycota</u> : <i>Peziza stercorea</i> P. and <i>Urula hartii</i> B. <u>Basidiomycota</u> : <i>Agaricus (Clitopilus) undatus</i> Fr., <i>Agaricus (Naucoria) bellotianus</i> B., <i>Agaricus (Omphalia)</i>	Northern Nunavut, Canada	Berkeley 1878

Second voyage of the Fram Expedition (1898-1902)	<p><i>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.</p> <p><u>Ascomycota</u>: <i>Mollisia graminis</i> (Desm.), <i>Niptera melatephra</i> (Lasch.), and <i>Sclerotinia vahliana</i> Rostr.</p> <p><u>Basidiomycota</u>: <i>Cantharellus lobatus</i> (Pers.), <i>Collybia dryophila</i> (Bull.), <i>Galera hypnorum</i> (Batsch), <i>Hebeloma fastibilis</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.).</p>	Ellesmere Island, Nunavut, Canada	Rostrup and Simmons 1906
Canadian Arctic Expedition (1913-1918)	<p><u>Ascomycota</u>: <i>Peziza micropus</i> Pers. var. <i>flavida</i> Phil., <i>Scleroderris fuliginosa</i> (Fr.) Karst., and <i>Scutellina scutellata</i> (L.). <u>Basidiomycota</u>: <i>Boletus scaber</i> Fr., <i>Cantharellus muscigenus</i> Fr., <i>Calvatia 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.</p>	Northern Regions of Nunavut, Northwest Territories, and the Yukon, Canada	Dearness 1923
Oxford Exploration Club's 1931 Expedition to Akpatok Island	<p><u>Ascomycota</u>: <i>Helvella lacunosa</i> Afz., <i>Peziza acetabulum</i> L., and <i>Sphaerospora asperior</i> (Nyl.) Sacc. <u>Basidiomycota</u>: <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 perlatum</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.</p>	Akpatok Island, Nunavut, Canada	Polunin 1934

Detailed Morphological Studies

Detailed mycological work that focused on Arctic fungi in North America includes researchers who focused on micromycetes, fungi that produce small, inconspicuous fruiting bodies, or researchers who focused on macrofungi, which produce large, conspicuous fruiting bodies. Usually mycologist focused their studies on

micromycetes or macrofungi, with little overlap between the two. Therefore, Arctic micromycetes and macrofungi are separated here to provide an overview of each group.

Arctic Micromycetes. Margaret Newton and J. P. Anderson undertook the first detailed morphological studies of cold-climate micromycetes in 1940. Their work expanded our understanding of plant parasitic fungi, mainly rusts, in the Northwest Territories and Northern Alaska (Estey 1994; Anderson 1940). Shortly after, in 1953, 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). As research into Arctic fungi began ramping up in the 1960s, Douglas Barton Osborne Savile, a prominent Canadian mycologist, focused on understanding the diversity of parasitic fungi in the Canadian Arctic (Savile 1961, 1963). His work highlighted the evolutionary history of these organisms by connecting plant parasitic fungi like *Puccinia* and *Ustilago* to their hosts, which contributed significantly to the taxonomic understanding of these groups. Savile's research would later be praised for initiating detailed mycological investigations into fungi of the Canadian Arctic (Kobayasi et al. 1967). Savile went on to collaborate with John A. Parmelee on parasitic micromycetes of Queen Elizabeth Island (Savile and Parmelee 1964) and later wrote a review of Arctic fungi (Savile 1972). Parmelee continued to describe micromycetes in the Canadian Arctic (Parmelee 1968), which further increased our understanding of the fungi on Central Baffin Island (Parmelee 1969) and in the Yukon (Parmelee and Ginns 1986). Parmelee's research on Arctic fungi culminated with his 1989 paper focused on the Uredinales (now

Pucciniales) of Arctic Canada, which contained excellent figures and a key to the order and all major genera (Parmelee 1989). Dr. Margaret Barr was the next mycologist to study micromycetes in the Canadian Arctic. She published a landmark paper on Pyrenomycetes that provided taxonomic clarification for the group and simplified identification (Barr 1959). Next, William Bridge Cooke surveyed soil and water for fungi in the Alaskan tundra near the Eskimo village of Napaskiak (Cooke and Fournelle 1960). Shortly after, Wehmeyer (1961) published a monograph of *Pleospora* and its allies, which included Arctic fungi.

Japanese mycologist Yosio Kobayasi yearned to visit the biologically diverse Arctic after a trip to Antarctica in 1963. In 1965, his opportunity arose and Kobayasi organized a small party to perform field work in the Alaskan Arctic. Kobayasi's team arrived in Point Barrow, Alaska on August 1, 1965 and began three weeks of exploration and experimentation at various sites in the region. During their research, they isolated fungi from soil, dung, water (water molds), plant material, animal bones, and insects (in an unsuccessful search for Trichomycetes). Kobayasi's team estimated that over 450 taxa of micromycetes were present in the Alaskan Arctic (Kobayasi et al. 1967). In all, the party collected 230 fungi representing 61 families and 136 genera; six species were new to science. Just as Lind (1910) noted, Kobayasi's party recognized that the harsh environmental factors and corresponding altered fungal appearance complicated identification.

Arctic Macrofungi. Up until the 1950's little research had focused on the larger fruiting bodies produced by the Ascomycota and the Basidiomycota in the Arctic,

otherwise known as macrofungi. In 1908 Elias J. Durand first confirmed Geoglossaceae 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 large distribution in Arctic regions. Hugh S. Spence and O. E. Jennings investigated the agarics of the Northwest Territories and on Southampton Island, respectively, and found species in the genera *Boletus*, *Calvatia*, *Cortinarius*, *Hydnum*, *Hygrophorus*, *Lactarius*, *Psathyrella*, *Russula*, and *Tubaria* (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 phaneograms.

During the 1950's several researchers began focusing on fungi in Northern Canada. James Walton Groves and colleagues published a series of articles starting with the Hypocreales and Discomycetes (Groves and Hoare 1954), followed by one on the Boletaceae (Groves and Thomson 1955), and lastly with a paper focused on the Amanitaceae, Hygrophoraceae, Rhodophyllaceae, and Paxillaceae (Groves et al. 1958). Groves research continued into the 1960s when he published a paper focused on the Gasteromycetes of Northern Canada with Constance A. Bowerman (Bowerman and

Groves 1962). Groves final paper, published one year after his death in 1970 in collaboration with M. E. Elliott, was on the Discomycetes of Northern Canada (Groves and Elliott 1971). During the same period, Howard E. Bigelow studied collections secured by government biological survey parties, which included some Arctic collections in the Tricholomataceae (Bigelow 1959). Bigelow also contributed to our knowledge of Arctic *Omphalina* in Alaska and Canada (Bigelow 1970).

Towards the end of the 1960s, Orson K. Miller Jr., a mycologist trained under Alexander Smith, became interested in Arctic fungi after a visit to Alaska with Robert L. Gilbertson in 1967 and 1968 (Cripps 2010). Miller's interest in Arctic fungi would last for the next 30 years, and Miller would inspire several mycologists to examine the understudied fungi in these remote areas. Miller published three papers focused on gasteromycetes from the Yukon territory and adjacent Alaska; he was considered an expert on this group by his peers (Miller 1968, 1969; Miller et al. 1980). Miller then turned his attention to Arctic and subarctic Basidiomycota in Canada and Alaska publishing on *Coprinus* with Roy Watling (Watling and Miller 1971), the genera *Omphalina*, *Laccaria*, and *Coprinus* with David F. Farr (Farr and Miller 1972), and on *Melanoleuca* with Linnea S. Gillman (Gillman and Miller 1977). Miller had several students who focused on the study of Arctic fungi. Robert K. Antibus studied fungal ecology in the Arctic and two other Miller students, Gary Laursen and T. G. Rau, who focused on soil fungi and fungal decomposition respectively in the Alaskan tundra (Laursen 1975; Rau 1977). Miller went on to publish a series of papers with Laursen, first on Arctic and alpine agarics in Alaska and Canada (Miller et al. 1973; Laursen et al.

1976); then on fungal hyphae belowground-biomass and distribution in Alaska (Miller and Laursen 1974; Laursen and Miller 1977); and lastly, on the function, distribution, and known plant associates of mycorrhizal fungi of the Alaskan tundra (Miller and Laursen 1978). Laursen would focus a large part of his early career on Arctic fungi, collaborating with several other mycologists. Laursen and Harold H. Burdsall Jr. found *Geopora cooperi* in association with *Salix alaxensis* in the Alaskan tundra, expanding its distribution to include Arctic regions (Laursen and Burdsall 1976).

In the 1980s, Laursen and Joe Ammirati studied *Lactarius*, *Cortinarius*, and Hygrophoraceae in the Alaskan Arctic tundra (Laursen and Ammirati 1982a; Ammirati and Laursen 1982; Laursen et al. 1987a). Miller continued publishing heavily on Arctic fungi into the '80s and '90s and this includes a review of the current taxonomic understanding of Arctic fungi at Point Barrow, AK (Bunnell et al. 1980). Miller studied higher fungi in the subarctic tundra of Alaska and the Yukon (Miller 1982a; Miller 1987), *Marasmius epidryas* with Canadian Mycologist Scott Redhead (Redhead et al. 1982), *Phaeogalera* and *Galerina* with prominent 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 et al. 1982). Miller continued to publish into the early 2000s when he focused on three *Hebeloma* species in the alpine tundra of Colorado, recognizing that these species were also present in the Arctic tundra in Europe (Miller and Evenson 2001).

While Miller and colleagues were exploring the Alaskan Tundra, Scott Redhead provided clarification for the Arctic species *Gerronema pseudogrisella* (Redhead 1980), published a detailed overview of *Arrhenia* in Arctic North America (Redhead 1984), 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, he noted that fungal species found in the high Arctic and in Arctic-alpine habitats have intercontinental distributions that match Arctic and alpine floristic patterns. Around the same time, Hutchinson, Summerbell, and Malloch (1988), who were intensively studying the fungi of Quebec, noticed that a majority of the fungi they collected in Northern Quebec were also present in Arctic regions of Greenland and Northern Europe (Gulden et al. 1985; Bresinsky 1987; Watling 1987). The collections of Durand (1908), Miller et al. (1982), Redhead (1984), and Hutchinson et al. (1988) further support 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 European mycologists have studied Arctic-alpine fungi in North America. H. Heikkila and P. Kallio from Finland showed that *Omphalina* is one of the most common genera in Arctic-alpine 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 16 new species in North America. Esteri

Ohenoja and Martti Ohenoja focused on the macromycetes in Arctic Canada during trips to the Hudson Bay in 1971 and 1974 (N.W.T. and Manitoba). Working independently and in collaboration with various authors they studied *Lactarius* (Ohenoja and Ohenoja 1993), *Inocybe* (Ohenoja et al. 1998), *Marasmius epidryas* (Redhead et al. 1982), Ascomycetes in Finland noting some distributions extending into North America (Ohenoja 1975), and the fungal diversity at Rankin Inlet (Ohenoja 1972). Ohenoja and Ohenoja (2010) then summarized all of their findings in the Canadian Arctic. Prominent Norwegian Mycologist Gro Gulden also contributed knowledge on Arctic and alpine species of *Lepista* from Alaska (Gulden 1983) and *Galerina* from Schafferville (Noordeloos and Gulden 1992).

Arctic and alpine Fungal Ecology. 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. Flanagan and Scarborough (1973, 1974) investigated fungal decomposition and Laursen and Chmielewski (1982) focused on the ecological significance of mutualistic and saprophytic soil fungi, all in the Arctic Tundra. During this same time mycorrhizal fungi started getting the attention of mycologists in Arctic and alpine regions (See Ectomycorrhizal Fungi and Hosts in Arctic-alpine environments). A. E. Linkins and Robert K. Antibus studied the ectomycorrhizal fungi of *Salix rotundifolia* following oil contamination of the soil. They found reduced numbers of viable mycorrhizae, an altered fungal mantle (Antibus and Linkins 1978), decreased root respiration rates, and reduced

adaptation to cold temperatures (Linkins and Antibus 1978); however, these effects were less prominent at a natural oil seep in Cape Simpson. Antibus and colleagues went on to investigate ectomycorrhizal synthesis of local and non-native fungi with *Salix rotundifolia* in Alaska (Antibus et al. 1981). Orson K. Miller Jr. also studied fungal biomass in Alaska in natural (Miller 1982b) and oil contaminated soils (Miller et al. 1978). The mycorrhizal status of plants in the Arctic Tundra and in alpine regions of Montana and Wyoming were assessed by Linkins and Antibus (1982) and Lesica and Antibus (1986a, 1986b). Antibus later reported on the physiology of ectomycorrhizal fungi from his earlier research, focusing on the effects of temperature, at Point Barrow (Antibus 2010).

Shortly after the turn of the century, Kernaghan and Harper (2001) began assessing edaphic factors, i.e. how ecological habitat change from subalpine to alpine affected ectomycorrhizal diversity in the Canadian Rockies. They reported that in alpine areas of the Front Range of the Rocky Mountains, fungi appeared to be non-host specific, forming mycorrhizal associations predominantly with conifers below treeline and with angiosperms like *Salix* and *Dryas* above treeline. They hypothesized that these interactions would facilitate upward movement of treeline due to pre-existing mycorrhizal fungi. The research of Schadt et al. (2003) marked a significant shift in the theoretical understanding of the biogeochemical processes in the alpine tundra of Colorado. Their research showed evidence of microbial communities, primarily consisting of fungi, maintaining significant biological activity under snow-cover, this

finding challenged our previous understanding of biogeochemical cycling in cold environments.

The International Symposium on Arctic and Alpine Mycology (1980 – 2016)

On August 16th, 1980, during the most productive fruiting period for Arctic and alpine fungi, an esteemed group of 25 mycologists from 9 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 pertinent 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 systems and the week-long meeting was an overwhelming success, providing detailed knowledge of the fungal community at Point Barrow (Laursen and Ammirati 1982a). Mycologists in attendance were required to submit a paper focusing on Arctic and/or alpine fungi for the proceedings. The format of the first meeting consisted of several days collecting fungi in the field followed by evening lectures to discuss proposed contributions. Because of the relative lack of knowledge on Arctic-alpine fungi, the first ISAM, focused on determining the fungi present. Fungal taxonomy would continue to dominate all subsequent meetings.

After the first ISAM, it was decided that a select group of professional Arctic and alpine mycologists would meet every four years on varying continents 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 conducted thus far and

more than 100 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 3 summarizes the research published in each proceeding that contributes information on Arctic and alpine mycology in North America.

Table 3. Research published in the proceedings of the ten International Symposia on Arctic and alpine mycology focused on North American fungi.

Symposium	Research on Arctic and alpine mycology in North America	Acting President	Editor(s)
1st ISAM, August 1980. Barrow, Alaska, U.S.A.	Basidiomycetes in subarctic Alaska (Miller 1982a), <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 Chmielewski 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 et al. 1987a)	Egon Horak	Laursen et al. (1987b)
3rd ISAM, August 1988. Svalbard	The 3 rd and 4 th ISAM were combined into one proceeding and the following research related to Arctic and alpine mycology in North America was included:	Sigmund Sivertsen	Petrini and Laursen (1993)
4th ISAM, August 1992. Lanslebourg, France	<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)	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 et al. 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 (Horak and Moser 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/Wyomi ng, U.S.A.	<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 et al. 2010), Larger fungi in Arctic and subarctic Canada (Ohenoja and Ohenoja 2010), <i>Inocybe (Malloocybe)</i> in the Rocky Mountain alpine (Cripps et al. 2010), Lycoperdaceae on the Beartooth Plateau (Kasuya 2010, Jalink 2010), and Mollisoid 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 et al. 2014) and <i>Lactarius</i> from the Rocky Mountain alpine zone (Cripps and Barge 2013)	Esteri Ohenoja	Ohenoja et al. (2018)
10th ISAM, August 2016. Kanazawa, Japan	<i>Inocybe</i> species distributed in the North American Alpine (Larsson et al. 2018)	Tamotsu Hoshino	Hoshino et al. (2018)

Fungi in the Rocky Mountain Alpine Zone

Many mycologists have focused their attention on Arctic fungi in Alaska and Canada over the last century; however, little attention was paid to the alpine fungi in the mountainous regions of the continent. At the beginning of the 20th century, researchers began reporting macromycetes from the Rockies (Overholtz 1919; Kauffman 1921; Seaver and Shope 1930; Solheim 1949); however, no research on true alpine fungi above treeline occurred until the 1980s when Meinhard Moser made a few brief visits to the North American alpine. Moser made several collecting trips to the Greater Yellowstone Area, which included alpine regions of Yellowstone National Park, the Beartooth Plateau in Montana and Wyoming, and the Windriver Mountains of Wyoming. Moser primarily described *Cortinarius* from these regions but also reported *Russula nana* for the first time from the Rocky Mountain alpine (Moser and McKnight 1987; Moser 1993; Moser et al. 1994, 1995). Redhead also reported *Arrhenia lobata* from Colorado after examining several of Alexander H. Smith's collections from the Rocky Mountain alpine; *A. lobata* is

a common Arctic-alpine species known from the Alps, Greenland, and Iceland (Redhead 1984).

Research into the diversity of lichens in the Rocky Mountain alpine started much earlier than research into the macro or micromycetes of the region. William A. Weber (1955) and Henry A. Imshaug (1957) provided historical accounts of lichenology in the Rocky Mountain alpine, starting as early as 1861. Imshaug also compiled a list of all the lichens present in alpine regions of the western United States and Canada, provided keys to alpine lichen identification and maps of their distribution (Imshaug 1957). Weber, a trained botanist who became obsessed with lichens in 1951, published a book on lichens of the Rocky Mountains that included alpine collections from the central and southern regions of the range (Corbridge and Weber 1998). Other researchers were also exploring the diversity of lichens in the Rockies; Eversman (1995) compiled a list of over 300 species of lichens in the alpine of the Beartooth Plateau and Erik D. Ahl's Master's Thesis focused on understanding how lichen diversity and abundance changes from alpine to subalpine sites at Rocky Mountain National Park in Colorado (Ahl 2016). With the start of the new millennium, research into the fungi present in Alpine regions of North America, and especially the southern Rocky Mountains, would increase substantially.

In 1996 Monique Gardes and Anders Dahlberg wrote a review on the diversity of mycorrhizal fungi in Arctic and alpine regions. They focused on the major mycorrhizal relationships in these systems including arbuscular mycorrhizae, dark septate fungi, ectomycorrhizae, and ericoid associations. The occurrence of these mycorrhizal types is highly variable and certain Arctic-alpine plants lack mycorrhizal associations completely

(Gardes and Dahlberg 1996). Gardes and Dahlberg (1996) identified mycorrhizal associations in cold-dominated environments as a potential model for understanding the evolution of mycorrhizal symbioses. They outlined future research questions requiring investigation, focused on the use of molecular tools to answer questions about the fungal species present, and mycorrhizal community structure and dynamics. Gardes and Dahlberg's review set the stage for future research into mycorrhizal fungi in Arctic and alpine areas.

In 1999 a survey of alpine fungi in the Rocky Mountains was initiated by Cathy Cripps and Horak with funding from a National Science Foundation Grant. Cripps is a professor at Montana State University in Bozeman and another former student of Miller's who was interested in Arctic and alpine fungi. Cripps and Horak were the first to survey alpine fungi in the Rocky Mountains on a large scale and their work focused on the central and southern Rockies. Later that same year a preliminary report on the agarics found in the Rocky Mountain alpine zone was presented at the International Botanical Congress (Cripps and Horak 1999). Cripps and Horak's investigation of the alpine fungi continued throughout the early 2000s and information on the distribution of ectomycorrhizal genera and their associated plant hosts in the Rocky Mountain alpine was disseminated at various conferences; genera discussed included: *Amanita*, *Inocybe*, *Russula*, *Lactarius*, and *Hebeloma* (Cripps and Horak 2002, 2005, 2007; Cripps 2003; Cripps et al. 2008). A review contributed information on the mycorrhizal status of alpine plants, including those of the Beartooth Plateau (Cripps and Eddington 2005). This review reported that 68% of alpine vascular plant species form mycorrhizal associations.

These associations included ectomycorrhizae, arbuscular mycorrhizae (AM), ericoid fungi, and arbutoid mycorrhizae; arbuscular mycorrhizal plant-fungal associations were the most common. Previously, Lesica and Antibus (1986a, 1986b) had only assessed arbuscular mycorrhizal root colonization on fell-field plant communities and on hemiparasitic vascular plants in alpine regions of the Rocky Mountains. Cripps and Horak (2006) reported the well-known Arctic-alpine species *Arrhenia auriscalpium* from Colorado; this species is known for its intercontinental distribution, and they reported the highest elevation and the furthest latitude south recorded for the fungus.

In 2008 Cripps and Horak published a preliminary list of alpine fungi in the Rocky Mountains in the proceedings of the seventh ISAM (Cripps and Horak 2008). At this date, their research revealed over 165 species from 46 genera and 11 families. They estimated that at least 75% of the macromycetes present in the Rocky Mountain alpine are known from other Arctic-alpine environments; the remaining 25% could be endemic. Based on these findings, the most diverse mycorrhizal groups in the Rocky Mountain alpine zone are the Cortinariaceae, Inocybaceae, and Hydnangiales with over 74 species. They 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 on the Beartooth Plateau (Cripps and Horak 2008).

Around this time, molecular DNA methods and phylogenetic analysis became cheaper and easier to use, providing researchers with a powerful and independent way to verify taxonomic determinations based on morphology. Armed with large molecular data sets and a basic understanding of the fungal diversity mycologists began investigating the

fungi in the Rocky Mountain alpine zone, focusing primarily on ectomycorrhizal genera. Cripps student Todd Osmundson investigated *Laccaria* in the Rockies (Osmundson et al. 2005). He utilized ribosomal DNA from the ITS region, along with morphological and cultural data; systematic analysis revealed five species in the Rocky Mountain alpine zone. *Laccaria laccata* var. *pallidifolia* and *L. nobilis* were reported for the first time in Arctic-alpine habitats and *L. pseudomontana* was new to science. Another Cripps student, Ed Barge, focused on the distribution and morphology of the genus *Lactarius* (Russulales, Russulaceae) in the Rocky Mountain alpine zone. Together they confirmed six species in the Rocky Mountain alpine zone, one new to science, found that most species were intercontinentally distributed in Arctic-alpine regions, and that species distribution may have been shaped by glaciation, host ranges, and long-distance dispersal (Barge et al. 2016; Barge and Cripps 2016). Additional molecular and morphological analyses have investigated the ectomycorrhizal genera *Hebeloma* (Beker et al. 2010; Cripps et al. 2019a), *Cortinarius* (Peintner 2008), and *Inocybe* (Cripps et al. 2010; Larsson et al. 2014; Larsson et al. 2018; Cripps et al. 2019b) in the Rocky Mountain alpine. All of the molecular studies listed above have confirmed intercontinental distributions and disjunct populations of numerous species, with the exception of Osmundson et al. (2005), in which this was not addressed. Although a few alpine *Russula* species have been reported from the Rocky Mountains (Cripps and Horak 2007; Cripps and Horak 2008; Cripps et al. 2016), detailed investigation is still needed to understand the true diversity of the genus in this region.

Ecological and Biogeographic Research on Arctic and Alpine Fungi in North America

In the last decade, there has been a dramatic increase in the number of studies concerned with 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% internal transcribed spacer 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). A few studies have hypothesized that long distance dispersal plays an important role in the distribution of Arctic fungal genera (Geml et al. 2012; Timling et al. 2014). Other recent studies have assessed how these fungi are affected by climate change and a warming Arctic (Deslippe and Simard 2011; Dislippe et al. 2012; Morgado et al. 2015; Geml et al. 2015, 2016; Semenova et al. 2016). Although not strictly concerned with North America, several reviews have addressed fungi in the Arctic. These reviews focus on cold adaptation (Robinson 2001), Basidiomycota decomposers (Ludley and Robinson 2008), the current status of fungal knowledge and species richness (Dahlberg and Bültmann 2013), the taxonomic and ecological structure of basidial macromycetes (Shiryaev et al. 2018), and fungi in polar regions (Tsuji and Hoshino 2019).

Prominent microbial ecologist, Steve K. Schmidt and colleagues have assessed the presence of dark-septate fungi and arbuscular mycorrhizal fungi in the Front Range of the Colorado Rocky Mountains (Schmidt et al. 2008). More recently Schmidt et al. (2012) examined the diversity of fungi in-between the alpine zone and the zone of permanent ice, which lacks plants and is referred to as the periglacial zone. They

compared fungal communities in the periglacial zone in Colorado, the Andes, and the Himalayas and found that zoosporic fungi in the order Spizellomycetales dominate (Schmidt et al. 2012). They go on to hypothesize that these fungi complete their lifecycle with the available free-moisture from snowmelt and then remain dormant for a majority of the year. Working closely with Schmidt, Ph.D. student Clifton P. Bueno de Mesquita, was the main author on multiple papers that investigated the arbuscular mycorrhizal fungi and root endophytes on Niwot Ridge in Colorado. They characterized the development of these fungi throughout the plant growing season (Bueno de Mesquita et al. 2018a) and found that colonization by these two groups of fungi was highly variable between plant species. They concluded that these fungi play important roles in the cycling of nitrogen and phosphorus in alpine systems (Bueno de Mesquita et al. 2018b).

Ectomycorrhizal Fungi and Plant Hosts in Arctic-Alpine Environments

Currently, the dominant hypothesis explaining the distribution of Arctic and alpine floras states that the alpine flora is derived from an ancient Arctic flora, which has moved up and down mountains due to changes in glaciation across North America (Billings 1974). Alternatively, Weber (2003) hypothesized that North American alpine floras have been around since the Tertiary period and therefore predate modern Arctic floras. This would imply that mountainous floral communities migrated into low-land Arctic communities following deglaciation. If Weber's (2003) hypothesis is true, large-scale migration and an Arctic origin of alpine floras may not explain the modern Arctic-alpine floral and fungal communities as proposed by Billings (1974). Based on Weber's (2003) hypothesis the term 'oroboreal' is a more appropriate descriptor than

‘circumpolar’ for describing the distribution of floral and fungal communities throughout the northern hemisphere because it implies a mountainous rather than Arctic origin.

Either way, plant communities in the alpine are in some ways similar to those in the Arctic and there is considerable overlap of species within the two regions (Billings 1974). However, Billings (1974) hypothesizes that alpine plant species are ecotypically different due to isolation during glacial phases of the Pleistocene and Chapin and Körner (1995) believe alpine communities have higher species richness due to niche differentiation.

Woody plants are particularly important in the alpine and in combination with grasses comprise the largest biomass in the biome (Körner 2003). A majority of the vascular-plant biomass is made up of less than ten species in most Arctic and alpine zones and most of the plant diversity will be present in 1 km² (Chapin & Körner 1995). These Arctic and alpine plants have adapted to the harsh conditions present in these cold-dominated regions (Körner 1999).

Most Arctic and alpine vascular plants form mutualistic relationships with fungi in what is called mycorrhizal symbiosis. The most abundant woody plants in these regions are the shrubs *Salix* L., dwarf *Betula* L. (Körner 2003), and *Dryas* L., which are known to form ectomycorrhizae (Trappe 1962; Miller et al. 1974; Chapin and Körner 1995; Cripps and Eddington 2005). A few plants such as *Bistorta vivipara* (L.) Delarbre and the sedge *Kobresia* Willd. are also known to form ectomycorrhizae (Trappe 1962, 1987; Lipson et al. 1999; Schadt 2002; Cripps and Eddington 2005; Ronikier and Mleczko 2006; Bjorbækmo et al. 2010; Thoen et al. 2019). In general, ectomycorrhizal fungi increase plant nutrient uptake (primarily nitrogen), ameliorate water relations,

protect roots from pathogen invasion, and can prevent heavy metal uptake. In return, the plant provides the fungus with photosynthetically derived sugars (Halling 2001; Smith and Read 2008). Hobbie and Hobbie (2006) reported that ectomycorrhizal fungi can provide up to 86% of the nitrogen required by the plant host in Arctic tundra and Lipson et al. (1999) showed that ectomycorrhizal fungi in association with *Kobresia* play an important role in the transfer of nitrogen in the form of amino acids. Ectomycorrhizal fungi also provide indirect benefits in Arctic and alpine regions where the mycelium aggregates and stabilizes soil (Graf and Brunner 1995). Ectomycorrhizal fungi are present in most major forest ecosystems in North America and Eurasia (Smith and Read 2008; Tedersoo et al. 2012), where they play an important role in seedling establishment, survival, and growth (Tedersoo et al. 2012). Concordantly, without these mutualistic fungi, most plants could not survive in harsh Arctic and alpine environments due to a short growing season, low temperatures, and poor soil nutrition (Haselwandter and Read 1980; Read and Haselwandter 1981; Gardes and Dahlberg 1996; Bjorbaekmo et al. 2010).

Shrubs are expanding into Arctic (Sturm et al. 2001, 2005) and alpine habitats (Formica et al. 2014) in response to changes in climate. Research has shown that fungal community composition can change under simulated climate change scenarios that increase temperature, alter nutrients, and increase snow cover, all of which can lead to a decline in species richness (Sturm et al. 2001, 2005; Semenova et al. 2016). Deslippe et al. (2011) reported that following warming of dwarf *Betula* in the Arctic, some groups of ectomycorrhizal fungi like *Cortinarius* (Pers.) Gray increased in abundance while others like the Russulaceae (*Russula* Pers. and *Lactarius* Pers.) decreased in abundance.

Semenova et al. (2016) found significant decreases in ectomycorrhizal species richness under experimentally increased snow-cover in the Arctic. Their research suggests that ectomycorrhizal fungi may not be entirely driven by vegetation, as previously thought (Dahlberg and Bültmann 2013) and that they may also be influenced by complex biotic and abiotic interactions in the soil.

As climatic warming continues to effect Arctic and alpine systems, the loss of entire plant functional groups could have large impacts on ecosystem function and health (Chapin & Körner 1995) leading to reduced stability due to decreases in community heterogeneity (Graae et al. 2018). These factors have important implications for the diversity of mycorrhizal species in Arctic and alpine regions. As climate change continues, ectomycorrhizal fungal communities will begin to shift or even decline. This could alter ecosystem functioning and highlights the importance of understanding ectomycorrhizal fungi in Arctic (Timling et al. 2014) and alpine environments (Formica et al. 2014).

The Rocky Mountains

The Rocky Mountains extend from northern Alaska to northern New Mexico and form a semi-contiguous alpine zone (Billings 1988). The Rocky Mountains were thrust up through thick sedimentary rocks and erosion exposed ancient granites and metamorphic rock. However, sedimentary rocks including shale, limestone, sandstone, and quartzite still remain, and make up entire subranges of the Rocky Mountains, basalt, andesite, and rhyolite can also be found (Retzer 1956). The semi-contiguous alpine zone of the Rockies creates isolated island populations (Kuchler 1964) where classic island

biogeography theory could apply to populations of animals, plants, and fungi; species richness is correlated with mountain top size and proximity of other alpine zones (MacArthur & Wilson 1967; Hadley 1987). It has been hypothesized (Weber 2003) that the Rocky Mountain flora is derived from Middle Asiatic flora and that these regions were connected by Greenland during the early Tertiary age. If true, it suggests that dry conditions in parts of the Rocky Mountains may have led to the attrition of the diverse Middle Asiatic floral communities, which could be true for fungi as well.

Many of the ectomycorrhizal plants that occur in the Rocky Mountain alpine zone have broad circumpolar distributions with disjunct components in alpine areas to the south of the Arctic (Hultén 1968). Historically, changes in climate have altered the geographic distributions of alpine floras; as warming continues, alpine floral communities are shifting upwards in elevation and may disappear completely as subalpine communities move toward the tops of mountains (Fagre 2009). As in other Arctic and alpine regions, *Salix* species are the most abundant ectomycorrhizal host in the central and southern Rocky Mountains, and dwarf *Betula* is found in restricted areas. Rocky Mountain ectomycorrhizal woody hosts include: *Betula glandulosa* Michx., *Dryas octopetala* L., *Salix arctica* Pall., *S. glauca* L., *S. planifolia* Pursh, and *S. reticulata* L.; *Betula glandulosa* is a close relative of the *B. nana* L. complex, which has a circumpolar distribution (Hultén 1968). *Salix reticulata* also has a circumpolar distribution in Arctic areas, excluding Greenland (Hultén 1968). Worldwide these species are 100% mycorrhizal with ectomycorrhizal fungi being present on roots a majority of the time (Newman and Reddell 1987; Cripps and Eddington 2005). In one Colorado study site, it

was shown that *Salix* species have expanded 441% in the last 62 years (Formica et al. 2014), highlighting the importance of gathering baseline data prior to large shifts in alpine ecosystem function. In the Rockies, the vegetation and geology have been well studied, but little is known of the ectomycorrhizal fungi associated with the alpine flora.

Over 200 macro-fungal species have now been documented in the Rocky Mountain alpine zone since Gardes and Dahlberg's (1996) review and over half are ectomycorrhizal species (Cripps and Horak 2008). The main diversity of ectomycorrhizal fungi with woody plants in the Rocky Mountain alpine are in the genera *Cortinarius* (Peintner 2008), *Entoloma* P. Kumm., *Hebeloma* (Fr.) P. Kumm. (Beker et al. 2010; Cripps et al. 2019a), *Inocybe* (Fr.) Fr. (Cripps et al. 2010; Larsson et al. 2014; Larsson et al. 2018; Cripps et al. 2019b), *Laccaria* Berk. & Broome (Osmundson et al. 2005), *Lactarius* (Barge et al. 2016), and *Russula*. The diversity of several of these genera has already been addressed. Here we propose to examine the diversity and ecology of the important ectomycorrhizal genus *Russula* in the Rocky Mountain alpine zone. This work will first provide an overview of the order (Russulales) and family (Russulaceae), in which *Russula* is classified, in order to better understand the importance of the genus.

Russulales Kreisel ex P.M. Kirk, P.F. Cannon & J.C. David (2001)

The order Russulales is one of the largest orders within the Agaricomycetes. Even though the Russulales contains one family that produces gilled mushrooms, it is distantly related to the Agaricomycetidae, which is the subclass containing most of the gilled fungi. The Russulales contains 98 genera, 10 families, and 4,436 accepted species (He et al. 2019). The Russulales are now understood to be an old lineage that began with a

polyporous habit, in which species radiated into an array of morphological forms.

Basidiocarps can be resupinate, effused-reflexed, discoid, clavarioid, or pileate-stipitate structures (Miller et al. 2006). Hymenophore types are also heterogenous and include smooth, hydroid, poroid, and lamellate forms. Families now in the Russulales were once thought to be unrelated because of this diversity of features.

The order was first described by Kreisel (1969) and at this time only included *Russula*, *Lactarius*, and related hypogeous taxa; also, it was not validly published. The modern Russulales was initiated by Donk (1964, 1971) who noticed that genera with vastly different macro-morphology such as lamellate Russulas and crust-like Gloeocystidiellums Donk shared unique microscopic characters such as gloeocystidia (cystidia with oily contents staining gray or black in sulfovanillin) and spores with amyloid ornamentation. Donk (1971) was later focused on the Hydnaceae s.l. and found that the genus *Hericium* Pers. also shared these features. He felt that gloeocystidia and amyloid spore ornamentation were important taxonomic characters for future classification. Oberwinkler (1977), on examining the microscopic characters of basidiomycetes, determined that the classification system at that time, did not reflect natural relationships. Building off of Donk's work, Oberwinkler (1977) grouped various families containing gloeocystidia and amyloid spores into the Russulales. The order was validly published by Kirk et al. (2001), and at that time included 11 families and 64 genera. This grouping is now widely accepted and strongly supported to be monophyletic using various taxon sampling methods and multiple genes (Hibbet and Donoghue 1995; Hibbett et al. 1997; Binder and Hibbett 2002; Larsson and Larsson 2003; Larsson et al.

2004; Binder et al. 2005; Miller et al. 2006; Larsson 2007; Matheny et al. 2007).

Researchers were drawn to sort out relationships within the Russulales using molecular techniques and focused on agaricoid, gasteroid, pleurotoid, and corticioid taxa (Miller et al. 2001, 2006; Larsson and Larsson 2003; Larsson 2007). Recently, the number of families has been reduced from eleven (Kirk et al. 2001) to ten, which includes the Albatrellaceae, Auriscalpiaceae, Bondarzewiaceae, Echinodontiaceae, Hericiaceae, Hybogasteraceae, Peniophoraceae, Russulaceae, Stereaceae, and Xenasmataceae (He et al. 2019). Currently, fifteen genera within the Russulales are classified as *incertae sedis* (He et al. 2019).

Phylogenetic analysis of the order has helped confirm the defining characteristics of the Russulales. The presence of gloecystidia is now accepted as a synapomorphic trait defining the russuloid clade. Amyloid spore ornamentation is frequently thought to be a synapomorphic character; however, this trait is not found in all of the Russulales and is found outside the order (Miller et al. 2006). Most fungi in the Russulales are saprotrophs, but two families are ectomycorrhizal (Russulaceae and Albatrellaceae), a few genera are root parasites (*Heterobasidion* and *Echinodontium*), and some species are insect symbionts (Klepzig et al. 2001). Recent research has examined the evolutionary shift from a saprophytic to mycorrhizal ecology and it is thought that the ectomycorrhizal habit evolved independently in the only two ectomycorrhizal families, Russulaceae and Albatrellaceae (Looney et al. 2018). These two families are also believed to harbor the highest diversity of hymenophore types (Miller et al. 2006). Thus, phylogenetics and

molecular techniques have provided systematists with a better understanding of the evolutionary relationships within the order, but much work still remains to be done.

Russulaceae Lotsy

The family Russulaceae is an old, highly specious, and morphologically diverse lineage of ectomycorrhizal fungi that has undergone rapid diversification (Looney et al. 2016). The family contains around 2,000 species (Kirk 2017; Miller et al. 2006; Hyde et al. 2016; Buyck et al. 2018) and seven genera (He et al. 2019). Four genera form pileate-stipitate structures including *Lactarius* (Persoon 1797), *Lactifluus* (Pers.) Roussel (Buyck et al. 2008), *Multifurca* Buyck & V. Hofst. (Buyck et al. 2008), and *Russula* (Persoon 1796) and three genera are crust fungi including *Boidinia* Stalpers & Hjortstam, *Gloeopeniophorella* Rick, and *Pseudoxenasma* K.H. Larss. & Hjortstam. The two most recognized genera, *Russula* and *Lactarius*, have been known since Persoon (1796, 1797). Both were originally described by Fries (1821) as tribes under the genus *Agaricus* L.: *Russula* under the tribe *Russula* and *Lactarius* under the tribe *Galorrheus* (Fr.) Fr. During the same year, Gray (1821) lifted both *Russula* and *Lactarius* to the generic level and both have remained stable. However, recent phylogenetic analyses have shown that these two genera as known do not form monophyletic groups; this led to the creation of the genus *Multifurca* and revision of the genus *Lactifluus* (Buyck et al. 2008), which are primarily tropical groups (De Crop et al. 2017; Wang et al. 2018).

Traditionally, the Russulaceae has been considered to be comprised primarily of pileate-stipitate species, other morphological forms are now included. *Macowanites* Kalchbr., *Gymnomycetes* Masse & Rodway, *Cystangium* Singer & A.H. Sm., and *Martellia*

Mattir. are hypogeous and gasteroid genera within the family that were once grouped together, separately from gilled taxa. Phylogenetic analysis has placed these genera within the pileate-stipitate *Russula* clade and all names have been synonymized with *Russula* (Elliot and Trappe 2018). The genera *Zelleromyces* Singer & A.H. Sm. and *Arcangeliella* Cavara were also erected to describe hypogeous taxa, but research has shown them to be phylogenetically within *Lactarius* (Miller et al. 2001); they have not yet been synonymized with *Lactarius*. The family Russulaceae is well-supported as a monophyletic group by multiple molecular phylogenetic studies (Miller et al. 2006; Larsson 2007; Phookamsak et al. 2019) and it is likely that this phylogenetic classification will remain stable. Because the Russulaceae is highly specious and has undergone rapid diversification many species still remain undescribed. To complicate the matter further, species recognition and delineation is difficult.

A synapomorphic trait for the Russulaceae is the presence of sphaerocysts (sometimes referred to as sphaerocytes); these are large round (isodiametric) cells that swell during basidiocarp development. Sphaerocysts are responsible for the brittle texture of mushrooms in the family (Buyck et al. 2018). Interestingly, sphaerocysts are only found in this family of the Russulales. Because both sphaerocysts and filamentous hyphae are present in the pileus, stipe, and lamellar trama, tissues of the Russulaceae are termed heteromerous.

The Russulaceae are easily defined based on a unique set of morphological characters but placing species in either *Russula* or *Lactarius* can be difficult. Verbeken (1996) looked at developmental differences between *Russula* and *Lactarius* and found

that *Lactarius* is composed of only one primary rosette complex of sphaerocysts; whereas, *Russula* is composed of many “agglomerate” rosettes. To clarify, *Lactarius* species do not contain sphaerocysts in the lamella (Heilmann-Clausen et al. 1998). This distinction has been used to place unknown taxa in either *Russula* or *Lactarius*. Although, other researchers have found this distinction to be of little use in tropical species (Henkel et al. 2000).

The presence of pseudocystidia in *Lactarius* and their absence in *Russula* appears to be a more reliable character for differentiation between the two genera (Miller et al. 2006). Pseudocystidia are cystidia located on the hymenium that lack basal septa because they are connected to the lactiferous system in basidiocarps of *Lactarius* (Heilmann-Clausen et al. 1998). Species in the genus *Lactarius* produce a milk or latex on cutting; whereas, *Russula* species do not, but this character can be obscured in drier climates. Research has determined that the acrid or hot tastes present in some *Russula* and *Lactarius* species are caused by sesquiterpenoid unsaturated dialdehydes (Vidari and Vita-Finzi 1995; Clericuzio and Sterner 1997; Clericuzio et al. 1998; Wang et al. 2006; Hanson 2008; Malagòn et al. 2014). The acrid/hot taste has been used as a character for placement within infrageneric classifications of *Russula* (Miller and Buyck 2002), but is variable in some species. Interestingly, the compounds responsible for the acrid or hot tastes in *Lactarius* have been shown to produce an anti-feeding response in some insects (Daniewski et al. 1993, 1995).

Members of the Russulaceae can be found from the Arctic (Knudsen et al. 2012) to the tropics (Henkel et al. 2000). They form ectomycorrhizal associations with various

plant hosts and are also known to be broadly associated with mycoheterotrophic plants in the genus *Hexalectris* Raf. (Kennedy et al. 2011). The Russulaceae are considered to be one of the most dominant families in ectomycorrhizal communities (Horton and Bruns 2001; Tedersoo et al. 2010). The family contains species that are thought to be late-stage colonizers of forests (Twieg et al. 2007). There is some debate regarding the temporal partitioning of species of *Russula* and *Lactarius*, some research shows that the latter is more abundant during the fall and the former is present year-round (Koide et al. 2007); however, there is evidence that contradicts this (Courty et al. 2008). In the tropics pleurotoid species of *Russula* and *Lactarius* were thought to be lignicolous based on the observation that these fungi fruited directly from tree trunks in elevated positions (Singer 1952, 1984; Dennis 1970; Pegler and Fiard 1979; Redhead and Norvell 1993; Verbeken 1998). However, more current research has matched sequences of ectomycorrhizae in the soil to basidiocarps, providing evidence that these species are ectomycorrhizal (Henkel et al. 2000).

The Russulaceae are widely distributed, ecologically valuable, and form mutualistic associations with important plant hosts. These characteristics indicate that the Russulaceae could be used as a model study system to understand the history, functionality, and role of ectomycorrhizal fungi in the environment (Looney et al. 2018). However, the fact that many species within the family still remain undescribed hinders the value of this model system and highlights the importance of first studying the species diversity within the Russulaceae, especially within the large genus *Russula*.

Russula Persoon

The ectomycorrhizal genus *Russula* contains hypogeous, sequestrate, and pileate-stipitate basidiocarps and is commonly cited as containing 750 species worldwide; however, this is known to be an underestimate of the true species diversity, which is estimated to extend to 3,000 species (Buyck 2007; Buyck et al. 2015; Kirk 2017; He et al. 2019). The type species of the genus is *R. emetica* (L.) Pers. *Russula* species have a colorful convex to funnel shaped pileus, attached lamellae that are not usually decurrent, a white to dark yellow spore print, no clamp connections, no latex, amyloid ornamented basidiospores, and sphaerocysts in a heteromerous trama (Romagnesi 1967; Singer 1986; Sarnari 1998–2005). *Russula* is an obligate mycorrhizal genus that requires a complex set of nutrients from its host plant for growth. Researchers still do not understand the growth requirements of *Russula* species and because of this they are considered unculturable. However, Hintikka and Niemi (1999) reported growing four different *Russula* species on commonly used media, but growth was slow. Historically, the taxonomy of *Russula* is complex and numerous publications produced by many authors have attempted to provide a usable and coherent classification for the genus.

Three major monographs on *Russula* have been written based on the morphological characters present in basidiocarps (Romagnesi 1967; Singer 1986; Sarnari 1998–2005). These monographs have produced complex infrageneric classifications that include subgenus, section, and subsection levels. Eleven subgenera within *Russula* are currently recognized, although the validity of some subgenera is still under debate; these include *Russula* subgenus *Russula* Buyck & V. Hofst., *R. subg. Compactae* (Fr.) Bon,

emend. Buyck & V. Hofst., *R. subg. Heterophyllidia* Romagnesi, *R. subg. Ingratula* Romagnesi, *R. subg. Amoenula* Sarnari, *R. subg. Incrustatula* Romagnesi, *R. subg. Archaea* Buyck & V. Hofst., *R. subg. Brevipes* Buyck & V. Hofst., *R. subg. Malodora* Buyck & V. Hofst., *R. subg. Crassotunicata* Buyck & V. Hofst., and *R. subg. Glutinosae* Buyck & X.H. Wang (Sarnari 1998–2005; Hongsanant et al. 2015; Das et al. 2017; Buyck et al. 2018, 2020). There are also many sections and subsections within the infrageneric classification of *Russula* and the most recent revision of the classification, based on morphology, was performed by Sarnari (1998–2005). The infrageneric classifications produced by Romagnesi (1967), Singer (1986), and Sarnari (1998–2005) all differ slightly and even the most recent classification has not resolved all observed clades in molecular phylogenetic analyses. Miller and Buyck (2002) showed that while some infrageneric classifications are well supported, others are not, and do not appear to be natural phylogenetically related assemblages of species. Due to these inconsistencies, the infrageneric classifications at the section and subsection level within *Russula* will not be listed here. Recently, molecular phylogenetic analysis using the ITS, LSU, mtSSU, *RPB1*, and *RPB2* regions has resolved eight major clades in the genus *Russula* (Looney et al. 2016; Buyck et al. 2018; Adamčík et al. 2019). These clades include the *Russula* crown clade, *Russula* core clade, *Malodora*, *Compacta*, *Archaea*, *Heterophyllidia*, *Crassotunicata*, and *Brevipes*. The *Russula* crown clade and *Russula* core clade together represent *R. subgenus Russula* and the remaining six clades phylogenetically represent the subgenera from which their names are derived. The ultimate goal of *Russula*

taxonomy is to create an infrageneric classification that matches strongly supported, multi-gene phylogenies (Adamčík et al. 2019).

The morphological and the molecular complexity within *Russula* has confused taxonomists who have had difficulty applying the correct names to taxa. This has led to the creation of many erroneous or superfluous names in the literature, further complicating *Russula* taxonomy. Buyck (2007) and Buyck et al. (2015) have discussed many of the issues facing the North American Russulologist, including the lack of specialists and the need for high quality type descriptions. There is no doubt that the genus *Russula* needs taxonomic and systematic revision within North America.

Mushrooms produced by certain species of *Russula* are economically important as edibles for humans. They are harvested around the world as a food source (Hu and Zeng 1992; Guo 1992; Rammeloo and Walley 1993; Buyck 1994) and are an important source of essential fatty acids (Sande et al. 2019). Worldwide there are 128 species of *Russula* that are considered edible or medicinal (Boa 2004). *Russula* mushrooms are unculturable; therefore, the medicinal and edible mushrooms produced hold substantial economic value. In small and rural communities, especially in Asia, mushroom foragers sell species like *R. virescens* (Schaeff.) Fr. for economic gain (Sitta and Davoli 2012). *Russula virescens* and other *Russula* species bring in high prices and a large market share, similar to highly regarded edibles like truffles (*Tuber* P. Micheli ex F.H. Wigg. spp.) and Matsutake (*Tricholoma matsutake* (S. Ito & S. Imai) Singer). *Russula* mushrooms also play important ecological roles in the diets of insects and larger mammals (Fogel 1975; Fogel and Trappe 1978; Lebel and Tonkin 2007).

Morphological Characters

Morphological observation of *Russula* species has continued since the time of Fries (1874) when he wrote *Hymenomycetes Europaei*. As with many other genera, Fries based his descriptions on characters found in/on the pileus, stipe, and lamellae. Unlike most genera these characters proved to be less informative or more difficult to interpret in *Russula*. Burlingham (1944) discussed how traditional characters like pileus color, which shows considerable color variation, might be useful in species delineation. However, she stressed the importance of taste, odor, and spore ornamentation in iodine for distinguishing species of *Russula*, indicating that these characters hold just as much importance as characters originally used by Fries.

Taste, odor, and spore ornamentation have indeed proven to be important characters in *Russula* and are now commonly used in descriptions and mapped onto molecular phylogenies (Romagnesi 1967; Singer 1986; Sarnari 1998–2005; Miller and Buyck 2002; Adamčík et al. 2019). The most well-known odors are the fishy smell that characterizes *R.* subsection *Xerampelinae* (Adamčík and Knudsen 2004) and the foul smell characteristic of the foetid *Russula* species (Shaffer 1972). Malagòn et al. (2014) noted that the origin of the compounds responsible for pungent or peppery taste in *Russula* may be useful in taxonomic classification. It is worth noting that species producing these hot or acrid tastes also tend to also produce a dark purple or black reaction in sulfovanillin when chemically tested (Favre-Bonvin and Bernillon 1982). Chemical reactions in *Russula* will be discussed later in more detail. Another character that has been observed by many mycologists in *Russula*, is the degree to which the cap cuticle can be peeled toward the pileal center before it separates, usually described as:

hardly peeling near margin (<20%), separable except at center (20–95%), or completely separable (Buyck 2019).

All the major monographs written on the genus also include in-depth descriptions of microscopic characters (Romagnesi 1967; Singer 1986; Sarnari 1998–2005). This includes spore shape and size, spore ornamentation type, and descriptions of the basidia, cystidia, pileocystidia (sterile cells on cap), and pileipellis (cap cuticle). The basidiospores range from globose to elliptic and possess ornamentation that includes spines (acute tips), warts (obtuse tips), ridges (linear elements connecting warts and spines), and/or wings (ridges > 2 μm tall) (Adamčík et al. 2019; Buyck 2019). A small area lacking ornamentation is present on the basidiospore adjacent to the apiculus, which is referred to as the suprahilar plage, its relative size and degree of amyloidity is often described (Buyck 2019). Basidia length and width are measured at the widest and tallest points. Basidia are usually clavate with a pedicellate base (Sarnari 1998–2005), but variation can occur, and basidia can have one to four sterigma. Cystidia length and width are measured as above and the shape is recorded as clavate, fusiform, mucronate (with appendage), or pedicellate; the refractive contents, and their staining in the presence of chemical compounds is noted. Pileocystidia are present in most groups and lacking in a few (*Incrustatula*). They are sometimes difficult to differentiate from hyphae but are usually more clavate and filled with refractive contents (Sarnari 1998–2005). The staining reaction of the pileocystidia is also noted in sulfovanillin. For the pileipellis, the depth and composition of the suprapellis (upper portion near surface containing pileocystidia and hyphae) and subpellis (portion between the suprapellis and trama) are also described

(Adamčík et al. 2019) (FIG. 1A). Details of the pileipellis and pileocystidia are still regarded today as some of the most important characters for differentiation of *Russula* species (Adamčík et al. 2016b). Kühner (1975) and Ruotsalainen and Vauras (1994) noted the importance of the pileal coating and other characters for differentiating *Russula* species. Recently, Bart Buyck has recently led the field in regard to examining the microscopic characters of *Russula*. Buyck (1991) published a paper on how to properly describe and measure the spores and basidia. Buyck (2007) and Buyck et al. (2015) emphasized the importance of proper microscopic examinations and drawings, especially for North American taxa that are not well known. Buyck also offers detailed information on how to describe Russulas on his website *Russulales News* (Buyck 2019).

Bazzicalupo et al. (2017) found a loose connection between morphological character states and species boundaries within *Russula*. This was done using a multivariate analysis that included molecularly delineated species of *Russula* and an extensive set of macro- and micro-morphological character information. The results explained some of the complexities that traditional taxonomists have faced. Morphological characters predicted genetic species only about 50% of the time. Their work pointed out that some common characters used in describing *Russula* did not vary enough to be informative, and this includes surface cap texture when wet or dry, and how far the cap cuticle could be peeled. Currently, Russulologists worldwide are working to produce a globally comprehensible *Russula* language to tackle some of the taxonomic needs of the genus (Adamčík et al. 2019). In order to produce a globally comprehensible *Russula* language, Adamčík et al. (2019) stress the importance of proper measurements,

drawings, and descriptions of the basidiospores, basidia, cystidia, pileocystidia, and pileipellis. Experts on the genus hope that using a thorough approach when describing *Russula* species, will help aid in the arduous process of delineating species.

Chemical Reactions

When working with *Russula* species, mycologists use various chemicals to produce macroscopic reactions on fresh basidiocarp material and microscopic reactions on basidiospores, basidia, cystidia, hyphae, and the pileipellis. Chemicals are used to aid in the taxonomic sorting of species. While chemicals are used in other fungal groups, chemical reactions can be especially useful in genera containing complex morphology and high species diversity such as *Russula*.

Chemicals used to invoke reactions on fresh basidiocarps include ferrous sulfate (FeSO_4), Phenol, and Gum Guaiac. Melzer and Zvara (1928) discovered a pinkish or greenish reaction caused by FeSO_4 when it is placed on the fresh context of some *Russula* species. Singer (1962) reported four different reactions when FeSO_4 was applied to the fresh material of *Russula*. These included a negative reaction in *R. cyanoxantha* (Schaeff.) Fr., a variable reaction in *R. ferrotincta* Singer, an olive-green reaction in *R. section Xerampelinae*, and a pink or salmon reaction in most *Russula* species. Watling (1971) hypothesized that the olive-green reaction in the *R. xerampelina* group may be directly related to the volatile compounds that produce the fishy odor. When applied to fresh fungal material, FeSO_4 becomes oxidized to a ferric salt that can react with phenolic compounds present. In a laboratory, ferric chloride produces a green color when exposed to catechol; however, this reaction has not been specifically studied in *Russula* (Watling

1971). Phenol is also used to test for various color reactions on fresh basidiocarp material: a chocolate or brownish reaction is present in most species within the Russulaceae (Watling 1971). Lastly, Gum Guaiac is used to test for a greenish to brownish oxidation reaction, which indicates a positive result. The positive reaction is present in most species, so a negative reaction can be taxonomically informative (Moser 1978).

There are five main chemicals that are used to test for microscopic reactions on tissues of *Russula*. These include carbolfuchsin, congo red, cresyl blue, Melzer's reagent, and sulfovanillin. The purpose of using these chemicals is outlined in Adamčík et al. (2019) and will be briefly reviewed here. Carbolufuschin is used to determine if acid-resistant incrustations are present in primordial hyphae (Romagnesi 1967). Congo red is used to help distinguish various structures in the hymenium and pileipellis (Heilmann-Clausen et al. 1998). Cresyl blue is used to test for a metachromatic reaction in the incrustations found in pileocystidia and hyphae of the pileipellis (Buyck 1989). Melzer's reagent causes the ornamentation on *Russula* spores to turn dark blue to black, a reaction referred to as amyloid; a reddish-brown reaction is called dextrinoid. This reaction is thought to be caused by an interaction between iodine in the solution and starch-like polysaccharides on the spore surface, although little research has investigated this (Watling 1971). These reactions are important in separating the Russulaceae from other agarics (Watling 1971). The amyloid reaction produced by Melzer's reagent was one of the first chemical tests to be widely accepted as having taxonomic value (Melzer and Zvára 1927; Donk 1964; Watling 1971) and helps differentiate species based on spore

ornamentation. Sulfovanillin is widely used to observe the microscopic features of *Russula* (Caboň et al. 2017) and its usefulness was first discovered in the Russulaceae (Donk 1964). Sulfovanillin will turn the contents of the pileocystidia and hymenial cystidia bluish gray to blackish in some species. When this reaction occurs in cystidia, they are referred to as gloeocystidia and this is a synapomorphic trait of the Russulales.

Ecology and Hosts

Russula species have a cosmopolitan distribution and can be found from the tropics (Buyck et al. 1996; Tedersoo and Nara 2010) to the Arctic (Knudsen et al. 2012; Geml et al. 2009). In tropical regions, the *Russula* species and their ectomycorrhizal host are vastly different from those in temperate, Arctic, and alpine regions (Buyck et al. 1996; Tedersoo and Nara 2010). This work focuses on *Russula* in Arctic and alpine habitats, and therefore will focus on the ecological interactions in these regions. *Russula* species form symbiotic mutualistic ectomycorrhizal associations with all major lineages of ectomycorrhizal hosts as well as some less common ectomycorrhizal shrubs and herbaceous species (Romagnesi 1967; Knudsen and Borgen 1982; Singer 1986; Buyck et al. 1996; Sarnari 1998–2005; Knudsen et al. 2012; Miller et al. 2012). Many *Russula* species are reported as generalists in the literature (Adamčík et al. 2006; Looney et al. 2016). A few species have been reported as host specialists with *Salix* (Adamčík and Knudsen 2004), *Fagus sylvatica* L., *Quercus* L., and *Betula* (Adamčík et al. 2006). A few studies used phylogenetics and ecological analysis to reveal niche partitioning of *Russula* species in different habitats and high species diversity in Alaska (Geml et al. 2010; Geml and Taylor 2013). Looney et al. (2016) analyzed metadata from *Russula* and relatives in

GenBank and found host specialization in some plant groups, including Fagaceae (25%) and Pinaceae (24%), while others were angiosperm generalists (12%) or associated with both angiosperms and Pinaceae (9%); the remainder had no host metadata. After phylogenetic analysis, Looney et al. (2016) determined that host association is highly variable in all of the *Russula* clades studied.

Russula species apparently originated in temperate regions with angiosperms and the highest rates of diversification are seen in extratropical taxa (Looney et al. 2016). This is contrary to trends observed in most flora and fauna, which are the most biodiverse in tropical regions (Hillebrand 2004). Looney et al. (2016) hypothesized that numerous abiotic and biotic factors promote *Russula* diversification in temperate regions, a major factor being the ectomycorrhizal hosts involved. They showed that *Russula* diversification corresponds with that of major ectomycorrhizal plant lineages like Betulaceae and Salicaceae.

In Arctic and alpine habitats, dwarf and shrubby species of *Salix* are the most common ectomycorrhizal hosts (Knudsen et al. 2012; Cripps and Horak 2008). DNA extracted from soil cores and grouped into OTUs using 97% sequence similarity has shown *Russula* to be one of the most abundant ectomycorrhizal associates of Arctic and alpine *Betula* (Deslippe et al. 2011) and to be the fourth most dominant ectomycorrhizal genus in moist tussock and dry tundra in Arctic Alaska (Morgado et al. 2015). Based on morphological data, a particular subset of *Russula* species is hypothesized to be intercontinentally distributed in Arctic and alpine environments, where they associate with *Salix* (Ohenoja 1972; Miller 1982a; Miller et al. 1973; Watling 2005; Ryberg et al.

2009, 2011), *Dryas* (Kernaghan and Currah 1998; Ryberg et al. 2009), *Bistorta* L. Scop. (Watling 2005; Mundra et al. 2016; Thoen et al. 2019), and *Betula* (Ohenoja 1972; Kernaghan and Currah 1998; Deslippe and Simard 2011; Voitk 2015).

For years researchers have been collecting basidiocarps of *Russula* near *Salix* in subalpine, alpine, and Arctic habitats. These include collections from Alaska (Miller et al. 1973), Canada (Miller et al. 1973), The Rocky Mountains (Cripps and Horak 2008), Svalbard (Skift 1989), Greenland (Knudsen and Borgen 1982; Lamoure et al. 1982; Adamčík and Knudsen 2004), Iceland (Hallgrímsson 1998), and Europe (Favre 1955; Adamčík and Knudsen 2004; Watling 2005; Ryberg et al. 2009, 2011) to name a few. There is no doubt that *Russula* species have a strong association with *Salix* in Arctic and alpine habitats; however, the importance of this host in subalpine or boreal habitats is less clear. Research aimed at understanding these associations with *Salix* may find that more *Russula* species are strictly associated with *Salix* in subalpine or boreal habitats, as was shown with *R. subrubens* (Adamčík and Knudsen 2004; Adamčík et al. 2016b). *Salix* is often overlooked in forests where tall trees are often assumed to host ectomycorrhizal fungi. Studies that dig up, sequence, and identify ectomycorrhizal components of *Salix* root tips will clarify these questions.

Much research has focused on understanding the ectomycorrhizal associations between *Russula* and *Betula* species in Arctic-alpine regions. *Russula* species have been reported to form ectomycorrhizal associations with *Betula nana* L., *B. glandulosa*, and *B. pubescens* Ehrh. in Alaska, Canada, Fennoscandia, and Greenland (Miller et al. 1973; Miller 1982b; Elborne and Knudsen 1990; De Groot et al. 1997; Deslippe et al. 2011;

Deslippe and Simard 2011). Some *Russula* species that associate with *Betula* in Greenland, also occur with the same host in Europe; these species are strictly associated with *Betula* (Elborne and Knudsen 1990).

Fertilization experiments have shown, that as ectomycorrhizal mutualists, *Russula* species require less carbon from *Betula nana* and provide better access to labile nitrogen compared to other ectomycorrhizal associates (Deslippe et al. 2011). Other work has shown that in a mycorrhizal community of *B. nana* dominated by *Russula* species, below-ground transfer of carbon is facilitated between separate *B. nana* individuals; however, no transfer of carbon was observed between or within other tundra plant species (Deslippe and Simard 2011). This suggests that *Russula* species are some of the most important ectomycorrhizal hosts of *B. nana*.

Research is beginning to assess how climate change will alter mycorrhizal fungal communities, but there is no consensus on how *Russula* species will be affected. Deslippe et al. (2011) reported that following experimental warming of dwarf *Betula* in the Arctic tundra, some groups of ectomycorrhizal fungi increased in abundance while others, especially *Russula* with a high affinity for labile nitrogen, decreased in abundance. In another experiment, Deslippe et al. (2012) showed that the genus *Russula* increased in abundance with warming treatments imposed on Arctic soils. Morgado et al. (2015) studied the effect of increased summer temperature on *Russula* species in the Alaskan tundra and did not observe any changes in fungal community composition, although there was a shift in extramatrical mycelium morphology.

Environments like the Arctic and alpine are seeing some of the largest negative impacts of climate change. As shrub expansion and nitrogen deposition continue in conjunction with changes in climate, the composition of ectomycorrhizal fungal communities will begin to shift. The functioning of individual ectomycorrhizal species is not redundant, with various species, even within the same genus, showing preferences for different forms of nitrogen (Antibus et al. 2018). It is also believed that warming will increase the growth and nutrient demand of ectomycorrhizal hosts like *Betula nana*, which would increase fungal density and decomposition (Deslippe et al. 2011). Ectomycorrhizal fungi will also play important roles in the spread of shrubby plant species as the climate warms (Deslippe and Simard 2011) and *Russula* species do have the ability to follow changes in plant host distribution due to climate change (Looney et al. 2019). These changes in ectomycorrhizal communities will alter basic microbial functioning across the landscape, which has important implications for plant ecology and plant processes over time (Cripps and Eddington 2005; Timling et al. 2014). All this underlines the importance of understanding the diversity and function of ectomycorrhizal genus *Russula* prior to large environmental shifts.

Russula in Arctic-alpine habitats of Europe,
Asia, and Arctic Islands

The study of the genus *Russula* has been dominated by European mycologists who have published extensively on the genus (Fries 1874; Killerman 1936; Lange 1937; Romagnesi 1967; Singer 1986; Sarnari 1998–2005). Although the study of the genus has been ongoing for around 150 years, European mycologist did not focus heavily on Arctic and alpine *Russula* until the 1950s. However, Killerman described one of the most well-

known and most common Arctic and alpine *Russula* species, *R. nana* Killerm. in 1936.

The most commonly reported species in Arctic or alpine habitats in Europe, Asia, and Arctic Islands are *R. nana*, (= *R. emetica* (Schaeff.) Pers., *R. alpina* (A. Blytt & Rostr.)

F.H. Møller & Jul. Schäff., and *R. emetica* var. *alpina* A. Blytt & Rostr.), *R. laccata*

Huijsman (= *R. norvegica* D.A. Reid), *R. pascua* (F.H. Møller & Jul. Schäff.) Kühner,

and *R. delica* Fr. TABLE 4 summarizes the reports of Arctic and alpine *Russula* species.

Table 4. Reports of Arctic-alpine *Russula* species in Eurasia, on Arctic Islands, and in North America. Names as reported, some are now changed or synonymized. Species with an * represent potential subalpine species that were only reported from Greenland.

References at end of table¹. AK = Alaska, CAN = Canada, DK = Denmark, GNLD = Greenland, ICLD = Iceland, JPN = Japan, EUR = Alps, Pyrenees or Carpathians, FNSC = Fennoscandia, FO = Faroe Islands, NL = Netherlands, PL = Poland, SCT = Scotland, SVBD = Svalbard, RM = Rocky Mountains, U.S.A., RUSS = Russia.

Taxa	Arctic-Alpine Locations
<i>R. aeruginea</i> Lindblad ex Fr.	CAN (63), GNLD (51, 65, 79)
<i>R. alnetorum</i> Romagn.*	GNLD (13)
<i>R. amoenipes</i> Romagn.	EUR (47), FNSC (47)
<i>R. alpina</i> (A. Blytt & Rostr.) F.H. Møller & Jul. Schäff.	FNSC (52), GNLD (45, 50, 51, 65, 79, 80), ICLD (18), SVBD (46)
<i>R. altaica</i> (Sing.) Sing.	CAN (63), GNLD (12, 13, 41, 50), RUSS (75), SVBD (46, 76)
<i>R. chamiteae</i> Kühner	EUR (27), FNSC (30), GNLD (12, 41, 50)
<i>R. citrinoclora</i> Singer*	GNLD (12, 13, 42), RUSS (43)
<i>R. claroflava</i> Grove*	GNLD (13, 41, 50, 51)
<i>R. claroflava</i> var. <i>viridis</i> Knudsen & T. Borgen*	GNLD (42)
<i>R. consobrina</i> (Fr.) Fr.*	GNLD (13, 42)
<i>R. cupreola</i> Sarnari	EUR (24)
<i>R. decolorans</i> (Fr.) Fr.*	GNLD (13, 51)
<i>R. delica</i> Fr.	AK (44), CAN (63), EUR (19, 72, 73), FNSC (28, 52), GNLD (12, 13, 41, 45, 50, 51, 65), ICLD (33), RM (20), RUSS (26), SVBD (46, 76)
<i>R. delica</i> var. <i>trachyspora</i> Romagn.	GNLD (41)
<i>R. dryadicola</i> R. Fellner & Landa	EUR (17, 23, 24), FNSC (17), GNLD (13), ICLD (33), RUSS (26)
<i>R. emetica</i> var. <i>alpestris</i> (Boud.) Singer	AK (55), EUR (21)
<i>R. felleaecolor</i> Bon & Jamoni	EUR (40)
<i>R. felleicolor</i> Bon & Jamoni	RUSS (26)
<i>R. flava</i> Romell	FNSC (52)

<i>R. fragilis</i> (Pers.) Fr.	AK (44), CAN (53)
<i>R. gracilis</i> var. <i>altaica</i> Singer	GNLD (51), RUSS (75)
<i>R. gracillima</i> Jul. Schäff.	GNLD (13), ICLD (18, 33)
<i>R. groenlandica</i> Ruots. & Vauras	GNLD (13, 70)
<i>R. heterochroa</i> Kühner	EUR (47, 66), FNSC (47)
<i>R. laccata</i> Huijsman	CAN (63), EUR (24), FNSC (28), NL (36), RM (20)
<i>R. laevis</i> Kälviäinen, Ruotsalainen & Taipale	FNSC (3)
<i>R. lundellii</i> Singer	ICLD (33)
<i>R. lutea</i> (Huds.) Gray	CAN (68), GNLD (51)
<i>R. maculata</i> subsp. <i>alpina</i> (Singer) Knudsen & T. Borgen	GNLD (42), RUSS (43)
<i>R. medullata</i> Romagn.*	GNLD (12, 13, 41, 50) AK (54), CAN (62, 63), EUR (1, 5, 6, 7, 8, 10, 15, 16, 19, 21, 22, 24, 32, 35, 38, 39, 47, 48, 49, 56, 64, 66, 71, 72, 73, 74, 77), FNSC (28, 29, 30, 34, 47, 61, 71), FO (78), GNLD (12, 13, 41, 50, 79), ICLD (33), NL (25), PL (67), RM (20, 57), RUSS (26, 43, 60), SCT (81), SVBD (30, 31, 76)
<i>R. nana</i> Killerm.	EUR (9)
<i>R. nana</i> var. <i>alpina</i> (A. Blytt & Rost.) Bon	EUR (72)
<i>R. nauseosa</i> (Pers.) Fr.	AK (44), GNLD (13, 41), ICLD (33)
<i>R. nitidia</i> (Pers.) Fr.	CAN (37), EUR (11, 14, 27), FNSC (30), GNLD (13, 41, 50, 79, 80), ICLD (33), JPN (59), RUSS (43), SCT (24, 81), SVBD (76)
<i>R. norvegica</i> D.A. Reid	FNSC (4, 69), RUSS (69)
<i>R. nuoljae</i> Kühner	GNLD (65, 79)
<i>R. obscura</i> (Romell) Peck*	CAN (53)
<i>R. ochroleuca</i> Fr.	EUR (9), GNLD (41, 65, 80), ICLD (33), RUSS (58)
<i>R. oreina</i> Singer	EUR (73), RUSS (26)
<i>R. pallidospora</i> J. Blum ex Romagn.	CAN (63)
<i>R. paludosa</i> Britzelm.	EUR (2, 4, 16, 24, 27, 67, 72, 73), FNSC (28), FO (2), GNLD (2, 13), PL (2, 4, 67), RM (20), RUSS (2), SCT (81)
<i>R. pascua</i> (F.H. Møller & Jul. Schäff.) Kühner	JPN (59)
<i>R. pectinatoides</i> Peck	GNLD (13), SCT (81)
<i>R. persicina</i> Krombh.	CAN (63)
<i>R. pubescens</i> A. Blytt	EUR (9, 67), GNLD (13, 41), PL (67)
<i>R. puellaris</i> Fr.	GNLD (41)
<i>R. pulchella</i> I.G. Borshch.*	EUR (69), FNSC (69)
<i>R. purpureofusca</i> Kühner	EUR (73), RM (57)
<i>R. queletii</i> Fr.	CAN (63)
<i>R. rivulicola</i> Ruots. & Vauras	EUR (7, 24, 66, 72, 73), FNSC (28, 34), FO (77), GNLD (13, 41, 50), ICLD (33), SVBD (76)
<i>R. saliceticola</i> (Singer) Kühner	JPN (59)
<i>R. sororia</i> (Fr.) Romell	

<i>R. sphagnophila</i> Kauffman	FNSC (52)
<i>R. sphagnophila</i> var. <i>heterosperma</i> Singer	GNLD (51, 65)
<i>R. subalpina</i> O.K. Mill.	AK (54)
<i>R. subrubens</i> (J.E. Lange) Bon	DK (4), EUR (4, 67), FNSC (4), GNLD (2, 13), PL (67)
<i>Russula</i> Subsection <i>Xerampelinae</i> Singer	CAN (63)
<i>R. versicolor</i> Jul. Schäff.*	GNLD (13, 51)
<i>R. violaceoincarnata</i> Knudsen & T. Borgen	CAN (63), GNLD (12, 13)
<i>R. xerampelina</i> (Schaeff.) Fr.*	GNLD (41, 51)
<i>R. xerampelina</i> var. <i>pascua</i> F.H. Møller & Jul. Schäff.	AK (55), EUR (21)
<i>R. xerampelina</i> var. <i>oreina</i> Sing.	FNSC (52)

¹References: 1. Adamčík 1998; 2. Adamčík and Knudsen 2004; 3. Adamčík et al. 2019; 4. Adamčík et al. 2016b; 5. Bon 1985; 6. Bon 1987; 7. Bon 1991; 8. Bon 2000; 9. Bon and Ballarà 1996; 10. Bon and Cheype 1987; 11. Bon and Noguera 1995; 12. Borgen 1993; 13. Borgen et al. 2006; 14. Bresinsky 1987; 15. Bresinsky et al. 2000; 16. Bresinsky et al. 1980; 17. Caboň et al. 2019; 18. Christiansen 1941; 19. Corriol 2008; 20. Cripps and Horak 2008; 21. Favre 1955; 22. Fellner and Landa 1991; 23. Fellner and Landa 1993a; 24. Fellner and Landa 1993b; 25. Geml et al. 2014; 26. Gorbunova 2014; 27. Graf 1994; 28. Gulden 2005; 29. Gulden and Lange 1971; 30. Gulden et al. 1985; 31. Gulden and Torkelsen 1996; 32. Gyosheva and Dimitrova 2011; 33. Hallgrimsson 1998; 34. Hansen and Knudsen 1992; 35. Horak 1960; 36. Huijsman 1955; 37. Hutchison et al. 1988; 38. Jamoni 1995; 39. Jamoni 2008; 40. Jamoni and Bon 1993; 41. Knudsen and Borgen 1982; 42. Knudsen and Borgen 1992; 43. Knudsen and Mukhin 1998; 44. Kobayasi et al. 1967; 45. Kobayasi et al. 1971; 46. Kobayasi et al. 1968; 47. Kühner 1975; 48. Kühner and Lamoure 1986; 49. Lamoure 1982; 50. Lamoure et al. 1982; 51. Lange 1957; 52. Lange and Skifte 1967; 53. Linder 1947; 54. Miller 1982a; 55. Miller et al. 1973; 56. Moreau 2002; 57. Moser and McKnight 1987; 58. Mueller and Wu 1997; 59. Nara et al. 2003; 60. Niezdoiminogo 2003; 61. Ohenoja 2000; 62. Ohenoja and Ohenoja 1993; 63. Ohenoja and Ohenoja 2010; 64. Peintner 1998; 65. Peterson 1977; 66. Ronikier 2008; 67. Ronikier and Adamčík 2009; 68. Rostrup and Simmons 1906; 69. Ruotsalainen and Huhtinen 2015; 70. Ruotsalainen and Vauras 1994; 71. Sarnari 1998–2005; 72. Schmid-Heckel 1985; 73. Schmid-Heckel 1988; 74. Senn-Irlet 1987; 75. Singer 1938; 76. Skifte 1989; 77. Tondl 1988; 78. Vesterholt 1998; 79. Watling 1977; 80. Watling 1983; 81. Watling 1987.

The literature on Arctic and alpine *Russula* can be grouped into two categories.

The first group comprises publications dedicated entirely to the study of *Russula* in Arctic and alpine environments. These include detailed reviews of species known from the European alpine zone (Kühner 1975; Jamoni 1995; Bon 2000; Knudsen et al. 2012), the Monte Rosa Massif (Bon 1993), Slovakia (Ronikier and Adamčík 2009; Adamčík et al. 2006), Poland (Ronikier and Adamčík 2009), Fennoscandia (Knudsen et al. 2012; Ruotsalainen and Huhtinen 2015), Germany (Bresinsky et al. 1980), Svalbard (Skifte 1989), Greenland (Knudsen and Borgen 1982; Borgen 1993) and Romania (Ronikier 2008). Another detailed review focused solely on *Russula* sect. *Xerampelinae* associated

with dwarf *Salix* in Europe and Greenland (Adamčík and Knudsen 2004). The second group includes research that focused broadly on the taxonomy and distribution of basidiomycota in Arctic and alpine habitats and listed one, two, or three *Russula* species. Examples of these studies are those from Switzerland (Favre 1995), Norway (Lange and Skifte 1967), Slovakia (Fellner and Landa 1993a, 1993b), Svalbard (Kobayasi et al. 1968; Gulden and Torkelsen 1996), and the Pyrenean range (Bon and Ballarà 1996). A majority of this research on the taxonomy and classification of Arctic and alpine *Russula* species in Europe was based entirely on morphology.

Many new species of *Russula* were described through this research in various Arctic-alpine regions of Europe; however, it was difficult to taxonomically place species based on morphology alone. Taxonomists relied on similarities to subalpine species found in the region. Most of the commonly reported species appeared to have wide ranges across Arctic and alpine habitats, while a few appeared endemic to particular regions. However, many identifications are likely incorrect, and many names may have been published superfluously, which complicates our understanding of *Russula* in Arctic and alpine regions. Modern molecular diagnostic tools can now provide insight into the diversity and phylogenetic relationships of fungi. Unfortunately, very few researchers have used these tools to understand the diversity and distribution of *Russula* species in Arctic and alpine habitats.

One of the first molecular phylogenies that included Arctic or alpine species of *Russula* was that of Miller and Buyck (2002); the Arctic-alpine species were *R. nana* and *R. pascua*. Another study analyzed DNA from sporocarps and soil samples to determine

that *Russula* was the fifth most species-rich genus in Svalbard (Geml et al. 2012). They proposed that long-distance, transoceanic dispersal occurs in Arctic fungi, in contrast to the more limited dispersal of temperate *Russula* species (Bazzicalupo et al. 2019). As molecular tools became easier to use and more reliable, researchers began to sort out and clarify certain groups of *Russula*. Although they did not deal directly with Arctic and alpine species, the work of Adamčík et al. (2016a) and Caboň et al. (2017) produced important insights into understanding species diversity and the evolution of important characters in the genus *Russula*. Their phylogenies often included Arctic and alpine species, which provided a deeper phylogenetic understanding of *Russula*. Adamčík et al. (2016a) found that *R. maculata* Quélet actually consisted of a complex of three closely related species. The following year, Caboň et al. (2017) produced a multi-locus phylogeny and ancestral state reconstruction of *Russula* subsect. *Rubrinae*. They hypothesized that mild taste is the ancestral state for both the crown clade and *Integrae* clade and that acrid taste likely evolved more recently in several lineages within the crown clade.

Adamčík et al. (2016b) did focus on Arctic and alpine species from Europe in the *R. clavipes* Velen. complex using molecular methods. This research determined that some traditional characters for delineating species, including pileus color and habitat preference, may be misleading. The *clavipes* complex consists of three closely related *Russula* species and metabarcoding approaches did not resolve ecological or biogeographical differences between two of these species. This indicates that even molecular approaches are not enough to understand *Russula* diversity unless coupled with

morphological, ecological, and biogeographical data. More recently, Caboň et al. (2019) determined that in boreal and Arctic environments of Eurasia the evolution of the *R. globispora* (J. Blum) Bon lineage has been shaped by glaciation events along with geographic and climactic disjunctions. Their work showed that European and North American collections of this species are nearly identical at the molecular level. *Russula laevis* Kälviäinen, Ruots. & Taipale was recently described from Arctic habitats of Finland and comparison to environmental sequences in GenBank indicate that this species is present in North America (Adamčík et al. 2019); it shares morphological similarities with the Arctic-alpine species *R. delica*, which has been reported from the Rocky Mountains (Cripps and Horak 2008)

In summary, the study of the genus *Russula* was initiated by, and has been dominated by, European mycologists. Europeans provided a basis for the study of the complex morphology of the genus and began to explore Arctic and alpine habitats, which expanded knowledge of *Russula* diversity. Molecular work has uncovered previously unknown clades and helped reshape infrageneric classifications within the genus. However, molecular analyses certainly have not solved all of the taxonomic problems in *Russula*. The research of Adamčík et al. (2016b) showed that molecular information alone fails to resolve true species diversity. Knowledge of *Russula* diversity in Arctic and alpine habitats in the northern hemisphere is far from complete, and this is especially true for North America. European names have been applied to North American collections of Arctic and alpine *Russula*, but the validity of these names has not been confirmed using rigorous approaches, including phylogenetic analysis.

North American studies of *Russula*

The study of *Russula* taxonomy in North America began in the 1870s with Peck, the botanist for the New York State Museum, who described *R. sordida* Peck (Peck 1873). Peck described 46 new species from the East Coast (Adamčík and Buyck 2014, Peck 1873, 1879, 1898, 1903, 1911) and reported many more (Peck 1906, 1907). W.A. Murrill also contributed significantly to the study of *Russula* when he described 110 species, mostly from Florida (Looney 2014); others also focused on Florida in the early-to mid-twentieth century (Beardslee 1934; Burlingham 1939; Murrill 1938, 1941, 1943, 1945a, 1945b, 1946). *Russula* diversity has also been examined in North Carolina (Beardslee 1918), the southern Appalachians (Bills and Miller 1984; Bills 1984, 1985, 1989), and northeastern Canada (Jennings 1936; Homola and Shaffer 1975). The genus has been covered more broadly in the East by (Peck 1906), Burlingham (1921, 1924, 1939, 1944), Singer (1942, 1943), and Fatto (2002). Kibby and Fatto (1990) also produced a key to *Russula* species found in Northeastern North America. Recently mycologist have begun to use molecular tools to understand the evolution and origins of *Russula* species in eastern regions, which are considered to have the highest diversity in North America (Looney et al. 2016; Looney et al. 2019). Buyck (2007) summarized the status of *Russula* research on the East Coast and determined that over 300 species have been described; he also provided a framework for future study of the genus.

The first species described from the West Coast was *R. nigrodisca* Peck from material collected on St. Paul Island in the Bering Sea (Macoun 1899). In the West, regionally-based studies focused on *Russula* taxonomy covered Arizona (Fatto 2000), California (Earle 1902; Peters 1962; Thiers 1997a, 1997b), Colorado (Burlingham 1915;

Shaffer 1975; Fatto 1999), Idaho (Singer 1948; Shaffer 1964), Oregon (Kauffman 1930; Smith and Lebel 2001), Washington (Grund 1965, 1979), Wyoming (Burlingham 1915, 1924, 1936; Singer 1939b), and the Pacific Northwest in general (Burlingham 1913; Woo 1989). *Russula* in western regions of Canada (Spence 1932; Roberts 2007) and Alaska (Wells and Kempton 1914; Brunner 1989) have also been taxonomically studied. In recent years, Bazzicalupo et al. (2017) examined the morphological variation and value of the characters used to delineate *Russula* species in the Pacific Northwest. They analyzed one of the largest *Russula* datasets present in North America, produced by Ben Woo. Their results indicate that there is only a loose connection between morphological character states and species boundaries. Buyck et al. (2015) summarized the current status of *Russula* in the Western United States in a short paper. Based on all of the above research, only 58 species of *Russula* have been described from the western United States (Buyck et al. 2015; Phookamsak et al. 2019). Considering that *Russula* is the second most speciose ectomycorrhizal genus (Kirk et al. 2008), it is likely that many more species are yet to be discovered, especially in under-sampled regions like the Rocky Mountains.

Burlingham (1915, 1924, 1936) and Singer (1938, 1939a, 1939b, 1948) provided general information on the genus in North America. Research has also focused on specific infrageneric groups of *Russula*, including *R.* subgenus *Compactae* (Shaffer 1962; Thiers 1994), *R.* subg. *Heterophyllidia* (Buyck and Adamčík 2011), *R.* subsection *Emeticinae* (Shaffer 1975), *R.* subsec. *Lactarioideae* (Shaffer 1964; Buyck and Adamčík 2013), *R.* subsec. *Foetentinae* (Shaffer 1972), *R.* subsec. *Nigricantes* (Adamčík and Buyck 2014), and *R.* subsec. *Roseinae* (Looney et al. 2019, 2020). Bergemann et al.

(2005, 2006) is the only researcher who appears to have performed population studies on *Russula*; she focused on *R. brevipes* Peck in North America. The *R. emetica* group (*R. montana* Shaffer) was briefly examined phylogenetically by Bazzicalupo et al. (2016).

Arctic and alpine research on *Russula* in North America

To date there has been little research focused on *Russula* in Arctic and alpine regions of North America. Researchers studying *Russula* in these regions have applied the names of taxa originally described from Europe to collections from North America. *Russula emetica* (likely *R. nana*) was one of the first names used to describe *Russula* found in Arctic northern Canada (Spence 1932; Jennings 1936). Since then, researchers have studied *Russula* species and their host associations in Arctic and alpine regions of Alaska, Canada, Greenland, and the Rocky Mountains.

Miller et al. (1973, 1982) studied *Russula* species and their host associations in Arctic and alpine regions of Alaska. In Canada, *Russula* species have been collected near Rankin Inlet (Ohenoja 1972), around Schefferville (Kallio 1980), in Québec (Hutchinson et al. 1988), near Hudson Bay, and broadly across Arctic regions (Miller et al. 1973, Ohenoja and Ohenoja 2010). Greenland is also considered part of the North American continent and *Russula* found in Arctic habitats on the island have been more thoroughly sampled than the rest of North America. *Russula* species in Greenland have been studied in northern (Watling 1977, 1983), western (Lamoure et al. 1982), and southern regions (Lange 1957; Kobayasi et al. 1971; Elborn and Knudsen 1990) (see TABLE 4 for the specific *Russula* species reported).

Petersen (1977) investigated the ecology and phenology of fungi in Greenland and found six species of *Russula* distributed throughout various habitats. He determined that frost-free period and temperature are directly related to solar irradiance, making this the most important factor determining fungal fruitification, including that of *Russula*, in this Arctic region. Although the insular characteristics of Greenland make it a unique Arctic region, solar irradiance is still expected to contribute significantly to fungal fruitification in other Arctic and alpine regions. Borgen (1993) produced detailed descriptions of many fungi including eight species of *Russula* from Greenland. Knudsen and Borgen (1982) focused an entire paper on the Russulaceae in Greenland, which included excellent descriptions and a key to thirteen *Russula* species and one variety. Elbone and Knudsen (1990) studied the fungi associated with *Betula pubescens* in Greenland and confirmed three species of *Russula* associated with the Arctic shrub. More recently Adamcik and Knudsen (2004) assessed the diversity of *R. sect. Xerampelinae* associated with dwarf *Salix* on Greenland. In total, twenty-six species names have been used to describe *Russula* species on Greenland.

Collecting in the Rocky Mountain alpine did not begin until much later when Moser and McKnight (1987) collected agarics at high elevations in Yellowstone National Park and the Beartooth Mountains. They reported *R. nana* for the first time from the Rocky Mountain alpine in association with *Salix*. This was the only report of alpine *Russula* in the Rockies until Cripps and Horak received a grant from the National Science Foundation in 1999 to study alpine Agaricales. Cripps and Horak began intensively surveying alpine fungi in the Rocky Mountains in 1999. Their work uncovered various

Russula species (Cripps and Horak 1999; Cripps 2003) and in 2007 they reported *R. cf. delica* Fr. for the first time from the Rocky Mountains in association with *Dryas octopetala* (Cripps and Horak 2007). The following year Cripps and Horak (2008) published their survey of agarics from the Rocky Mountain alpine zone focusing on the central and southern regions. In addition to *R. cf. delica*, they also provided the first formal reports of *R. laccata* and *R. cf. pascua* in the region and reported *R. nana* from the central and southern Rockies. Both *R. nana* and *R. laccata* were primarily associated with *S. reticulata*, and *R. cf. pascua* with *S. glauca*. Based on morphological characters Cripps and Horak (2008) reported five species of *Russula*, including one unidentified species.

Overall, studies suggest that at least four taxa of *Russula* occur in the central and southern Rocky Mountain alpine zone and many more have been reported from Arctic and alpine areas of Canada and Alaska. The *Russula* species reported in Arctic and alpine areas of North America associate with a variety of hosts including *Dryas octopetala*, *Bistorta vivipara*, *Betula glandulosa* and several species of dwarf and shrubby *Salix*. All of the aforementioned research on taxonomy and systematics on *Russula* in Arctic and alpine habitats of North America has been based on morphological characters.

Morphology alone suggests that at least some of the *Russula* species in Arctic and alpine habitats of North America are the same as those found in similar habitats in Europe (Lamoure et al. 1982; Knudsen and Borgen 1982; Borgen 1993; Elbone and Knudsen 1990; Adamčík and Knudsen 2004). However, these species and their potential intercontinental distributions have not been confirmed by modern molecular analyses. One recent paper dealt directly with taxonomy and systematics of the genus *Russula* in

Arctic and boreal habitats of North America and Europe using molecular phylogenetic methods but, this paper only covered the *R. globiospora* lineage (Caboň et al. 2019). They determined that *R. dryadicola* Fellner & Landa has an intercontinental distribution based on phylogenetic clustering of European material from the Alps and North American ITS sequences from Alaska. However, *R. dryadicola* has not yet been collected in North America.

Research has indicated that morphological analyses often fail to recognize the true *Russula* diversity in a region (Buyck 2007). Other studies have found high diversity and species partitioning within *Russula* in the Arctic using a 97% ITS sequence similarity cutoff (Geml et al. 2010; Geml and Taylor 2013). These results indicate that the true diversity and function of *Russula* in Arctic and alpine habitats may not be fully understood. It is likely that there are more than the four species of *Russula* previously reported from the central and southern Rocky Mountain alpine, and that undescribed species are present in this region.

To gain an accurate and stable understanding of *Russula* in the Rocky Mountain alpine, rigorous systematic approaches need to be applied. The goal of this research was to assess the diversity of *Russula* in the central and southern Rocky Mountains using morphological, ecological, and biogeographical data, along with molecular phylogenetics. This was done by comparing Rocky Mountain alpine *Russula* collections to type and reference material from Arctic, alpine, and subalpine habitats of North America and Europe.

CHAPTER TWO

SYSTEMATIC ANALYSIS OF *RUSSULA* IN THE NORTH AMERICAN ROCKY
MOUNTAIN ALPINE ZONEIntroduction

Arctic and alpine regions make up 5% and 3% of land on earth, respectively (Chapin & Körner 1995; Körner 1999; Körner 2003) and are collectively referred to as the Arctic-alpine biome (Bliss 1962; Billings 1973; Löve & Löve 1974; Bliss 1988; Chapin & Körner 1995; Murray 1995). Arctic and alpine regions are defined as the open, vegetated areas beyond the climatic limit of tree growth (Bliss 1988; Chapin & Körner 1995) or above tree line in mountainous regions worldwide (Körner 2003). The Arctic includes northern areas of Russia, Norway, Svalbard, Iceland, Greenland, Canada, and the United States of America (USA), which together comprise a circumpolar habitat (Callaghan et al. 2005). Alpine zones are found on high elevation mountain tops near the equator and at lower and lower elevations as you approach the poles, eventually merging with the Arctic (Billings 1974; Körner 1995). Research suggests that Arctic and alpine environments are being disproportionately affected by global warming compared to other systems (Serreze and Barry 2011; IPPC 2014). The temperature in Arctic regions is increasing 0.1° C per year (Anisimov et al. 2007; Comiso and Hall 2014), which is altering microbial function (Chapin et al. 1995) and leading to large scale changes in plant distributions (Sturm et al. 2001). As the climate warms, alpine communities will be restricted to ever-decreasing areas on mountain tops or will even disappear completely

(Grabherr et al. 1995). Most alpine regions are highly fragmented, disconnected, and contained within small areas of land, and the species present are often adapted to the harsh conditions found at high elevations (Anthelme & Lavergne 2018).

Fungi play important ecological roles in Arctic and alpine habitats where they 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 (Haselwandter and Read 1980; Read and Haselwandter 1981; Gardes and Dahlberg 1996; Bjorbækmo et al. 2010; Haselwandter 2007). A knowledge of fungal biodiversity in these systems can be used as a model to understand larger biological trends regarding the distribution and evolutionary history of Arctic and alpine communities (Gardes and Dahlberg 1996). This information can also help scientists and regulators make informed decisions concerning the conservation needs of these sensitive systems which are increasingly threatened by climate change (Grabherr et al. 1995). Therefore, gaining baseline data on Arctic and alpine fungi is essential so that future change can be detected and considered in management plans (Dahlberg and Bültmann 2013).

One of the most important fungal guilds in Arctic and alpine habitats are the ectomycorrhizal fungi that form mutualistic relationships with woody plants, which allows plants to survive in these cold-dominated habitats. In Arctic and alpine habitats, woody plants are ecologically important and in combination with grasses comprise the largest biomass in the biome (Körner 2003). In general, ectomycorrhizal fungi increase plant nutrient uptake (primarily nitrogen), ameliorate water relations, protect roots from

pathogen invasion, and can prevent heavy metal uptake. In return, the plant provides the fungus with photosynthetically derived sugars (Halling 2001; Smith and Read 2008). The most abundant ectomycorrhizal woody plants in these cold-dominated regions are the shrubs *Salix* L., dwarf *Betula* L. (Körner 2003), and *Dryas* L. (Trappe 1962; Miller et al. 1974; Chapin and Körner 1995; Cripps and Eddington 2005). One herb, *Bistorta vivipara* (L.) Delarbre, and sedges in the genus *Kobresia* Willd. are also known to form ectomycorrhizae (Trappe 1962, 1987; Lipson et al. 1999; Schadt 2002; Cripps and Eddington 2005; Ronikier and Mleczko 2006; Bjorbækmo et al. 2010; Thoen et al. 2019).

Members of the ectomycorrhizal fungal family Russulaceae play important roles in nutrient cycling across a variety of ecosystems worldwide. The Russulaceae has been proposed as a model family to explore ecosystem function and evolutionary diversification in ectomycorrhizal fungi (Looney et al. 2018). However, this model cannot be fully realized until species in the family are known and currently there is a knowledge gap. One of the largest ectomycorrhizal genera in the Russulaceae is *Russula* Pers. which is commonly reported to contain 750 species worldwide; however, this is known to be an underestimate of the true species diversity, which may extend to 3000 species (Buyck 2007; Buyck et al. 2015; Kirk 2017; He et al. 2019). *Russula* is most diverse in temperate zones where the genus apparently originated (Looney et al. 2016), but its species exist from the tropics to the Arctic.

Russula is an important ectomycorrhizal genus in Arctic and alpine habitats. It is reported to be one of the most abundant ectomycorrhizal associates of *Betula* in Arctic and alpine regions (Deslippe et al. 2011) and is the fourth most dominant ectomycorrhizal

genus in moist tussock and dry tundra in Arctic Alaska (Morgado et al. 2015). A study that analyzed the DNA from sporocarps and soil samples, found *Russula* to be the fifth most species-rich genus in Svalbard, a large Arctic island (Geml et al. 2012). Two studies of *Russula* in boreal regions of Alaska found high diversity (42 nonsingleton OTUs in one study) and that there was species partitioning by habitat using ITS sequence similarity to environmental and physical collections (Geml et al. 2010; Geml and Taylor 2013). These studies suggest that the diversity of *Russula* may be high in Arctic and alpine habitats, and that the true number of *Russula* species in northern latitudes is not fully realized.

The genus *Russula* comprises species with hypogeous, sequestrate, and pileate-stipitate basidiocarps, but only the latter has been reported from Arctic and alpine habitats. Pileate-stipitate *Russula* species have colorful, convex to funnel shaped pilei, attached lamellae that are not usually decurrent, a white to dark yellow spore print, no clamp connections, no latex, amyloid ornamented basidiospores, and sphaerocysts in a heteromerous trama (Romagnesi 1967; Singer 1986; Sarnari 1998–2005). The taxonomy of *Russula* is complex and several monographs have attempted to provide usable and coherent classifications for the genus (Romagnesi 1967; Singer 1986; Sarnari 1998–2005). The type species for the genus is *R. emetica* (L.) Pers. and eleven subgenera are currently recognized phylogenetically; however, the validity of some is still under debate (Sarnari 1998–2005; Hongsanant et al. 2015; Das et al. 2017; Buyck et al. 2018, 2020).

The study of *Russula* has been dominated by European mycologists who have published extensively on the genus (Fries 1874; Killerman 1936; Lange 1937; Romagnesi

1967; Singer 1986; Sarnari 1998–2005). Although these studies have continued for around 150 years, European mycologists did not focus heavily on Arctic and alpine species of *Russula* until the 1950s. In Arctic and alpine regions of Eurasia, *Russula* species have been reported from the European Alps (Kühner 1975; Jamoni and Bon 1993; Jamoni 1995, 2008; Bon 2000; Adamčík and Knudsen 2004; Knudsen et al. 2012; Adamčík et al. 2016b), the Monte Rosa Massif (Bon 1993), the Pyrenean range (Bon and Ballarà 1996; Corriol 2008), Slovakia (Fellner and Landa 1993a, 1993b; Ronikier and Adamčík 2009; Adamčík et al. 2006), Poland (Ronikier and Adamčík 2009; Adamčík et al. 2016b), Fennoscandia (Favre 1955; Lange and Skifte 1967; Knudsen et al. 2012; Ruotsalainen and Huhtinen 2015; Adamčík et al. 2016b), Germany (Bresinsky et al. 1980), Svalbard (Kobayasi et al. 1968; Skifte 1989; Gulden and Torkelsen 1996), Romania (Ronikier 2008), Denmark (Adamčík et al. 2016b), the Faroe Islands (Vesterholt 1998; Adamčík and Knudsen 2004), Scotland (Fellner and Landa 1993b; Watling 1987), and Iceland (Christiansen 1941; Hallgrímsson 1998).

The majority of the taxonomy and classification of Arctic and alpine *Russula* species has been based almost entirely on morphology. Around 50 names have been used to describe *Russula* taxa in Arctic and alpine habitats worldwide, based mostly on basidiocarp surveys (TABLE 4, Chapter 1). However, this is likely an overestimate as some names have been synonymized and others have been incorrectly applied to Arctic and alpine *Russula* collections. That being said, it is also possible that *Russula* diversity has not been completely explored in Arctic and alpine regions. Morphological analyses often fail to recognize the true diversity of *Russula* in a region (Buyck 2007).

In North America, *Russula* diversity has been investigated in cold habitats to a limited extent in Alaska (Miller et al. 1973, 1982), Canada (Ohenoja 1972; Miller et al. 1973; Kallio 1980; Hutchinson et al. 1988; Ohenoja and Ohenoja 2010), and extensively in Greenland (Lange 1957; Kobayasi et al. 1971; Watling 1977; 1983; Knudsen and Borgen 1982; Lamoure et al. 1982; Elborne and Knudsen 1990; Borgen 1993; Adamcik and Knudsen 2004). Virtually nothing was known of *Russula* species in the central and southern Rocky Mountain alpine region until the last two decades. *Russula nana* was reported above treeline in Wyoming by Moser and McKnight in 1987, and it remained the only *Russula* known from the Rocky Mountain alpine until the early 2000s. Four species of alpine *Russula* were later reported from a large-scale survey of alpine Agaricales focused on the central and southern Rocky Mountains (Cripps and Horak 1999, 2008; Cripps 2003). This includes *R. nana* along with the first formal reports for *Russula* cf. *delica* Fr., *R. laccata* Huijsman, and *R. cf. pascua* (F.H. Møller & Jul. Schöff.) Kühner for the Rocky Mountains (Cripps and Horak 2008). These four species were found in association with a variety of hosts, including *Dryas octopetala* L., *Bistorta vivipara*, and species of shrubby (*S. glauca* L. and *S. planifolia* Pursh) and dwarf willows (*S. reticulata* L. and *S. arctica* Pall.) (Moser and Mcknight 1987; Cripps and Horak 2008). Most *Russula* species reported from the Rocky Mountain alpine appear to be in *R.* subgenus *Russula* and *R.* subgenus *Brevipes*. All of the taxonomic work on *Russula* in Arctic and alpine habitats of North America up to this time has been based solely on morphological characters. These species, their distribution, and their phylogenetic placement were not confirmed by molecular analyses.

Based on morphology, species in other genera previously reported from the Rocky Mountain alpine (Miller et al. 1973; Moser and McKnight 1987; Cripps and Horak 2008, 2010a, 2010b; Osmundson et al. 2005) are mostly those known from alpine habitats in Europe and the Arctic (Lamoure et al. 1982; Knudsen and Borgen 1982; Borgen 1993; Elbone and Knudsen 1990; Adamčík and Knudsen 2004). More recently, molecular research on *Lactarius* Pers., *Inocybe* (Fr.) Fr., and *Hebeloma* (Fr.) P. Kumm. has confirmed that most species from the Rocky Mountain alpine are also present in the alpine of Europe and the Arctic, although a few appear to be North American endemics (Barge et al. 2016; Cripps et al. 2019, 2020). All this suggests that there may be at least some overlap between *Russula* species in the Rocky Mountain alpine and those in similar habitats of Europe and the Arctic. If *Russula* species in the Rocky Mountain alpine are the same as those in Arctic and alpine habitats of Europe, this implies that these species have large, intercontinental distributions. Large, intercontinental distributions have been molecularly confirmed for other ectomycorrhizal genera from the Rocky Mountain alpine, including *Hebeloma* (Beker et al. 2010; Cripps et al. 2019), *Cortinarius* (Pers.) Gray (Peintner 2008), *Inocybe* (Cripps et al. 2010; Larsson et al. 2014; Larsson et al. 2018; Cripps et al. 2019), and *Lactarius* (Barge et al. 2016; Cripps and Barge 2016).

While fungal communities in the Rocky Mountain alpine have certainly been shaped by glaciation and other abiotic factors, ectomycorrhizal fungi also need to follow their plant host. One of the primary hosts for ectomycorrhizal fungi, including *Russula*, in northern cold-dominated habitats are Arctic and alpine species of *Salix* (Knudsen et al. 2012; Cripps and Horak 2008); these species are known to have large, circumpolar

distributions in Arctic and alpine habitats (Hultén 1968). Some of these willow species are present in the disjunct isolated areas that comprise the Rocky Mountain alpine. As further evidence, *Russula* distributions have even been shown to shift in response to changes in plant host distribution due to climate change (Looney et al. 2019, 2020). We also know that *Russula* diversification corresponds with that of major ectomycorrhizal plant lineages such as Betulaceae and Salicaceae (Looney et al. 2016), both of which occur in Arctic and alpine regions. Thus, it is likely that alpine species of *Russula* in the Rocky Mountains have at least the potential to occur wherever their host exists, which could result in large distributions in the case of *Salix*-associated species.

Large, intercontinental distributions have already been confirmed for two species of *Russula*. *Russula dryadicola* Fellner & Landa and *R. laevis* Kälviäinen, Ruots. & Taipale are reported in boreal and Arctic environments of Europe and confirmed in North American using molecular comparison to environmental sequences (Adamčík et al. 2019; Caboň et al. 2019). *Russula laevis* was previously reported from the southern Rocky Mountains as *R. cf. delica* which extends the range of this species (Cripps and Horak 2008). Therefore, we hypothesize that the *Russula* species that occur in the Rocky Mountain alpine will have large intercontinental distributions. Long distance, transoceanic dispersal has been hypothesized to explain minimal molecular differences in Arctic species of ectomycorrhizal fungi (Geml et al. 2012), in contrast to the more limited dispersal of temperate *Russula* species (Bazzicalupo et al. 2019). However, long distance dispersal is a problematic explanation for fungal distributions in disjunct alpine areas. The central and southern Rocky Mountains, which is the primary collecting sites for this

study, are thousands of miles from the Arctic and an explanation for large intercontinental distributions in Arctic-alpine fungi is outside the scope of this project.

There are several possibilities for how *Russula* species came to occur in relatively young available Arctic and alpine habitats. Did one or a few species arrive and diversify like Darwin's finches? Or did they originate from various subalpine lineages scattered throughout the *Russula* phylogeny? Molecular phylogenetics can elucidate the evolutionary history of these species within the entire *Russula* clade. Based on morphology alone, the few *Russula* species that have been reported in the Rockies appear to be distantly related (Moser and McKnight 1987; Cripps and Horak 2008), and do not appear to share a recent common ancestor. Thus, given the data so far, it appears most likely that *Russula* species in the Rocky Mountain alpine do not share a recent common ancestor unique to this group but instead evolved independently from more than one lineage into alpine habitats.

Despite being a diverse genus, only about 58 species of *Russula* have been newly described from the western United States in all habitats (Buyck et al. 2015). This is certainly an under representation. It is also likely that there are more than the four species of *Russula* previously reported in the Rocky Mountain alpine zone, and that additional species remain to be found. To gain an accurate and stable understanding of *Russula* taxonomy, rigorous systematic approaches need to be applied. This research integrated morphological, ecological, and biogeographical data along with molecular phylogenetics to elucidate the true diversity of *Russula* in alpine regions of the Rockies. We hypothesize that 1) the species reported from the Rocky Mountain alpine will be the same

as those reported in Arctic and alpine habitats of Europe based on molecular and morphological data, 2) the *Russula* species present in the Rocky Mountain alpine will have large, intercontinental distributions, similar to the Arctic and boreal species studied molecularly in Europe, and 3) the *Russula* species in the Rocky Mountains have independently colonized alpine habitats and do not form a monophyletic group.

This research analyzed the morphological and molecular characters of over 130 *Russula* collections (collected from 1997 to 2018) from the Rocky Mountain alpine in Montana, Wyoming, and Colorado and compared them to type and reference material from several herbaria throughout the world. Detailed morphological descriptions were created for each species; scanning electron microscope and compound microscope photos accompany descriptions. The diversity of *Russula* in the Rocky Mountain alpine was assessed with a multi-locus phylogeny, using the nuclear ribosomal ITS1-5.8S-ITS2 region (ITS barcode) and the second largest subunit of the RNA polymerase II gene (*RPB2*). Species distributions are addressed, and some *Russula* species are reported for the first time in the Rocky Mountain alpine and in North America. A key was created to help identify the *Russula* species present in the Rocky Mountain alpine zone using macro- and micromorphological features.

Methods

Study Sites

The goal of this study was to determine which species of *Russula* occur in the central and southern Rocky Mountain alpine zone. The Rocky Mountains extend from northern Alaska to northern New Mexico and host a semi-contiguous alpine zone, which

consists of open, vegetated areas above treeline (Billings 1988). The vegetation is often variable, but consists of perennial grasses, sedges, forbs, low-growing prostrate shrubs and cushion plants; mosses and lichens are also abundant (Körner 2003). The Rocky Mountains were thrust up through thick sedimentary rocks and erosion exposed ancient granites and metamorphic rock. However, sedimentary rocks including shale, limestone, sandstone, and quartzite still remain, and make up entire subranges of the Rocky Mountains; basalt, andesite, and rhyolite can also be found (Retzer 1956). High elevation alpine environments in the Rockies often experience cold temperatures, high winds, and a majority of their moisture occurs as snow fall (Billings 1973; Körner 1999; Körner 2003); these factors lead to a short growing season. In the Rocky Mountain alpine, the ectomycorrhizal hosts include the shrubby willows *Salix glauca* and *S. planifolia*, and the dwarf willows *S. reticulata* and *S. arctica*. Other important hosts include *Betula glandulosa* Michx., *Dryas octopetala*, and *Bistorta vivipara* (Cripps and Eddington 2005; Cripps and Horak 2008). These hosts are found at most alpine field sites in the Rocky Mountains with the exception of *B. glandulosa*, which is more common in the southern Rockies of Colorado and the northern Rockies of Alaska, and less common in the central Rockies.

This study was based on specimens collected in the Rocky Mountain alpine as well as reference material collected and obtained (through herbaria) from Arctic and alpine regions of Europe. A majority of the fungi used in this study were collected in the central and southern Rocky Mountains of Montana, Wyoming, and Colorado; a few collections came from Alaska. The main collecting sites for the central Rocky Mountains

are located in the Beartooth Mountains, which lie on the border of Montana and Wyoming. The Mountain range is part of the Absaroka-Beartooth Wilderness, which is located within the Custer, Gallatin, and Shoshone National Forests. The Beartooth Mountains are home to Granite Peak (3904 m), which is the highest point in the state of Montana. The mountain range includes multiple high elevation alpine plateaus. The Beartooth Plateau is considered one of the most biologically unique regions in North American and is the highest elevation alpine plateau in the forty-eight conterminous United States. Collecting sites located on the Beartooth Plateau include the Billings Fen (44°58'16.9" N, 109°26'07.3" W, 3230 m), Birch Site (45°01'26.64" N, 109°24'29.164" W, 2990–3020 m), Highline Trail (45°00'21.36" N, 109°24'23.22" W, 3060–3100 m), Frozen Lakes (44°57'55.92" N, 109°28'59.88" W, 3190–3200 m), Solifluction Terraces (44°58'22.32" N, 109°26'48.6" W, 3258 m), and Wyoming Creek (45°00'10.62" N, 109°24'30.06" W, 3200 m). Two other collecting locations in Montana were at Cinnabar Basin (45°07'21.07" N, 110°48'59.17" W, 1930 m) in the Absaroka Mountains and Hellroaring Plateau (45°03'31.79" N, 109°28'36.58" W, 3166 m) in the Beartooth Mountains.

Study sites in the southern Rocky Mountains are in alpine areas of Colorado and include Independence Pass (39°06'36" N, 106°33'36" W, 3600–3700 m) and Cottonwood Pass (38°49'12" N, 106°24'00" W, 3700 m) in the Sawatch Range; Black Bear Basin (37°24'00" N, 107°42'00" W, 3760 m), California Gulch (37°55'30" N, 107°35'06" W, 3941 m), Cinnamon Pass (37°55'48" N, 107°31'48" W, 3700–3850 m), Engineer Pass (37°58'19.2" N, 107°35'2.4" W, 3901 m), Mineral Basin (38°45'38.16" N, 106°23'57.12"

W, 3900 m), and Stony Pass (37°46'48" N, 107°31'48" W, 3700 m) in the San Juan Mountains; Blue Lake area (40°05'24" N, 105°37'12" W, 3572 m), Loveland Pass (39°39'36" N, 105°52'48" W, 3700m), Mt. Evans (39°35'17.88" N, 105°38'37.68" W, 4310 m), and Niwot Ridge (40°03'34.92" N, 105°37'00.84" W, 3748 m) in the Front Range. Study sites in Alaska include Crow Pass road (61°04'26" N, 149°07'28" W, 457 m) near Girdwood and Alpine Glen (61°05'26.16" N, 149°39'55.08" W, 1070 m) on Flattop Mountain outside Anchorage.

Taxon Sampling and Processing

Basidiocarps of *Russula* were collected in the Rocky Mountain alpine during July and August from 1997 to 2018. All collections were described when fresh and photographed when possible. Habitat, possible mycorrhizal hosts, location, and date were noted for all collections. Spore prints were obtained when possible. All basidiocarps were dried on a standard dehydrator and deposited in the Montana State University herbarium (MONT), Bozeman, Montana 59717–3150. Other Rocky Mountain alpine collections of *Russula* were obtained from the Denver Botanic Gardens' Sam Mitchel Herbarium of Fungi, Denver, Colorado (DBG). Reference collections were obtained from the University of Michigan fungal herbarium, Ann Arbor, Michigan (MICH), the New York Botanical Garden, Bronx, New York (NY), the Botanical Museum, University of Oslo, Norway (O), the Arctic University of Norway, Norway (TROM), and Åbo Akademi University, Finland (TURA). Herbarium Codes are from <http://sweetgum.nybg.org/ih/> (Thiers B., continuously updated).

Our collections were initially identified based on morphological species concepts when possible, using taxonomic keys (Jamoni 1995; Sarnari 1998–2005; Bon 2000; Moreau 2002; Adamčík et al. 2016b) and personal expertise (Cripps pers. com. 1997–2020). Detailed morphological descriptions were made for each collection and compiled for each species. Morphological descriptions include most of the characters traditionally described by fungal taxonomists, even if characters like the pileus color and the degree to which the cap cuticle peels have been determined to be less informative for species delineation in *Russula* (Bazzicalupo et al. 2017). Final species determinations were based on a combination of morphological, molecular, and ecological data, with the goal being concordance between all data types. If there were disagreements between particular datasets, we looked for concordance between as many independent data points as possible while taking the species taxonomic history into account.

Morphological Descriptions

Macromorphological characters were described using fresh material and micromorphological characters were assessed following observation of dried, rehydrated material. Macromorphological descriptions of the pileus, lamellae, stipe, and context follow Buyck (2019). The odor and taste of fresh material were included when possible. Spore print colors are described and compared to Romagnesi's (1967) color code for spores. Chemical tests for ferrous sulfate (FeSO_4), Phenol, and Gum Guaiac were done by placing one drop of each chemical on a small section of fresh context; reactions were observed for five minutes (Melzer and Zvara 1928; Watling 1971; Moser 1978). Exsiccata were also described. The degree to which the cap cuticle can be peeled was

described as: hardly peeling near margin (<20%), separable except at center (20–95%), or completely separable (Buyck 2019). The number of lamellae (L) refers to those that reach the stipe on select basidiocarps. A lower-case n was used to denote the number of basidiocarps from which lamellae were counted.

A Leica DMLS research microscope was used for all microscopic observations and measurements. The micromorphology was examined for collections listed in TABLE 5. Micromorphological characters described and measured include basidiospores, basidia, hymenial cystidia, pileipellis, and pileocystidia. Hymenial cystidia refer to the sterile cells on the surface of the lamellae (Romagnesi 1967; Thiers 1994; Sarnari 1998–2005; Adamčík and Knudsen 2004; Adamčík et al. 2016b). Pileocystidia are unique terminal cells in the pileipellis with granular (and possibly gelatinous) contents of usually a larger width than hyphal terminations (Sarnari 1998–2005). For microscopic examination, fungal tissue was first reconstituted in 70% ethanol. Basidiospores were then observed in Melzer's reagent (0.5 g iodine, 1.5 g potassium iodide, 20ml dH₂O, 2 ml chloral hydrate) (Melzer and Zvara 1927) and basidia, hymenial cystidia, and pileocystidia were observed in 3% KOH and sulfovanillin. When observing features in sulfovanillin, a few crystals of vanillin were placed next to a reconstituted scalp section of the pileipellis or a piece of lamella and mixed with one drop of sulfuric acid and observed for five minutes; the reaction was recorded as: none, slightly graying, graying, slightly blackening, or blackening.

On average, 20 basidiospores were measured at random from the apex of the stipe or directly from the lamellae. For each basidiospore, the length and width were measured

at the widest point under a 100× oil-immersion lens (1000× magnification); the apiculus and ornamentation were not included in measurements. The length to width ratio (Q) was calculated for each basidiospore and the average Q value was used to describe the spore shape: subglobose (Q = 1.05–1.15), broadly ellipsoid (Q = 1.16–1.3), ellipsoid (Q = 1.31–1.45), narrowly ellipsoid (Q = 1.46–1.6), oblong (Q>1.6) (Adamčík et al. 2019). The height of basidiospore ornamentation was recorded from at least five spores and the range recorded. Degree of amyloidity and relative size was recorded for the suprahilar plage. Ornamentation terminology follows Adamčík et al. (2019), and includes: spines (acute tips), warts (obtuse tips), ridges (linear elements connecting warts and spines), and/or wings (ridge > 2µm tall). The general appearance of the ornamentation was described as: isolated warts, clustered warts, individual lines, branched, subreticulate, or reticulate (Adamčík et al. 2019). Ten basidia, hymenial cystidia, and pileocystidia were randomly measured under a 40× lens (400× magnification) to determine length and width at the widest points; the contents were also described. Mucronate appendages on hymenial cystidia were measured, when encountered, and the range recorded. Within the pileipellis, the suprapellis (upper portion near surface containing pileocystidia and hyphae) and subpellis (portion between the suprapellis and context) were measured and the general form of each layer described (FIG. 1A). The general shape and width of the hyphal terminations located in between the supra- and subpellis were also described. On select taxa the length and width of the terminal cells of hyphae in the pileipellis were recorded from ten hyphal ends at the pileus margin and near the pileus center. Photographs of some of the micromorphological features are shown in FIG. 1. After

macro- and micromorphological descriptions were complete for each collection, they were combined for each species as determined by morphological, ecological, and molecular phylogenetic analyses. Then, the minimum measurement, standard deviation, average, average – standard deviation, average + standard deviation, and maximum measurement was calculated for basidiospores (length, width, and Q), basidia, hymenial cystidia, pileocystidia, and for hyphal terminations when applicable for each species; average values are italicized.

Figure 1. Select microscopic features in *Russula*. A. Important microscopic features present in the pileipellis in 3% KOH (400×). B. Sphaerocysts in 3% KOH (1000×). C. Pileocystidia showing a blackening reaction in sulfovanillin, indicated by arrow (200×). D. Hymenial cystidia showing a blackening reaction in sulfovanillin, indicated by arrow (400×).

Scanning Electron Microscopy

Morphological descriptions were complemented with scanning electron microscope (SEM) photographs of the basidiospores for most species found in the Rocky Mountain alpine (FIG. 17). These were included to provide detailed images of the basidiospore ornamentation, which can be useful for taxonomic identification and for understanding intraspecific morphological variation. The scanning electron microscope and associated equipment were provided by the Imaging and Chemical Analysis Laboratory at Montana State University. Dried pieces of lamella about 2 mm² were attached to glass coverslips using double-stick tape. They were either iridium or gold sputter-coated for 45 seconds at 35 milliamps to achieve a coating thickness of 15 nm. Basidiospores were examined using a field emission scanning electron microscope (Zeiss SUPRA 55VP) at 1.00 KV. Photos were edited in Adobe Lightroom 3 and Photoshop v. 21.0.1. A scale bar was created by modifying the scale produced by the SEM.

Compound Microscope Photography

Morphological descriptions were complemented with compound microscope photographs of the basidiospores for all species found in the Rocky Mountain alpine (FIG. 18). These were included for the same reasons as the SEM photographs, but also to replicate what is observed under the compound microscope because most researchers won't have access to SEM images. Basidiospores were photographed using a Sony $\alpha 7$ III camera with a Full Frame 2x DSLR/ML Microscope Camera Adapter on a Leica DMLS research microscope. Three to five separate photographs were taken at various focal depths of the same image to increase depth of field. Photographs were focus-stacked in

Helicon Focus 7 and edited in Photoshop v. 21.0.1. Photographs were taken of the eyepiece reticle scale so a 10 μ scale could be added to the basidiospore photographs.

Table 5. Collections whose micromorphological features were examined¹ or were included in the phylogenetic analyses². Type specimens are bolded. ITS or *RPB2* is bolded if the sequence was generated in this study. Herbarium Codes from <http://sweetgum.nybg.org/ih/>.

Taxon	Voucher	Date	Location	Host or Habitat	ITS	<i>RPB2</i>
<i>Lactarius deceptivus</i> ²	AFTOL ID 682	NA	MA, U.S.A.	NA	AY854089	AY803749
<i>Multifurca ochricompacta</i> ²	PC0723654	20 Jun 2014	Newton County, TX, U.S.A.	NA	MH063878	MH061175
<i>R. aeruginea</i> ²	AT2003017	NA	Sweden	NA	DQ421999	DQ421946
<i>R. albonigra</i> ²	AT2002064	NA	Sweden	NA	DQ422029	DQ421966
<i>R. aff. alpigenes</i> ²	CLC 3822B (MONT)	22 Aug 2018	Crow Pass Rd. Girdwood, AK, U.S.A.	<i>Dryas, Salix</i>	Yes	Yes
<i>R. aff. alpigenes</i> ²	CLC 3821 (MONT)	22 Aug 2018	Crow Pass Rd. Girdwood, AK, U.S.A.	<i>Salix</i>	Yes	Yes
<i>R. altaica</i> ^{1,2}	333753 (NY)	5 Aug 1937	Russia	<i>Salix, Betula</i>	Yes	NA
<i>R. altaica</i> ^{1,2}	CLC 1608 (MONT)	2 Aug 2001	Blue Lake Dam, CO, U.S.A.	<i>Betula, Dryas</i>	Yes	Yes
<i>R. altaica</i> ^{1,2}	CLC 1618 (MONT)	3 Aug 2001	Blue Lake Dam, CO, U.S.A.	<i>Betula, Salix</i>	Yes	Yes
<i>R. amara</i> ²	FH 12213	18 Aug 2012	Hildesheim, Germany	NA	KT933998	KT933930
<i>R. amoenipes</i> ²	309IS77	NA	NA	NA	AY061656	NA
<i>R. cf. amoenoides</i> ²	Sav_F_1340	NA	Italy	NA	KU205284	NA
<i>R. aquosa</i> ²	TROM_F_17338	8 Sept 2017	Norway	<i>Picea</i>	UDB037477	NA
<i>R. aquosa</i> ²	TU 101719	NA	NA	NA	KX579813	NA
<i>R. atrorubens</i> ²	TU 101728	9 Sept 2011	Varstu vald, Võru maakond, Estonia	<i>Picea</i>	UDB011308	NA
<i>R. atrorubens</i> ²	TU 101718	NA	NA	NA	KX579812	NA
<i>R. betularum</i> ²	PC BB2004-235	NA	Great Smoky Mountains National Park, TN, U.S.A.	NA	EU598183	NA
<i>R. betularum</i> ²	SAV:F-20026	6 Oct 2014	Apuseni Mts., Romania	<i>Betula, Picea</i>	KY582694	KY616687
<i>R. betularum</i> ²	JV 30628	17 Aug 2014	Tolola, Saukkovaara, Paltamo, Kainuu, Finland	<i>Picea, Betula, Salix, Pinus</i>	Yes	NA
<i>R. betularum</i> ²	BPL 269	8 Aug 2012	Great Smoky Mountains National Park, TN, U.S.A.	<i>Tsuga carolinensis, Abies, Picea, Betula</i>	KT933969	KT933900
<i>R. cf. brevipes</i> ²	321965	4 Jul 2018	Point Reyes National Seashore, CA, U.S.A.	<i>Pseudotsuga menziesii</i>	MH714879	NA
<i>R. cf. brevipes</i> ²	RK8	NA	Canada	NA	KF007188	NA

<i>R. brevipes</i> ^{1,2}	CLC 2730 (MONT)	5 Aug 2011	Alaska, U.S.A.	<i>Dryas</i>	Yes	Yes
<i>R. brevipes</i> ^{1,2}	CRN 063 (MONT)	18 Sept 2017	Hyalite Canyon, MT, U.S.A.	<i>Picea, Abies</i>	Yes	NA
<i>R. brevipes</i> ²	18598 (DBG)	6 Jul 1996	Boulder, CO, U.S.A.	<i>Pinus ponderosa</i>	Yes	Yes
<i>R. brevipes</i> ²	TENN:070667	16 Jul 2015	Great Smoky Mountains National Park, NC, U.S.A.	NA	KY848511	NA
<i>R. camarophylla</i> ²	PAM01081108	NA	France	NA	DQ421982	DQ421938
<i>R. chamiteae</i> ¹	24741 (DBG)	23 Aug 2010	Glacier Lake, Near Roosevelt N.F., CO, U.S.A.	Conifers, <i>Salix</i>	Yes	NA
<i>R. aff. chloroides</i> ²	FH 12273	10 Oct 2012	Belgium	NA	KT934015	KT933947
<i>R. chloroides</i> ²	ue68 (TUB)	NA	Germany	<i>Fagus sylvatica</i>	AF418604	NA
<i>R. chloroides</i> ²	205Rus24	NA	NA	NA	AY061663	NA
<i>R. chloroides</i> ²	RUS-12091401	14 Sept 2012	Ireland	NA	KF432954	NA
<i>R. claroflava</i> ²	FH 12212	18 Aug 2012	Hildesheim, Germany	NA	KT933997	KT933929
<i>R. clavipes</i> ²	FR:652	NA	RheinLahnKreis, Germany	<i>Betula, Populus, Picea</i>	KU205304	NA
<i>R. clavipes</i> ²	SAV:F-1327	NA	W. Carpathians, Slovakia	<i>Picea, Abies, Sphagnum</i>	KU205292	NA
<i>R. compacta</i> ²	BPL 242	2 Aug 2012	Great Smoky Mountains National Park, TN, U.S.A.	<i>Betula, Tsuga</i>	KT933960	KT933890
<i>R. compacta</i> ²	BPL 227	30 Jul 2012	TN, U.S.A	<i>Tsuga</i>	KT933952	KT933881
<i>R. cremeirosea</i> ²	BPL 289	2 Oct 2012	Knoxville, TN, U.S.A.	<i>Quercus</i>	KT933983	KT933915
<i>R. cuprea</i> ²	SAV:HK12050	17 Aug 2012	Gotland Island, Sweden	<i>Quercus</i>	KU886591	NA
<i>R. cuprea</i> ²	FH 12250	31 Aug 2012	Rudigsdorf, Germany	NA	KT934010	KT933942
<i>R. cuprea</i> ²	LM-18	14 Sept 2006	Ledmore Oakwood, Spinningdale, Sutherland, Scotland	<i>Quercus petraea, Betula</i>	UDB002420	NA
<i>R. cf. cyanoxantha</i> ²	BPL 280	10 Aug 2012	TN, U.S.A	<i>Tsuga</i>	KT933976	KT933908
<i>R. decolorans</i> ²	FH 12196	2 Aug 2012	Ilmenau, Germany	NA	KT933992	KT933924
<i>R. aff. delica</i> ²	FH 12266	3 Oct 2012	Walkenried, Germany	NA	KT934014	KT933946
<i>R. aff. delica</i> ²	UE24.08.2004-20	NA	NA	NA	DQ422005	NA
<i>R. cf. delica</i> ²	UBC F30260	2 Nov 2014	Canada	NA	KX812852	NA
<i>R. delica</i> ²	TU116211	22 Jul 2013	Tartu, Estonia	NA	UDB025023	NA
<i>R. delica</i> ²	hue22 (TUB)	NA	NA	<i>Fagus sylvatica</i>	AF418605	NA
<i>R. delica</i> ²	FH 12-272	10 Oct 2012	Belgium	NA	KF432955	NA
<i>R. dryadicola</i> ²	PAM95082603	26 Aug 1995	Svoie, France	<i>Dryas octopetala</i>	MG386715	MG386741
<i>R. earlei</i> ²	BPL 245	3 Aug 2012	Great Smoky Mountains National Park, TN, U.S.A.	<i>Quercus, Fagus, Tsuga, Pinus</i>	KT933961	KT957331

<i>R. emetica</i> ²	Iw081	15 Oct 1996	Nationalpark Bayerischer, Germany	<i>Picea</i>	UDB000300	NA
<i>R. emetica</i> ²	JV 25569	5 Oct 2007	Finland	<i>Pinus sylvestris</i>	Yes	NA
<i>R. emetica</i> ²	Buyck 2444 (517IS76)	NA	Europe	NA	AY061673	NA
<i>R. emetica</i> ²	UBC F30056	NA	NA	NA	KX579781	NA
<i>R. emeticicolor</i> ²	FH 12253	5 Sept 2012	Erfurt, Aspenbusch, Germany	NA	KT934011	KT933943
<i>R. faginea</i> ²	Sav:F-1336	NA	Slovakia	NA	KU205285	NA
<i>R. farinipes</i> ²	UE28.09.2002.4	NA	France	NA	DQ421983	DQ421939
<i>R. favrei</i> ²	IB1995/0098	NA	Tirol, Austria	Conifers	KU205318	NA
<i>R. foetens</i> ²	FH 12277	27 Aug 2012	Keula, Germany	NA	KT934016	KT933948
<i>R. font-queri</i> ²	FH 12223	30 Aug 2012	Rudigsdorf, Germany	NA	KT934003	KT933935
<i>R. fragilis</i> ²	FH 12197	18 Aug 2012	Hildesheim, Germany	NA	KT933993	KT933925
<i>R. gigasperma</i> ²	438/BB 07.280	NA	NA	NA	NA	KU237787
<i>R. globispora</i> ²	GENT FH2007 BT111	8 Sept 2007	Thuringen, Germany	NA	KU928144	KY616671
<i>R. gracillima</i> ²	JV 32758F	5 Oct 2007	Finland	<i>Picea, Betula</i>	Yes	NA
<i>R. gracillima</i> ²	TU101698	6 Sept 2011	Krabi, Estonia	<i>Picea, Betula</i>	UDB011284	NA
<i>R. gracillima</i> ²	UE23.08.2004-14	NA	NA	NA	DQ422004	NA
<i>R. gracillima</i> ²	FH 12-264	NA	Germany	NA	KR364094	NA
<i>R. graminea</i> ²	KKJV 26121F (MONT)	16 Aug 2008	Finland	<i>Picea, Betula, Pinus sylvestris</i>	Yes	NA
<i>R. graveolens</i> ²	Sav:F-1343	NA	Slovakia	NA	KU205298	NA
<i>R. grisescens</i> ²	MxM R-0838	26 Jul 2008	Österreich (Tirol), Austria	<i>Picea abies</i>	UDB031192	NA
<i>R. grisescens</i> ²	JV 32642F	30 Aug 2018	Tololanmäki, Paltamo, Kainuu, Finland	<i>Betula, Alnus, Picea, Populus</i>	Yes	NA
<i>R. heterochroa</i> ^{1,2}	CLC 1723 (MONT)	12 Aug 2001	Cottonwood Pass, CO, U.S.A.	Alpine <i>Dryas</i>	Yes	Yes
<i>R. heterochroa</i> ^{1,2}	CLC 1919 (MONT)	21 Aug 2002	Nordensklods Land, Adventdalen, Todalen, Svalbard	Arctic <i>Salix polaris</i> , <i>Dryas octopetala</i>	Yes	Yes
<i>R. heterochroa</i> ^{1,2}	CLC 1918 (MONT)	21 Aug 2002	Nordensklods Land, Adventdalen, Todalen, Svalbard	Arctic <i>Salix polaris</i> , <i>Dryas octopetala</i>	Yes	Yes
<i>R. heterophylla</i> ²	UE20.08.2004-2	NA	Sweden	NA	DQ422006	NA
<i>R. integra</i> ²	FH 12172	1 Aug 2012	Erfurt, Aspenbusch, Germany	NA	KT933984	KT933916
<i>R. cf. intermedia</i> ^{1,2}	CLC 2759 (MONT)	9 Aug 2011	Near Girdwood, AK, U.S.A.	<i>Dryas, Salix</i>	Yes	Yes
<i>R. cf. intermedia</i> ^{1,2}	CLC 3784 (MONT)	20 Aug 2018	Alpine Glen, Flattop, AK, U.S.A.	<i>Dryas, Salix</i>	Yes	Yes
<i>R. cf. intermedia</i> ^{1,2}	CLC 3822 (MONT)	22 Aug 2018	Crow Pass Rd., Girdwood, AK, U.S.A.	<i>Dryas</i>	Yes	Yes

<i>R. intermedia</i> ²	Sav:F-3093	6 Sept 2009	Dovre fjell National Park, Dovre, Oppland, Norway	<i>Betula pendula</i>	KU928147	NA
<i>R. intermedia</i> ²	JV 32189F	27 Aug 2017	Melalahti, Paltamo, Kainuu, Finland	<i>Picea, Betula</i>	Yes	NA
<i>R. aff. laccata</i> ¹	23923 (DBG)	30 Aug 2007	Squaw Pass Road, CO, U.S.A.	<i>Salix, Picea</i>	Yes	Yes
<i>R. cf. laccata</i> ²	UBC F30302	8 Nov 2014	Canada	NA	KX812849	NA
<i>R. laccata</i> ¹	JV 23194	26 Aug 2005	Oulanka National Park, Kuusamo, Koillismaa, Finland	<i>Salix</i>	Yes	NA
<i>R. laccata</i> ¹	CLC 1381 (MONT)	19 Aug 1999	Birch Site, Beartooth Plateau, MT, U.S.A.	Alpine <i>Salix planifolia</i>	Yes	Yes
<i>R. laccata</i> ¹	CLC 1465 (MONT)	6 Aug 2000	Independence Pass, CO, U.S.A.	Alpine	Yes	NA
<i>R. laccata</i> ¹	CLC 1467.1 (MONT)	6 Aug 2000	Independence Pass, CO, U.S.A.	Alpine	Yes	NA
<i>R. laccata</i> ¹	CLC 2275 (MONT)	1 Aug 2005	Niwot Ridge, CO, U.S.A.	Alpine	Yes	Yes
<i>R. laccata</i> ¹	CLC 2371 (MONT)	6 Aug 2008	Wyoming Creek, Beartooth Plateau, WY, U.S.A.	Alpine	Yes	Yes
<i>R. laccata</i> ¹	CLC 3617 (MONT)	23 Aug 2017	Billings Fen Site, Beartooth Plateau, MT, U.S.A.	Alpine <i>Salix</i>	Yes	Yes
<i>R. laccata</i> ¹	CRN 133 (MONT)	7 Aug 2018	Billings Fen Site, Beartooth Plateau, MT, U.S.A.	Alpine <i>Salix</i>	Yes	Yes
<i>R. laccata</i> ¹	CRN 157 (MONT)	10 Aug 2018	Highline Trailhead, Beartooth Plateau, MT, U.S.A.	Alpine <i>Salix reticulata</i>	Yes	NA
<i>R. laccata</i> ¹	CRN 166 (MONT)	19 Aug 2018	Loveland Pass, CO, U.S.A.	Alpine <i>Salix planifolia</i>	Yes	NA
<i>R. laccata</i> ¹	CRN 175 (MONT)	21 Aug 2018	Niwot Ridge, CO, U.S.A.	Alpine, <i>Salix planifolia</i>	Yes	NA
<i>R. laccata</i> ^{1,2}	CLC 1378 (MONT)	19 Aug 1999	Birch Site, Beartooth Plateau, MT, U.S.A.	Alpine <i>Salix</i>	Yes	Yes
<i>R. laccata</i> ^{1,2}	CLC 1487 (MONT)	9 Aug 2000	Loveland Pass, CO, U.S.A.	Alpine	Yes	NA
<i>R. laccata</i> ^{1,2}	21511 (DBG)	21 Aug 2003	Loveland Pass, CO, U.S.A.	Alpine <i>Salix</i>	Yes	Yes
<i>R. laccata</i> ^{1,2}	21608 (DBG)	21 Aug 2003	Loveland Pass Lake, CO, U.S.A.	Alpine <i>Salix</i>	Yes	Yes
<i>R. laccata</i> ^{1,2}	CRN 114 (MONT)	6 Aug 2018	Solifluction Site, Beartooth Plateau, WY, U.S.A.	Alpine <i>Salix</i>	Yes	Yes
<i>R. laccata</i> ^{1,2}	CRN 128 (MONT)	7 Aug 2018	Highline Trailhead, Beartooth Plateau, MT/WY, U.S.A.	Alpine <i>Salix reticulata</i>	Yes	Yes
<i>R. laccata</i> ^{1,2}	CRN 168 (MONT)	20 Aug 2018	Niwot Ridge, CO, U.S.A.	Alpine <i>Salix planifolia</i> , <i>S. reticulata</i>	Yes	Yes
<i>R. laccata</i> ^{1,2}	CRN 186 (MONT)	24 Aug 2018	Blue Lake, CO, U.S.A.	Alpine <i>Salix planifolia</i>	Yes	Yes
<i>R. laccata</i> ²	GC_1b_III	Jun 2005	Sweden	<i>Salix</i>	JQ724003	NA
<i>R. laccata</i> ²	TU101871	22 Aug 2008	Savukoski, Finland	<i>Salix, Betula</i>	UDB016024	NA
<i>R. laccata</i> ²	23.08.2004-6	24 Aug 2004	Abisko, Lappland, Sweden	<i>Salix, Betula</i>	UDB000915	NA

<i>R. laccata</i> ²	F-73860 (O)	24 Aug 2004	Finse, Ulvik, Hordaland, Norway	NA	Yes	NA
<i>R. laccata</i> ²	F-127987 (O)	27 Jul 1979	Sør-Varanger, Finnmark, Norway	Marsh	Yes	NA
<i>R. laevis</i> (Holotype)²	JR4016	21 Aug 1995	Lapponia Enontekiönensis, Kilpisjärvi, Finland	<i>Betula, Salix</i>	MN130091	NA
<i>R. laevis</i> ^{1,2}	CLC 1146 (MONT)	17 Aug 1997	Niwot Ridge, CO, U.S.A.	Alpine <i>Salix</i>	Yes	Yes
<i>R. laevis</i> ^{1,2}	CLC 1642 (MONT)	4 Aug 2001	Cottonwood Pass, CO, U.S.A.	Alpine <i>Salix glauca</i> , <i>S. arctica</i> , <i>Dryas</i>	Yes	Yes
<i>R. laevis</i> ^{1,2}	CLC 1690 (MONT)	9 Aug 2001	Stony Pass, CO, U.S.A.	Alpine <i>Salix reticulata</i> , <i>S. arctica</i>	Yes	Yes
<i>R. laevis</i> ^{1,2}	CLC 1740 (MONT)	13 Aug 2001	Independence Pass, CO, U.S.A.	Alpine <i>Dryas</i>	Yes	Yes
<i>R. laevis</i> ^{1,2}	CLC 1883 (MONT)	18 Aug 2002	Longyearbyn, Svalbard	Arctic <i>Salix polaris</i>	Yes	Yes
<i>R. laevis</i> ^{1,2}	CLC 2271 (MONT)	1 Aug 2006	Niwot Ridge, CO, U.S.A.	Alpine <i>Bistorta</i>	Yes	Yes
<i>R. laevis</i> ^{1,2}	CLC 2981 (MONT)	12 Aug 2013	Mt. Evans, CO, U.S.A.	<i>Salix arctica</i> , <i>Bistorta</i>	Yes	Yes
<i>R. laevis</i> ²	F-5917 (TROM)	20 Jul 1961	Nordkapp, Finnmark, Norway	<i>Dryas</i>	Yes (partial)	NA
<i>R. laevis</i> ²	27685 (DBG)	20 Aug 2013	Summit Lake, CO, U.S.A.	Alpine <i>Salix arctica</i> , <i>S. glauca</i>	Yes	Yes
<i>R. cf. maculata</i> ²	HJB 10019	NA	Europe	NA	DQ422015	NA
<i>R. mairei</i> ²	FH 12262	2 Oct 2012	Walkenried, Germany	NA	KT934013	KT933945
<i>R. montana</i> (Holotype)^{1,2}	12231 (MICH)	10 Aug 1972	Perigo, CO, U.S.A.	<i>Pseudotsuga menziesii</i> , <i>Picea</i>	Yes	NA
<i>R. montana</i> ¹	3596 (DBG)	15 Aug 1974	Perigo, CO, U.S.A.	NA	Yes	NA
<i>R. montana</i> ^{1,2}	CLC 1624 (MONT)	2 Aug 2001	Blue Lake Dam, CO, U.S.A.	<i>Betula glandulosa</i>	Yes	Yes
<i>R. montana</i> ^{1,2}	19236 (DBG)	18 Aug 1997	Copper Mtn., CO, U.S.A.	<i>Pinus contorta</i> , <i>Picea</i>	Yes	Yes
<i>R. montana</i> ^{1,2}	19170 (DBG)	15 Aug 1997	Shrine Pass, Copper Mtn., CO, U.S.A.	Burned wood, moss	Yes	NA
<i>R. montana</i> ^{1,2}	19556 (DBG)	4 Aug 1998	Squaw Pass, CO, U.S.A.	<i>Picea</i> , <i>Abies</i>	Yes	NA
<i>R. montana</i> ^{1,2}	9654 (MICH)	13 Aug 1972	Jefferson Lake, CO, U.S.A.	<i>Picea</i> , <i>Abies</i>	Yes	NA
<i>R. montana</i> ²	JV 9788	24 Sept 1994	Hammaudda, Jomala, Åland, Finland	<i>Picea</i> , <i>Pinus</i> , <i>Betula</i>	Yes	NA
<i>R. montana</i> ²	NL GM15A-018	NA	NA	NA	KX579801	NA
<i>R. montana</i> ²	UBC F30293	8 Nov 2014	Canada	NA	KX812853	NA
<i>R. nana</i> ²	01930708 (NY)	27 Aug 1984	Switzerland	<i>Salix retusa</i>	Yes	NA
<i>R. nana</i> ¹	CLC 1101 (MONT)	28 Jul 1997	Birch Site, Beartooth Plateau, MT, U.S.A.	Alpine <i>Salix</i>	Yes (partial)	Yes
<i>R. nana</i> ¹	CLC 1156 (MONT)	16 Aug 1997	Niwot Ridge, CO, U.S.A.	Alpine <i>Salix</i>	Yes	Yes
<i>R. nana</i> ¹	CLC 1426 (MONT)	31 Jul 2000	Engineer Pass, CO, U.S.A.	Alpine <i>Salix planifolia</i>	Yes (partial)	Yes

<i>R. nana</i> ¹	CLC 1467.2 (MONT)	6 Aug 2000	Independence Pass, CO, U.S.A.	Alpine	Yes	Yes (partial)
<i>R. nana</i> ¹	CRN 135 (MONT)	7 Aug 2018	Billings Fen Site, Beartooth Plateau, MT, U.S.A.	Alpine <i>Salix planifolia</i>	Yes	Yes
<i>R. nana</i> ¹	CRN 154 (MONT)	10 Aug 2018	Highline Trailhead, Beartooth Plateau, MT, U.S.A.	Alpine <i>Salix planifolia</i> , <i>S. reticulata</i>	Yes (partial)	Yes
<i>R. nana</i> ¹	CLC 3575B (MONT)	17 Aug 2017	Frozen Lakes, Beartooth Plateau, WY, U.S.A.	<i>Salix reticulata</i>	Yes	NA
<i>R. nana</i> ¹	CLC 1544 (MONT)	20 Aug 2000	Sismiut, Greenland	Arctic <i>Salix herbacea</i>	Yes	Yes (partial)
<i>R. nana</i> ¹	CLC 1875 (MONT)	31 Jul 2002	California Gulch, CO, U.S.A.	Alpine <i>Salix arctica</i>	Yes	Yes (partial)
<i>R. nana</i> ^{1,2}	CLC 1440 (MONT)	1 Aug 2000	Cinnamon Pass, CO, U.S.A.	Alpine <i>Salix planifolia</i> , <i>S. reticulata</i>	Yes	Yes
<i>R. nana</i> ^{1,2}	CLC 1450 (MONT)	3 Aug 2000	Black Bear Basin, CO, U.S.A.	Alpine	Yes	Yes
<i>R. nana</i> ^{1,2}	CLC 1812 (MONT)	27 Jul 2002	Cinnamon Pass, CO, U.S.A.	Alpine <i>Salix arctica</i>	Yes	Yes
<i>R. nana</i> ^{1,2}	CLC 2330 (MONT)	14 Aug 2007	Hellroaring Plateau, MT, U.S.A.	Alpine <i>Salix</i>	Yes	Yes
<i>R. nana</i> ^{1,2}	CLC 3619 (MONT)	23 Aug 2017	Frozen Lakes, Beartooth Plateau, MT, U.S.A.	Alpine <i>Salix reticulata</i>	Yes	Yes
<i>R. nana</i> ^{1,2}	21359 (DBG)	6 Aug 2003	Independence Pass, CO, U.S.A.	Alpine <i>Salix</i>	Yes	Yes
<i>R. nana</i> ²	01943297 (NY)	12 Sept 1978	Scotland	<i>Salix herbacea</i>	Yes	Yes (partial)
<i>R. nana</i> ²	F-127873 (O)	7 Jul 1980	Finse, Ulvik, Hordaland, Norway	<i>Salix herbacea</i>	Yes	NA
<i>R. nana</i> ²	EC 17.08.2011	17 Aug 2011	Belluno, Italy	Alpine <i>Salix reticulata</i> , <i>S. retusa</i>	Yes	NA
<i>R. nana</i> ²	CRN 177 (MONT)	23 Aug 2018	Niwot Ridge, CO, U.S.A.	Alpine <i>Salix</i>	Yes	Yes
<i>R. nana</i> ²	TU 101701	NA	NA	NA	KX579809	NA
<i>R. nana</i> ²	TU 101878	18 Sept 2006	Pori, Finland	<i>Betula</i>	UDB016029	NA
<i>R. nauseosa</i> ²	FH 12173	1 Aug 2012	Erfurt, Aspenbusch, Germany	NA	KT933985	KT933917
<i>R. nigricans</i> ²	UE20.09.2004-7	NA	NA	NA	DQ422010	NA
<i>R. nitida</i> ²	2-1148IS79	NA	NA	NA	AY061696	NA
<i>R. nitida</i> ²	UPS:UE08.07.2004-2	NA	Sweden	NA	KU205269	NA
<i>R. nitida</i> ²	FH 12218	18 Aug 2012	Hildesheim, Germany	NA	KT934001	KT933933
<i>R. norvegica</i> ²	10183	5 Aug 2000	Italy	NA	JF908687	NA
<i>R. norvegica</i> ²	12163	23 Aug 2000	Italy	NA	JF908690	NA
<i>R. nuoljae</i> ²	UPS:UE24.08.2004-09	23 Aug 2000	Lappland, Sweden	<i>Betula</i>	KU205270	NA

<i>R. nuoljae</i> ²	UPS:UE23.08.2004-10	23 Aug 2000	Lapland, Sweden	<i>Betula, Salix</i>	UDB002430	NA
<i>R. nuoljae</i> ²	UPS:UE25.08.2004-06	24 Aug 2000	Lapland, Sweden	<i>Betula, Salix, Picea</i>	UDB002540	NA
<i>R. cf. ochrophylla</i> ²	BPL 231	31 Jul 2012	Great Smoky Mountains National Park, TN, U.S.A.	<i>Quercus, Tsuga</i>	KT933953	KT933883
<i>R. pallescens</i> ²	146/2002 (TUR)	NA	Norway	<i>Picea, Pinus sylvestris</i>	DQ421987	DQ421941
<i>R. pallidospora</i> ²	rw1901	14 Sept 1996	Bombergstraat, Turnhout, Belgium	<i>Quercus robur</i>	UDB002459	NA
<i>R. paludosa</i> ²	FH 12216	18 Aug 2012	Hildesheim, Germany	NA	KT934000	KT933932
<i>R. aff. pascua</i> ¹	CLC 1220 (MONT)	8 Aug 1998	Highline Trailhead, Beartooth Plateau, MT, U.S.A.	Alpine	Yes	Yes
<i>R. aff. pascua</i> ^{1,2}	CLC 2274 (MONT)	1 Aug 2006	Niwot Ridge, CO, U.S.A.	Alpine	Yes	Yes
<i>R. aff. pascua</i> ^{1,2}	CRN 138 (MONT)	8 Aug 2018	Frozen Lakes, Beartooth Plateau, MT, U.S.A.	Alpine <i>Salix reticulata</i>	Yes	Yes
<i>R. aff. pascua</i> ^{1,2}	CRN 146 (MONT)	8 Aug 2018	Billings Fen Site, Beartooth Plateau, MT, U.S.A.	Alpine <i>Salix reticulata</i>	Yes	Yes
<i>R. pascua</i> ²	JV 32526F	14 Aug 2018	Sweden	<i>Salix</i>	Yes	NA
<i>R. pascua</i> ²	IB:2005/1153	NA	Tirol, Austria	<i>Salix, Polygonum</i>	KU205312	NA
<i>R. pascua</i> ²	IB:2004/0149	NA	Dolomites, Italy	<i>Salix, Dryas</i>	KU205315	NA
<i>R. pascua</i> ²	KRAM:F-45052	NA	S. Carpathians, Romania	<i>Dryas, Salix, Polygonum</i>	KU205327	NA
<i>R. peckii</i> ²	BPL 270	8 Aug 2012	Great Smoky Mountains National Park, TN, U.S.A.	<i>Tsuga caroliniana, Abies, Picea, Betula</i>	KT933970	KT933901
<i>R. pubescens</i> ^{1,2}	JV 31657F (MONT)	24 Aug 2016	Finland	<i>Picea, Betula, Pinus sylvestris</i>	Yes	NA
<i>R. pulchra</i> ²	BPL 226	30 Jul 2012	Great Smoky Mountains National Park, TN, U.S.A.	<i>Quercus, Tsuga</i>	KT933951	KT933880
<i>R. purpureofusca</i> ^{1,2}	CLC 3820 (MONT)	22 Aug 2018	Crow Pass Rd. Girdwood, AK, U.S.A.	<i>Salix, Dryas</i>	Yes	Yes (partial)
<i>R. purpureofusca</i> ^{1,2}	CRN 164 (MONT)	19 Aug 2018	Loveland Pass, CO, U.S.A.	Alpine <i>Salix planifolia</i>	Yes	Yes
<i>R. purpureofusca</i> ^{1,2}	CRN 165 (MONT)	19 Aug 2018	Loveland Pass, CO, U.S.A.	Alpine <i>Salix planifolia</i>	Yes	Yes
<i>R. purpureofusca</i> ²	JV 32876F	22 Aug 2019	Sweden	<i>Dryas, Salix</i>	Yes	NA
<i>R. purpureofusca</i> ²	H6042234	30 Aug 2013	Tromsø, Troms, Norway	<i>Salix herbacea</i>	UDB022579	NA
<i>R. purpureofusca</i> ²	F-60573 (O)	21 Aug 1998	Levanger, Nord-Trøndelag, Norway	NA	Yes	NA
<i>R. pusilla</i> ²	BPL 267	7 Aug 2012	Great Smoky Mountains National Park, TN, U.S.A.	<i>Pinus, Tsuga, Quercus, Betula</i>	KT933968	NA
<i>R. aff. queletii</i> ^{1,2}	CLC 1616 (MONT)	3 Aug 2001	Blue Lake Dam, CO, U.S.A.	<i>Betula, Abies</i>	Yes	NA
<i>R. queletii</i> ²	FH 12237	30 Aug 2012	Elendstal, Germany	NA	KT934007	KT933939

<i>R. queletii</i> ²	CLC 1616	2 Aug 2002	Blue Lake, CO, U.S.A.	<i>Betula, Abies</i>	Yes	NA
<i>R. queletii</i> ²	hue168	1 Oct 1998	Villingen, Baden-Württemberg, Germany	<i>Picea</i>	UDB000316	NA
<i>R. renidens</i> ^{1,2}	JV 31542F (MONT)	15 Aug 2016	Sweden	Alpine <i>Salix, Betula</i>	Yes	NA
<i>R. renidens</i> ^{1,2}	CLC 2871 (MONT)	27 Aug 2012	Near Utsjoki, Finland	Boreal, <i>Betula</i>	Yes	NA
<i>R. renidens</i> ²	UWBM:WTU-F-038601	24 Sept 1983	Priest Lake, ID, U.S.A.	NA	KX813140	NA
<i>R. rubellipes</i> ²	BPL 240	1 Aug 2012	Great Smoky Mountains National Park, TN, U.S.A.	<i>Picea, Betula</i>	KT933958	KT933888
<i>R. cf. rugulosa</i> ²	BPL 237	1 Aug 2012	Great Smoky Mountains National Park, TN, U.S.A.	<i>Picea</i>	KT933955	KT933885
<i>R. saliceticola</i> ¹	CRN 125 (MONT)	7 Aug 2018	Highline Trailhead, Beartooth Plateau, MT/WY, U.S.A.	Alpine <i>Salix reticulata</i>	Yes	Yes
<i>R. saliceticola</i> ¹	CRN 134 (MONT)	7 Aug 2018	Billings Fen Site, Beartooth Plateau, MT, U.S.A.	Alpine <i>Salix</i>	Yes	NA
<i>R. saliceticola</i> ¹	CRN 140 (MONT)	8 Aug 2018	Billings Fen Site, Beartooth Plateau, MT, U.S.A.	Alpine <i>Salix planifolia</i>	Yes	NA
<i>R. saliceticola</i> ¹	CRN 144 (MONT)	8 Aug 2018	Billings Fen Site, Beartooth Plateau, MT, U.S.A.	Alpine <i>Salix planifolia</i>	Yes	NA
<i>R. saliceticola</i> ¹	CLC 3575C (MONT)	20 Aug 2017	Birch Site, Beartooth Plateau, MT, U.S.A.	<i>Salix planifolia</i>	Yes	NA
<i>R. saliceticola</i> ^{1,2}	CLC 1137 (MONT)	29 Jul 1997	Birch Site, Beartooth Plateau, MT, U.S.A.	Alpine <i>Salix</i>	Yes	Yes (partial)
<i>R. saliceticola</i> ^{1,2}	CLC 2370 (MONT)	6 Aug 2008	Wyoming Creek, Beartooth Plateau, WY, U.S.A.	Alpine	Yes	Yes
<i>R. saliceticola</i> ^{1,2}	CLC 3616 (MONT)	23 Aug 2017	Billings Fen Site, Beartooth Plateau, MT, U.S.A.	Alpine <i>Salix reticulata</i>	Yes	NA
<i>R. saliceticola</i> ^{1,2}	CRN 143 (MONT)	8 Aug 2018	Billings Fen Site, Beartooth Plateau, MT, U.S.A.	Alpine <i>Salix</i>	Yes	Yes
<i>R. saliceticola</i> ^{1,2}	CRN 155 (MONT)	10 Aug 2018	Highline Trailhead, Beartooth Plateau, MT, U.S.A.	Alpine <i>Salix planifolia</i>	Yes	Yes
<i>R. saliceticola</i> ^{1,2}	CRN 173 (MONT)	20 Aug 2018	Niwot Ridge, CO, U.S.A.	Alpine <i>Salix planifolia</i>	Yes	Yes
<i>R. saliceticola</i> ^{1,2}	CRN 184 (MONT)	24 Aug 2018	Blue Lake, CO, U.S.A.	Alpine <i>Salix planifolia</i>	Yes	Yes
<i>R. saliceticola</i> ²	01782831 (NY)	30 Aug 1984	Albula Pass, Switzerland	Alpine	Yes (partial)	NA
<i>R. saliceticola</i> ²	F-127988 (O)	4 Aug 1980	Holtålen, Sør-Trøndelag, Norway	<i>Salix herbacea</i>	Yes (partial)	NA
<i>R. saliceticola</i> ²	F-74342 (O)	27 Aug 2005	Finse, Ulvik, Hordaland, Norway	<i>Salix herbacea, S. lanata</i>	Yes	Yes
<i>R. saliceticola</i> ²	JV 32515F	13 Aug 2018	Arjeplog, Lycksele lappmark, Sweden	<i>Salix, Betula</i>	Yes	NA
<i>R. saliceticola</i> ²	IB 05 150	NA	NA	NA	NA	NA
<i>R. sanguinea</i> ²	FH 12240	30 Aug 2012	Elendstal, Germany	NA	KT934008	KT933940
<i>R. sardonias</i> ²	FH 12215	18 Aug 2012	Kolshorner Moor, Germany	NA	KT933999	KT933931

<i>R. silvestris</i> ²	NL 15.09.08.av01	NA	NA	NA	KX579800	NA
<i>R. silvestris</i> ²	NL 15.09.06.av04	NA	NA	NA	KX579798	NA
<i>R. sphagnophila</i>	256930 (MICH)	1936	St. Petersburg, Russia	NA	Yes	NA
<i>R. sphagnophila</i> (Holotype)¹	12254 (MICH)	6 Sept 1905	Bay View, Emmet, MI, U.S.A.	<i>Pseudotsuga menziesii</i> , <i>Abies</i> , <i>Picea</i>	NA	NA
<i>R. sphagnophila</i> ^{1,2}	CLC 3779 (MONT)	19 Aug 2018	Crow Pass Rd. Girdwood, AK, U.S.A.	<i>Betula nana</i> , <i>Hemlock</i> , <i>Picea</i>	Yes	NA
<i>R. subalpina</i> (Holotype)¹	01919735 (NY)	24 Aug 1976	Eagle Summit, AK, U.S.A.	Subalpine tundra, <i>Betula nana</i>	NA	NA
<i>R. subrubens</i> ¹	CLC 1218 (MONT)	8 Aug 1998	Highline Trailhead, Beartooth Plateau, MT, U.S.A.	Alpine <i>Salix</i>	Yes	Yes
<i>R. subrubens</i> ¹	CLC 1219 (MONT)	8 Aug 1998	Highline Trailhead, Beartooth Plateau, MT, U.S.A.	Alpine <i>Salix</i>	Yes	Yes
<i>R. subrubens</i> ¹	CLC 1382 (MONT)	19 Aug 1999	Birch Site, Beartooth Plateau, MT, U.S.A.	Alpine <i>Salix</i>	Yes	NA
<i>R. subrubens</i> ¹	CLC 1464 (MONT)	6 Aug 2000	Independence Pass, CO, U.S.A.	Alpine <i>Salix planifolia</i>	Yes	Yes (partial)
<i>R. subrubens</i> ¹	CLC 3597 (MONT)	22 Aug 2017	Frozen Lakes, Beartooth Plateau, MT, U.S.A.	Alpine <i>Salix planifolia</i> , <i>S. glauca</i>	Yes	Yes
<i>R. subrubens</i> ¹	CLC 3601 (MONT)	22 Aug 2017	Frozen Lakes, Beartooth Plateau, MT, U.S.A.	Alpine <i>Salix planifolia</i>	Yes	Yes
<i>R. subrubens</i> ¹	20848 (DBG)	3 Aug 2000	Independence Pass, CO, U.S.A.	<i>Salix</i>	Yes	Yes
<i>R. subrubens</i> ¹	CRN 137 (MONT)	7 Aug 2018	Billings Fen Site, Beartooth Plateau, MT, U.S.A.	Alpine <i>Salix</i>	Yes	NA
<i>R. subrubens</i> ¹	CRN 156 (MONT)	10 Aug 2018	Highline Trailhead, Beartooth Plateau, MT, U.S.A.	Alpine <i>Salix planifolia</i> , <i>S. reticulata</i>	Yes	NA
<i>R. subrubens</i> ¹	CRN 185 (MONT)	24 Aug 2018	Blue Lake, CO, U.S.A.	Alpine <i>Salix planifolia</i>	Yes	NA
<i>R. subrubens</i> ^{1,2}	CLC 1466 (MONT)	6 Aug 2000	Independence Pass, CO, U.S.A.	Alpine <i>Salix planifolia</i> , <i>S. glauca</i>	Yes	NA
<i>R. subrubens</i> ^{1,2}	CLC 1488 (MONT)	9 Aug 2000	Loveland Pass, CO, U.S.A.	Alpine	Yes	Yes
<i>R. subrubens</i> ^{1,2}	CLC 1666 (MONT)	7 Aug 2001	Mineral Basin, CO, U.S.A.	Alpine <i>Salix arctica</i>	Yes	Yes
<i>R. subrubens</i> ^{1,2}	CLC 1719 (MONT)	11 Aug 2001	Black Bear Basin, CO, U.S.A.	Alpine <i>Salix arctica</i>	Yes	Yes
<i>R. subrubens</i> ^{1,2}	CLC 1808 (MONT)	27 Jul 2002	Cinnamon Pass, CO, U.S.A.	Alpine <i>Salix arctica</i>	Yes	Yes
<i>R. subrubens</i> ^{1,2}	CLC 3550 (MONT)	17 Aug 2017	Birch Site, Beartooth Plateau, MT, U.S.A.	Alpine <i>Salix glauca</i>	Yes	Yes
<i>R. subrubens</i> ^{1,2}	CLC 3588 (MONT)	21 Aug 2017	Highline Trailhead, Beartooth Plateau, MT, U.S.A.	Alpine <i>Salix planifolia</i>	Yes	Yes

<i>R. subrubens</i> ^{1,2}	23519 (DBG)	6 Aug 2006	Independence Pass, CO, U.S.A.	Alpine <i>Salix</i>	Yes	Yes
<i>R. subrubens</i> ^{1,2}	CRN 139 (MONT)	8 Aug 2018	Billings Fen Site, Beartooth Plateau, MT, U.S.A.	Alpine <i>Salix reticulata</i>	Yes	Yes
<i>R. subrubens</i> ^{1,2}	CRN 174 (MONT)	20 Aug 2018	Niwot Ridge, CO, U.S.A.	Alpine <i>Salix planifolia</i>	Yes	Yes
<i>R. subrubens</i> ^{1,2}	CRN 187 (MONT)	24 Aug 2018	Blue Lake, CO, U.S.A.	Alpine <i>Salix planifolia</i>	Yes	Yes
<i>R. subrubens</i> ²	JV 02-624	30 Sept 1998	NW Jutland, Denmark	<i>Salix, Alnus</i>	UDB002536	NA
<i>R. subrubens</i> ²	JV 98-294	26 Aug 1994	Central Jutland, Denmark	<i>Salix</i>	UDB002537	NA
<i>R. subtilis</i> ²	BPL 275	9 Aug 2012	Great Smoky Mountains National Park, TN, U.S.A.	<i>Quercus, Pinus, Fagus, Tsuga</i>	KT933974	KT933906
<i>R. suecica</i> ^{1,2}	JR 9092 (MONT)	6 Sept 2013	Finland	Primeval forest	Yes	NA
<i>R. suecica</i> ²	MATC_N24	Jul 2007	Toolik Lake, AK, U.S.A.	<i>Betula nana</i>	GU997948	NA
<i>R. velenovskyi</i> ²	NL GM15c-061	NA	NA	NA	KX579803	NA
<i>R. cf. versicolor</i> ²	FH 12259	2 Oct 2012	Walkenried, Germany	NA	KT934012	KT933944
<i>R. vesicatoria</i> ²	PC0124666	NA	TX, U.S.A.	NA	KY800359	NA
<i>R. aff. vinosa</i> ^{1,2}	CLC 3778 (MONT)	19 Aug 2018	Crow Pass Rd. Girdwood, AK, U.S.A.	<i>Betula</i>	Yes	NA
<i>R. vinosa</i> ²	500RUS26	NA	NA	NA	AY061724	NA
<i>R. virescens</i> ²	HJB9989	NA	Belgium	NA	DQ422014	DQ421955
<i>R. xerampelina</i> ²	24138 (DBG)	4 Aug 2011	Independence Pass, CO, U.S.A.	<i>Picea</i>	Yes	Yes
<i>R. xerampelina</i> ²	20531 (DBG)	1 Sept 1999	Mt. Goliath Nature Trail, Arapaho N.F., CO, U.S.A.	<i>Picea, Abies</i>	Yes	Yes
<i>R. xerampelina</i> ²	S. Miller 9772 (2-684RUS28)	NA	Europe	NA	AY061734	NA
<i>R. zvarae</i> ²	FH 12175	1 Aug 2012	Erfurt, Aspenbusch, Germany	NA	KT933986	KT933918

DNA Extraction, PCR Amplification, DNA Purification, and Sequencing

For molecular analyses, we extracted and amplified the ITS and *RPB2* gene regions. The ITS region was chosen because it is the universal barcode for species identification in fungi (Schoch et al. 2012). The ITS region is 600–800 base pairs in length and present in multiple copies making it easy to amplify (White et al. 1990). However, because it is a multicopy gene, variation can exist between populations or individuals, which has the potential to complicate phylogenetic analyses (Smith et al.

2007). The ITS is a spacer region containing ITS1 and ITS2, which are transcribed but excised prior to translation, the highly conserved 5.8S gene sits between the two spacers (White et al. 1990; Gardes and Bruns 1993). These characteristics allow the ITS to undergo mutations freely, which makes the region variable between species, but conserved within species, making it useful for identification at the species level (Schoch et al. 2012). The *RPB2* region was chosen to complement the ITS region because it is a conserved protein coding region; in general, these regions have more species resolving power, but are more difficult to amplify using PCR (Schoch et al. 2012). The *RPB2* region encodes the second largest subunit of RNA polymerase II (Liu et al. 1999; Matheny 2005). The ITS-*RPB2* combination has also been suggested as a target DNA barcode for *Russula* because it has sufficient intra- and inter-specific variation for species identification and high rates of successful PCR amplification (Guo-Jie et al. 2019). For the broad dataset described below, the nuclear ribosomal 28S large subunit (LSU) and the gene responsible for encoding the largest subunit of RNA polymerase II (*RPB1*) were included in the analysis; this data was extracted from Looney et al. (2016). LSU is a large gene region adjacent to the ITS and *RPB1* is a slowly diverging, protein coding gene that is universally present (Tanabe et al. 2002). Both are commonly used in fungal phylogenetics (James et al. 2006).

The ITS and *RPB2* gene regions were amplified from dried basidiocarps, portions of which were placed in a clean 2ml screw cap tube. DNA was extracted following the procedure in the Sigma-Aldrich® Extract-N-Amp™ Plant PCR kit: manufacturer instructions were followed except a 1:2 (25:50 µl) ratio was used for the

extraction:dilution solution. A CTAB (Cetyltrimethylammonium bromide) extraction was used for older herbarium material or when extractions produced poor sequences using the previous method. This extraction method followed a slightly modified version of Nguyen et al. (2013) and used CTAB buffer to lyse cells followed by a chloroform extraction and ethanol precipitation. The CTAB extraction protocol with pertinent lab notes can be found in Appendix A. The ITS region was amplified using only the primers ITS1-F and ITS4 or a combination of primers ITS1-F and ITS2 and/or ITS3 and ITS4 to amplify the ITS1 and ITS2 regions separately (White et al. 1990; Gardes and Bruns 1993). When the ITS1 and ITS2 regions were amplified separately from the same collection each region was analyzed using a Standard Nucleotide BLAST® provided by NCBI (<https://blast.ncbi.nlm.nih.gov/Blast.cgi>) to check for the possible ITS contamination. If no contamination was present, the ITS1 and ITS2 regions were combined into one sequence for phylogenetic analysis and missing portions of the 5.8S region between them was filled with Ns (ambiguous nucleotides). For these collections, the alignment was carefully examined to ensure correct positioning within related sequences. When amplified separately the ITS1 and ITS2 regions will be uploaded separately to GenBank. Primer sequences are in TABLE 6. All primer sequences used were ordered from Integrated DNA technologies (<https://www.idtdna.com/pages>) and were prepared following the protocol in Appendix B.

Table 6. Primer sequences used in this study.

Primer	Sequence (5' – 3')	Reference
ITS1-F	CTTGGTCATTAGAGGAAGTAA	White et al. 1990, Gardes and Bruns 1993
ITS2	GCTGCGTTCTTCATCGATGC	White et al. 1990, Gardes and Bruns 1993
ITS3	GCATCGATGAAGAACGCAGC	White et al. 1990, Gardes and Bruns 1993
ITS4	TCCTCCGCTTATTGATATGC	White et al. 1990, Gardes and Bruns 1993
fRPB2-7cR	CCCATRGCTTGYTTRCCCAT	Liu et al. 1999
bRPB2-6f	TGGGGYATGGTNTGYCCYGC	Matheny 2005

For the polymerase chain reaction (PCR) amplification (Mullis et al. 1986; Saiki et al. 1988), the reaction mix was combined in 0.2 ml ThermoGrid™ strip PCR tubes following Barge et al. (2016): 7.5 µl of molecular grade water, 12.5 µl of Extract-N-Amp PCR ReadyMix, 1.0 µl forward primer (10 µM), 1.0 µl reverse primer (10 µM), and 3.0 µl of fungal DNA. DNA amplification of the ITS region using PCR was done in a Thermocycler running with the following settings: 94 °C for 2 minutes, followed by 30 cycles of 94 °C for 30 seconds, 55 °C for 1 minute, and 72 °C for 1 minute, followed by a final 5-minute elongation step at 72°C.

The *RPB2* region was amplified using the primers fRPB2-7cR and bRPB2-6f (Liu et al. 1999; Matheny 2005), (TABLE 6). For PCR amplification of the *RPB2* region, the following was combined in 0.2 ml ThermoGrid™ strip PCR tubes following Barge et al. (2016): 5.5 µl of molecular grade water, 12.5 µl of Extract-N-Amp PCR ReadyMix, 3.0 µl forward primer (10 µM), 3.0 µl reverse primer (10 µM), and 1.0 µl of fungal DNA. DNA amplification of the *RPB2* region using PCR was done in a Thermocycler running with the following settings: 94 °C for 90 seconds, followed by 40 cycles of 94 °C for 30 seconds, 55 °C for 90 seconds, and 68 °C for 3 minutes, followed by a final 5-minute elongation step at 68°C.

PCR products were verified using gel electrophoresis. A 1.5% gel was made using molecular grade agarose and 1XTBE buffer, 0.5 μ l of Ethidium Bromide (EtBr) or GelRed was added to bind the DNA so bands could be visualized under UV (ultraviolet) light. Next, 5–10 μ l of PCR product was added to the gel, which was run for 1 hour at 96 volts and viewed with a trans-illuminator. Once PCR products were verified, PCR purification was performed using the QIAquick Kit (Qiagen) following the manufactures instructions. Purified PCR product concentrations were quantified using the spectrophotometer NanoDrop™ 2000.

DNA for each gene was sent to Genscript® in Piscataway, New Jersey for sequencing. DNA was diluted to 2 ng/ μ l as specified by the “DNA Sequencing Sample Submission Guidelines – Genscript” and added to two 0.2 ml ThermoGrid™ strip PCR tubes, one containing 2.5 μ l (10 μ M) of the forward primer and another containing 2.5 μ l (10 μ M) of the reverse primer. Enough molecular grade water was added to each tube to bring the total volume to 15 μ l. DNA was sequenced at Genscript® using Sanger DNA sequencing. Forward and Reverse complemented sequences were loaded into SeqTrace v. 0.8.1 (Stucky 2012); SeqTrace protocol can be found in Appendix C. Chromatograms were examined and contig sequences were constructed. Nucleotide sequences were trimmed at the ends until 8 out of 10 nucleotides were supported with at least a 30% confidence score. Ambiguous nucleotide positions were replaced by N's. Positions where nucleotides were less ambiguous (could be 1 of 2 overlapping peaks) were coded as follows: W (A or T), S (C or G), M (A or C), K (G or T), R (A or G), or Y (C or T). NCBI BLAST® search was used for tentative identification of fungal isolates and to

check for similar sequences; sequences were then subjected to phylogenetic analysis. We searched for similar sequences in BLAST but did not add them to the phylogenies because of the need to examine morphology and take ecological data into account when delineating *Russula* species. Highly similar sequences in public databases were discussed under species observations when necessary.

For particular species in the phylogenetic analyses, a UNITE species hypothesis was included in the phylogenetic analysis. UNITE is an online database that connects vouchered collections to well annotated sequences for ectomycorrhizal fungi (Kõljalg et al. 2005). A species hypothesis is species-level group that shares a certain degree of sequence similarity like an operational taxonomic unit. UNITE species hypotheses are included in groups containing significant taxonomic confusion or lacking reference specimens.

Sequence Alignment and Phylogenetic Analyses

The goal of the phylogenetic analyses was to determine phylogenetic placement of the species of *Russula* found in the Rocky Mountain alpine zone based on the genetic loci studied. The ITS and *RPB2* sequences produced in this study were aligned using the online or desktop version of MUSCLE (<http://www.ebi.ac.uk/Tools/msa/muscle/>) (Madeira et al. 2019) using default parameters. For the desktop version of MUSCLE, an example of the code required to run the program can be found in Appendix D. Sequences were then inspected using PhyDE v.0.9971 (<http://www.phyde.de/index.html>) and misaligned regions were manually adjusted. Four phylogenetic trees were produced using the ITS-*RPB2* data from this study. All datasets were analyzed using both the maximum

likelihood and Bayesian analysis methods described below. The phylogeny produced using the Bayesian method was selected to represent the tree because there were no significant differences in the topologies regarding the species clades studied here. All of the maximum likelihood phylogenies can be found in Appendix E. The bootstrap support from maximum likelihood and the Bayesian posterior probability was annotated onto each branch in the Bayesian phylogeny.

A phylogeny representing a broad overview of the genus *Russula*, including eight well-recognized clades, was produced using select taxa from the multi-locus dataset (including ITS, LSU, *RPB1*, and *RPB2* gene regions) published by Looney et al. (2016) in addition to ITS and *RPB2* sequences generated in this study. The sequences of select taxa from Looney et al. (2016) were chosen to represent the relative diversity of the eight well-recognized clades within the genus *Russula*. The clade names used here follow Adamčík et al. (2019), and all represent the subgenera for which they are named. The *Russula* clade is divided into two large clades, the crown clade and core clade, which represent *Russula* subgenus *Russula*. The crown clade represents the large, highly diverse, apically resolved clade (FIGS. 2, 3). We realize that the use of crown clade here is inconsistent with the traditional use of crown clade defined as: a clade containing the most distant extant members of a group including the most recent common ancestor of that group and all its descendants (Budd and Jensen 2000). However, we use the term *Russula* crown clade to be consistent with recent literature (Looney et al. 2016; Adamčík et al. 2019; Buyck et al. 2020). The multi-locus dataset containing eight well-recognized clades within the genus *Russula* will be referred to as the broad dataset or phylogeny and

includes 61 taxa with the maximum number of characters being 4416; this alignment file along with all others will be uploaded to TreeBase.

A multi-locus phylogeny that includes the ITS and *RPB2* gene regions was also produced for the *Russula* crown clade (95 taxa and 1656 characters), *Russula* core clade (81 taxa and 1567 characters), and *Brevipes* clade (29 taxa and 1568 characters) in order to take a closer look at species relationships. Only the ITS and *RPB2* data was used for these detailed datasets due to the lack of LSU and *RPB1* sequences available for type and references collections relevant to this study. Collections included in the phylogenetic analyses are indicated in TABLE 5. Bayesian analysis was performed using MrBayes v. 3.2.2 (Ronquist et al. 2012). Throughout this project several multi-locus trees, including time trees, were also produced in Beast v.2.4.8 (Bouckaert et al. 2019); these data are not included in this thesis but the protocol for Beast can be found in Appendix F. For Bayesian, analysis all loci in each dataset were partitioned so that each locus or each codon position in a protein coding gene is allowed different rates of nucleotide evolution, which has been shown to improve tree topology (Kainer and Lanfear 2015). The broad dataset was divided into the following partitions: ITS, LSU, and the 1st, 2nd, and 3rd codon positions of *RPB1* and *RPB2*. For Bayesian analysis, the *Russula* crown clade, *Russula* core clade, and *Brevipes* clade were divided into the following partitions: ITS and the 1st, 2nd, and 3rd codon positions of *RPB2*. The *RPB1* and *RPB2* regions were partitioned into the 1st, 2nd, and 3rd codon positions in Mesquite (Maddison and Maddison 2018) with the goal being to minimize stop codons in the beginning and middle of the coding region (Bazzicalupo pers. com. 2/1/19). This was done in Mesquite by selecting characters > list

of characters > select all > codon position > set codon position > and minimizing stop codons. The Display tab was selected followed by > color matrix cell > color nucleotide by Amino Acid. In the *RPB2* alignment a large ambiguously aligned intron was removed prior to phylogenetic analysis to improve the overall alignment. The final ITS and *RPB2* data sets were concatenated manually in Notepad++. Using PartitionFinder v.2.1.1 (Lanfear et al. 2012), the best substitution model was calculated for each partition in each dataset; the selected substitution models can be found in Appendix G.

In MrBayes, the command block used the partitions set by PartitionFinder. Two independent runs of 30 million generations were sampled every 100 000 runs with the first 25% of samples discarded. The number of chains was set to four. Both independent runs reached likelihood stationarity and the convergence of runs was visually assessed using the Trace function in Tracer version 1.5 (Rambaut et al. 2014).

The maximum likelihood (ML) analyses were performed in RAxML GUI version 1.5 (Silvestro and Michalak 2012). The alignment was loaded into RAxML as a PHYLIP file and analyzed as a partitioned data set. The broad dataset was again partitioned into the ITS, LSU, and each codon position of the *RPB1* and *RPB2* region; whereas, the detailed datasets were partitioned into the ITS and each codon position of the *RBP2* region. Branch lengths were not calculated independently for each partition due to the obviously flawed topologies produced using this setting. The dataset was analyzed using the ML + rapid bootstrap option (default option) using the GTRGAMMAI model with 1000 bootstrap iterations. The BS brL option was not checked. The outgroup was

manually selected. The tree files from each analysis were viewed and edited in TreeGraph 2 (Stöver and Müller 2010) and annotated in Adobe Illustrator v 23.0.2.

Maps of *Russula* Species Distributions

Maps were created to visualize the observed, geographic distribution of each *Russula* species studied here. Maps only include collection locations that are confirmed in the phylogenetic analyses (FIGS. 3, 4). The maps were created in R Studio (<https://rstudio.com/>) using ggmap, which is part of the ggplot2 package (Wickham 2016). An example of the code used to create each map can be found in Appendix H.

Results

Phylogenetic Analysis

In total 138 ITS and 83 *RPB2* sequences were generated from 143 collections in this study (TABLE 5). An ITS1 and ITS2 sequence was generated for the *R. montana* Shaffer holotype (MICH 12231). The *R. laveis* holotype sequence (JR 4016) was included in the phylogenetic analyses (FIGS. 2, 5) (Adamčík et al. 2019). Sequences were not successfully obtained from the holotypes of *R. sphagnophila* Kauffman (MICH 12254) or *R. subalpina* O.K. Mill. (NY 01919735). Other types could not be obtained; however, sequences were generated or received for collections from the type locality or type country from reliable sources for most species. The alignments and multi-locus trees produced in this study will be uploaded to TreeBase.

The topology of all the phylogenetic trees produced using the maximum likelihood and Bayesian phylogenetic methods were consistent in regard to the following

trends. Ten species of *Russula* were resolved from the Rocky Mountains. Nine of these species were resolved as monophyletic and eight species clades were strongly-supported. All analyses indicate that alpine species of *Russula* in the Rocky Mountains are distantly related from each other, and do not share a recent common ancestor that is unique to this group. All species studied were consistently resolved in either *R.* subgenus *Russula* or *R.* subgenus *Brevipes*.

A few small differences in tree topology and support between the phylogenies produced here and other studies are worth noting. The topology leading to the clade containing *R. altaica* (Singer) Singer is weakly-supported and paraphyletic in the broad phylogeny (FIG. 2) and strongly-supported and monophyletic in the *Russula* core clade phylogeny (FIG. 4). This variation may be due to the fewer number of sequences included in this clade in the broad phylogeny compared to the *Russula* core clade phylogeny. The clade containing *R. altaica*, *R. gracillima* Jul. Schäff., and *R. queletii* Fr. forms a polytomy in the broad analyses with the remainder of the *Russula* core clade and the *Russula* crown clade (FIG. 2); whereas, in the *Russula* core clade phylogeny and in previous studies (Looney et al. 2016; Adamčík et al. 2019), this clade is strongly-supported and resolved within the *Russula* core clade. There was also some variation in the topology and weak-support for deeper nodes at the subgeneric level within the broad phylogeny (FIG. 2) compared to previous studies (Looney et al. 2016; Adamčík et al. 2019). For example, our analysis resolved the *Crassotunicata* and *Heterophyllidia* clades as the most basal clades of the genus *Russula*; whereas, Looney et al. (2016) and Adamčík et al. (2019) resolved the *Brevipes* clade as the most basal. We believe that the

broad phylogeny has varying topology and low-support for deeper nodes at the subgeneric level due to the absence of LSU and *RPB1* sequence data for the species studied here and closely related reference sequences. Other studies (Looney et al. 2016; Adamčík et al. 2019; Buyck et al. 2020) produced strong-support for nodes at the subgeneric level using four or five loci including the LSU and *RPB1* regions which are highly conserved throughout the genus *Russula*.

A phylogeny representing a broad overview of *Russula*, including eight well-recognized clades, was produced using select taxa from the multi-locus dataset published by Looney et al. (2016) in addition to ITS and *RPB2* sequences generated in this study. *Multifurca ochricompacta* (Bills & O.K. Mill.) Buyck & V. Hofst. (PC0723654) and *Lactarius deceptivus* Peck (AFTOL ID 682) were used as outgroups. The *Russula* crown and core clades in the broad phylogeny (FIG. 2) correspond to *Russula* subgenus *Russula* and the remaining six clades correspond to the subgenera for which they are named. The topology of the broad phylogeny is similar to that produced in recent taxonomic studies focused on *Russula* (Looney et al. 2016; Buyck et al. 2018; Adamčík et al. 2019). The broad phylogeny was used to determine the subgeneric placement of *Russula* species from the Rocky Mountain alpine zone. The *Russula* species found to occur in the Rocky Mountain alpine zone in this study occur in two subgenera: nine are in *R.* subgenus *Russula* and one is in *R.* subgenus *Brevipes*.

Figure 2. Bayesian phylogeny of the genus *Russula* produced using select sequences from the multi-locus dataset produced by Looney et al. (2016) in addition to ITS and *RPB2* sequences generated in this study. Support values for bootstrap support (BS) and Bayesian posterior (PP) probabilities are indicated above or below branches. Thickened branches lead to clades receiving $\geq 75\%$ bootstrap support (BS) and Bayesian posterior probabilities (PP) ≥ 0.95 . Bolded tip labels represent Rocky Mountain alpine collections. AA = Arctic-alpine habitats. Each gray box is labeled with a well-recognized clade in the genus *Russula* following Adamčík et al. (2019). Bolded tip labels represent Rocky Mountain collections. AA = Arctic-alpine habitats.

Subgenus *Russula*. The subgenus *Russula* consists of two large clades, the *Russula* crown clade and the *Russula* core clade (Looney et al. 2016; Adamčík et al. 2019; Buyck et al. 2020), which is confirmed here. A multi-locus phylogeny that included the ITS and *RPB2* gene regions was produced for each clade to take a closer look at species relationships. Five species from the Rocky Mountain alpine (*R. subrubens*, *R. cf. pascua*, *R. saliceticola*, *R. heterochroa*, and *R. purpureofusca*) are in the *Russula* crown clade as represented in Adamčík et al. (2019) and *R. fragilis* Fr. (FH 12197) was used as the outgroup (FIG. 3). The five *Russula* species in the crown clade have primarily red and magenta pilei, ocher or yellow spore prints, and isolated or subreticulate spore ornamentation. All species studied in the crown clade are represented by at least two collections observed in this study and are supported in both phylogenetic analyses (FIG. 3). *Russula* subsection *Xerampelinae* forms a clade within the *Russula* crown clade and contains species with reddish-brown pilei, fishy odors, and a greenish reaction in the context when exposed to ferrous sulfate. This group includes the well-known edible *R. xerampelina* (Schaeff.) Fr., which has been recognized because of these unique characteristics since Singer (1938) (Adamčík and Knudsen 2004).

In the *Russula* crown clade, the analysis produced a weakly-supported clade containing species originally identified as *R. saliceticola* (Singer) Kühner ex Knudsen & T. Borgen from Switzerland (NYBG 01782831), Norway (F-74342), and Sweden (JV 32515F) along with several collections from the Rocky Mountain alpine zone. The *R. saliceticola* clade also contains two sequences labeled *R. nitida* (AY061696 and FH 12218). The *R. saliceticola* clade forms a polytomy within a strongly-supported clade that also contains *R. nitida* (Pers.) Fr. and *R. sphagnophila* Kauffman. Within subsection *Xerampelinae*, a strongly-supported clade contains collections identified as *R. subrubens* (J.E. Lange) Bon from the Rocky Mountains as well as a collection from western Jutland, Denmark (C JV02-624), the epitype locality of *R. subrubens* (Adamčík et al. 2016b). Also, within *R.* subsection *Xerampelinae* is a strongly-supported clade containing three collections identified as *R. cf. pascua* from the Rocky Mountain alpine that form a polytomy with members of the closely related *R. clavipes* complex (Adamčík et al. 2016b). The *R. clavipes* complex is known to have little molecular differentiation between three closely related species; our collections in this complex were identified based on the key in Adamčík et al. (2016b), which focuses on characters in the pileipellis and ecology. The *Russula* crown clade also contains a strongly-supported clade containing collections identified as *R. purpureofusca* Kühner from the Rocky Mountain alpine zone and reference material from Norway (F-60573) and Sweden (JV 32876F), including a collection (FIPUTO23) examined by Ruotsalainen and Huhtinen (2015) who recently synonymized *R. purpureofusca* with *R. cupreola* Sarnari based on examination of type material. The *R. purpureofusca* clade is sister to a strongly-supported clade

containing *R. dryadicola* R. Fellner & Landa and *R. globispora* (J. Blum) Bon, which have been referred to as the *R. globispora* lineage (Adamčík et al. 2019). One of our collections from the Rocky Mountains and two from Svalbard identified as *R. heterochroa* form a strongly-supported clade sister to a strongly-supported clade containing several sequences of *R. cuprea* (FH 12250, UDB002420, KU886591) and one sequence of *R. gigasperma* Romagn. (KU237787).

Figure 3. Bayesian phylogeny of the *Russula* crown clade combining ITS and *RPB2* data. Support values for bootstrap support (BS) and Bayesian posterior (PP) probabilities are indicated above or below branches. Thickened branches lead to clades receiving $\geq 75\%$ bootstrap support (BS) and Bayesian posterior probabilities (PP) ≥ 0.95 . Bolded tip labels represent Rocky Mountain alpine collections. Each gray box indicates a species found in the Rocky Mountains. AA = Arctic-alpine habitats. Collections in quotation marks indicate questionable identifications.

Four species from the Rocky Mountain alpine are placed in the *Russula* core clade as represented in Adamčík et al. (2019) and *R. subtilis* Burl. (BPL 275) was used as the outgroup (FIG. 4). These species all have red or magenta pilei, white to pale cream spore prints, an acrid or mild taste, and spores with various types of ornamentation. All species studied are represented by at least two collections in the phylogeny. Our Rocky Mountain alpine collections originally identified as *R. laccata* form a strongly-supported clade with collections from Norway (F-127987, F-73860, type country of *R. norvegica* D.A. Reid = *R. laccata*), Finland (JV 23194, UDB016024), Sweden (UDB000915, JQ724003), Italy (10183, 12163), and Canada (UBC:F30302). The *R. laccata* clade is sister to a strongly-supported clade containing *R. atrorubens* Quél. and is located within a strongly-supported, larger clade containing *R. emetica* (Shaeff.) Pers., *R. silvestris* (Singer) Reumaux, *R. fragilis*, and *R. betularum* Hora. The *Russula* core clade also includes collections originally identified as *R. nana*, which form a strongly-supported clade that includes specimens from the Rocky Mountain alpine zone as well as reference sequences from Italy (EC 17.08.2011, type country), Scotland (NYBG 1943297), and Switzerland (NYBG 1930708). The *R. nana* clade forms a polytomy with numerous collections originally identified as *R. montana* or *R. grisescens* (Bon & Gaugué) Marti. Within this polytomy, our analysis includes several collections identified as *R. montana* from

Colorado, including the holotype (MICH 12231) as well as several collections identified as *R. grisescens* from Austria (UDB031192) and Finland (JV 9788, JV32642F). All of the collections identified as *R. montana* or *R. grisescens*, except for one (F-127873, identified as *R. nana* from Norway with *Salix*) were collected in subalpine habitats, usually with conifers. Last in the *Russula* core clade is a weakly-supported clade identified as *R. altaica*, which contains two of our collections from the Rocky Mountain alpine zone along with a reference sequence from Russia identified as *R. altaica* (NYBG 00333753) by Singer, who described the species. The *R. altaica* clade contains species associated with *Betula* and is sister to a strongly-supported clade containing four sequences labeled *R. gracillima*, from Germany (FH 12264), Finland (JV 32758F), Estonia (UDB011284) and one without locality data (UE23.08.2004-14). The sequence from Estonia (UDB011284) represents the UNITE species hypothesis for *R. gracillima*.

Figure 4. Bayesian posterior probability phylogeny of the *Russula* core clade combining ITS and *RPB2* data. Support values for bootstrap support (BS) and Bayesian posterior (PP) probabilities are indicated above or below branches. Thickened branches lead to clades receiving $\geq 75\%$ bootstrap support (BS) and Bayesian posterior probabilities (PP) ≥ 0.95 . Bolded tip labels represent Rocky Mountain alpine collections. Each gray box indicates a species found in the Rocky Mountains. AA = Arctic-alpine habitats. Collections in quotation marks indicate questionable identifications.

Subgenus *Brevipes*. *Russula* subgenus *Brevipes* contains species with dense flesh, a white pileus that browns in age, a white spore print, and lamellae that are somewhat decurrent. One multi-locus phylogeny of the *Brevipes* clade, which represents subgenus *Brevipes*, was produced as represented in Adamčík et al. (2019) and *R. nigricans* Fr. (UE2009200407) was used as the outgroup (FIG. 5). The *Brevipes* clade contains sequences representing the UNITE species hypothesis for *R. delica* Fr. (UDB025023) and *R. chloroides* (Krombh.) Bres. (AF418605) along with the Rocky Mountain species *R. laevis* and several sequences with questionable identifications (FIG. 5). *Russula* subgenus *Brevipes* is known to contain species that have been difficult for mycologist to sort taxonomically (Buyck and Adamčík 2013). Collections originally identified as *R. cf. delica* from the Rocky Mountain alpine zone form a strongly-supported clade along with the holotype sequences of *R. laevis* (JR4106). *Russula laevis* is newly described (Adamčík et al. 2019) from Finland with *Salix* and represents an Arctic-alpine species. The sequence representing the UNITE species hypothesis for *R. delica* forms a clade by itself sister to the clade containing *R. laevis* and two collections labeled *R. cf. brevipes*. Within the *Brevipes* clade is the *R. chloroides* complex, which is a strongly-supported clade containing the sequence representing the UNITE species hypothesis for *R. chloroides*. Two sequences from Montana that were morphologically identified as *R.*

receiving $\geq 75\%$ bootstrap support (BS) and Bayesian posterior probabilities (PP) ≥ 0.95 . Bolded tip labels represent Rocky Mountain alpine collections. AA = Arctic-alpine habitats.

Ecology of *Russula* in the Rocky Mountain alpine

This study recorded potential ectomycorrhizal hosts near most fungal collections and some broad host patterns emerged. In alpine habitats of the Rocky Mountains the most common ectomycorrhizal hosts are dwarf (*Salix reticulata* and *S. arctica*) and shrubby (*S. glauca* and *S. planifolia*) *Salix* species (Cripps and Eddington 2005; Knudsen et al. 2012; Cripps and Horak 2008). In this study, a majority of the species in the alpine zone were associated with *Salix*. These include *R. nana*, *R. laccata*, *R. purpureofusca*, *R. saliceticola*, *R. cf. pascua*, and *R. subrubens*. In the Rocky Mountain alpine zone, *R. laevis* was commonly reported with *Bistorta vivipara* and *Dryas octopetala*, occasionally it was reported with *Salix*. *Russula heterochroa* was collected with *Dryas* in Colorado and with *Salix polaris* Wahlenb. and *Dryas octopetala* in Svalbard. Nine of the ten *Russula* species found in the Rocky Mountains were conspecific with European collections from Arctic and alpine regions. These European collections were reported in association with species of *Salix* that are not found in the Rocky Mountains including dwarf (*S. polaris* and *S. herbacea* L.) and shrubby (*S. retusa* L. and *S. lanata* L.) species.

Taxonomy

All descriptions are based on collections from the Rocky Mountain alpine zone.

Russula altaica (Singer) Singer

FIGS. 6, 16D, 18D, 20D

Lilloa 22:715 1951 ('1949')

= *Russula gracilis* subsp. *altaica* Singer, Bull. trimest. Soc. mycol. Fr. 54(2):143
1938

= *Russula gracillima* f. *altaica* (Singer) Vassilkov, in Novin (Ed.), Ecologiya i
Biologiya Rastenii Vo.vtochnoevropeskot Lesotundry, Pt. 1 (Leningrad):60 1970

Macromorphology. Pileus 10–40 mm wide, convex, then dished, occasionally umbonate, mottled olive yellow, olive green, grayish magenta, darker at center to umber or lighter to pinkish, smooth, greasy; margin not striate or indistinctly striate in age, can be lighter in color. Cuticle thick, gelatinous, separable except at center. Lamellae narrowly attached, crowded, L = 100–120 (n = 3), rather thick, white, graying somewhat, occasionally forking. Lamellulae absent. Stipe 20–30 × 5–15 mm, clavate or equal, white, with or without pink blush or strong pink coloring, slightly hoary. Context watery white, slightly graying, vinaceous beneath cuticle; stipe stuffed. Odor indistinct or absent. Taste mild, possibly bitter, and not hot. Exsiccata: Pileus with solid green or grayish ruby colors or mottled ruby, grayish ruby, olive green, greenish black, ocher, ruby under pileus cuticle, darker over disk or at margin. Lamellae deep yellow, yellow orange, browning or graying in age. Stipe pale yellowish, ocher, crème, with pink tints over entire surface, and brown stains near base. Chemical reactions: Not available.

Micromorphology. Basidiospores reported as pale cream (IIa-IIb) (Knudsen et al. 2012; Sarnari 1998–2005), (7.1–)7.4–7.9–8.5(–9.6) × (5.1–)5.8–6.1–6.5(–7.1) µm, broadly ellipsoid to ellipsoid, Q = (1.1–)1.2–1.3–1.4(–1.5); ornamentation of numerous,

isolated, conical, amyloid warts (rarely as spines), <0.5 – 1 μm high, occasionally fusing, without thin lines or ridges, not reticulate; apiculus truncate and inamyloid; suprahilar plage medium, weakly amyloid. Basidia $(38.1\text{--})41.9\text{--}46.1\text{--}50(\text{--}58.4) \times (7.6\text{--})8\text{--}8.6\text{--}9.3(\text{--}10.2)$ μm , clavate, 4-spored, some possibly 2-spored; basidiola slightly clavate. Hymenial cystidia $(53.3\text{--})61.2\text{--}72.4\text{--}83.6(\text{--}91.4) \times (7.6\text{--})8.7\text{--}9.7\text{--}10.7(\text{--}12.7)$ μm , clavate-pedicellate, apically subacute, often mucronate, with swollen, 5.1 – 8.9 μm long appendage; contents granular or crystalline, orange-brown, red-brown, brown to black in sulfovanillin. Pileipellis sharply delimited from underlying context; suprapellis weakly gelatinized, ca. 38 – 76 μm thick, composed of loosely to tightly interwoven, generally erect, hyphae and pileocystidia, well-defined or gradually transitioning to subpellis; subpellis strongly gelatinized, ca. 50 – 64 μm thick, composed of horizontally oriented, hard to differentiate hyphae. Hyphal terminations clavate or cylindrical, occasionally tapering, ca. 2.5 – 4 μm wide at apex, apically obtuse, difficult to observe. Pileocystidia near the pileus margin rarely septate, cylindrical to slightly clavate, $57.3\text{--}134.5\text{--}211.72(\text{--}411.5) \times (3.8\text{--})4.7\text{--}5.5\text{--}6.2(\text{--}7.6)$ μm , apically subacute or obtuse, occasionally forking; contents gelatinous, granular, or crystalline, more granular and orangish red in Congo Red, blackening in sulfovanillin. Pileocystidia at center slightly longer, otherwise similar, $(63.5\text{--})66.3\text{--}155.3\text{--}244.3(\text{--}467.4) \times 4.7\text{--}5.7\text{--}6.7(\text{--}8.9)$ μm , rare in some areas, abundant in others, occasionally forking below apex.

Figure 6. *Russula altaica* (CLC 1618). A. with *Betula*, Blue Lake Dam, Colorado. B. same collection photographed on a gray card. Scale = 2 cm.

North American Ecology. Likely with *Betula glandulosa* at treeline in Colorado, also with *Salix* and *Dryas* species nearby. Aug.

Material Examined. USA. COLORADO. Summit County, Blue Lake Dam, with *Betula glandulosa* and *Dryas*, 2 Aug 2001, *C. Cripps CLC 1608* (MONT); loc. cit., with *Betula* and *Salix* species, 3 Aug 2001, *C. Cripps CLC 1618* (MONT). RUSSIA. Arkhangelsk, Ostrov Artura, with *Betula*, *Salix*, and *Carix*, 5 Aug 1937, *R. Singer and Vasilieva 00333753* (NYBG).

Observations. Singer described *Russula gracilis* subsp. *altaica*, from the Altai Mountains of central Asia with *Betula* and *Dryas* in 1938, and later designated it *R. altaica* (Singer) Singer (1951 '1949'). Singer's species was subsequently reported with *Salix* and *Betula* in Arctic and alpine habitats of Greenland (Knudsen and Borgen 1982; Lamoure et al. 1982; Borgen 1993) and Svalbard (Kobayasi et al. 1968; Skifte 1989). Knudsen and Borgen (1982) believed that Kühner's (1975) description of *R. amoenipes* Romagn. was synonymous with *R. altaica* (Sing.) Sing., and if true this would extend this species distribution to the Alps and Swedish Lapland; however, this conclusion has been rejected by others (Singer 1986, Sarnari 1998–2005). Kobayasi et al. (1967) reported *R. fragilis* in wet tundra in Alaska during August but notes that this species is similar to *R. altaica* (Sing.) Singer (1951). More recently, *Russula altaica* has been reported in Arctic and alpine habitats in Greenland (Borgen et al. 2006), Canada (Ohenoya and Ohenoya 2010), and the Alps (Moser and Jülich 1985–2005).

A similar species, *Russula gracillima*, was described by Schäffer in 1931 from Germany and it is well known in Europe from low elevations near *Betula*. Some consider

Russula altaica to be merely a synonym of *R. gracillima*, although significantly, Sarnari (1998–2005) and Romagnesi (1967) do not. *Russula gracillima* is associated with *Betula* (Adamčík et al. 2006) and has been reported based on morphology in Slovakia (Adamčík et al. 2006), Greenland (Borgen et al. 2006), and Iceland (Christiansen 1941, Hallgrímsson 1998). Geml et al. (2010) sequenced soil cores from Alaska and reported *R. gracillima* based on only 97% sequence similarity to data available in public databases.

Both *R. gracillima* and *R. altaica* are reported to have a variable pileus color with combinations of red, dark red, purple, olive green, and ocher, a pink-flushed stipe, a weakly acrid taste, indistinct odor, and light-colored spores with isolated warts; this matches our collections except that we reported a mild taste. Our mature specimens are notable for olive-green and purple colors, unlike other *Russula* species in the Rocky Mountain alpine, however young specimens were dark reddish purple. Moser and Jülich (1985–2005) show a much redder pileus for *R. altaica*, and a resemblance to the dark red subalpine species *R. queletii* has been noted (Knudsen and Borgen 1982). However, Greenland collections also have green, pink, and gray coloration (Knudsen and Borgen 1982). *Russula altaica* may have slightly wider spores ($7\text{--}8.5(10) \times 6\text{--}7.8(8.5) \mu\text{m}$) in the original latin description compared to *R. gracillima* ($7.2\text{--}8.5 \times 5.2\text{--}6.5 \mu\text{m}$) (Romagnesi 1967).

Our phylogenetic analysis produced a strongly-supported clade with two clusters: one with sequences labeled as *R. gracillima* (DQ422004, AY061678, and KR364094), and the second with two collections from Colorado along with a reference sequence from Russia identified as *R. altaica* by Singer himself (00333753), although in the broad

phylogeny our collection (CLC 1618) was sister to the clade containing *R. altaica* (NYBG 333753) and *R. gracillima* (DQ422004) (FIG. 2). Singer's collection was found with *Salix* and *Betula* on an Arctic Island near Russia. In the alignment our collections from the Rocky Mountain alpine have eight conserved base pairs in the ITS1 and ITS2 regions that are not shared with the *R. altaica* sequence, most of which are also different from the *R. gracillima* sequences. The average spore size of Singer's collection is 8×6.4 μm and the spore size and morphology match that of our collections from the Rockies. Given the data presented above we elect to call our collections *R. altaica* at this time. There are no sequences of *R. altaica* in Genbank or UNITE, and the type is in Russia. Our reference collection (00333753, NYBG) was collected and determined by Singer was collected in 1937 and will be the first publicly available sequence of this species. This is the first report of *R. altaica* from the Rocky Mountains. Interestingly, there is a known floristic relationship between the Altai and the Southern Rocky Mountains (Weber 2003) and we hypothesize that there may be a mycological connection as well. There is a possibility that *R. altaica* is synonyms with *R. gracillima*, but the type material of *R. gracillima* needs to be examined. For now, we elect to call our Rocky Mountain collections *R. altaica* due to the morphological similarities and phylogenetic clustering with Singer's *R. altaica* collection.

Our collections and Singer's were found near *Betula*. *Betula glandulosa* is present in the Rockies but rare on most of the sites sampled, except for a few shrubs on the Beartooth Plateau and in a few areas of Colorado such as near Blue Lake Dam where our collections were found at treeline. This is the only *Russula* we report with *Betula* from

these areas, however, our Alaskan collections of red-capped Russulas are primarily with *Betula*, and this includes *R. cf. alpigenes* (Bon) Bon, *R. purpureofusca*, *R. cf. intermedia* P. Karst., *R. sphagnophila*, and *R. vinosa* Lindblad. These should be considered when collecting in the Rocky Mountains near *Betula* (see Addendum).

Russula heterochroa Kühner

FIGS. 7, 17D, 18I, 21B

Bull. trimest. Soc. mycol. Fr. 91(3):389 1975

Macromorphology. Pileus 20–40 mm wide, convex to shallow convex with or without slight depression, mottled dark red brown, ruby, dark magenta, ocher and yellow, can be pale but disk remaining dark, viscid, smooth, not striate or indistinctly so; cap cuticle separable except at center. Lamellae narrowly attached, adnate, on av. 100–120 L (n = 3), whitish to medium yellow cream, somewhat thick, occasionally forking. Lamellulae absent. Stipe 25–40 × 10–20 mm, clavate or equal, central, white, with or without faint pink tint. Context white, pink underneath cap cuticle. Odor fruity or very faintly fishy. Taste mild not hot. Exsiccata: Pileus orange brown to dark brown, nearly uniform in color. Lamellae light yellow to darker orange yellow. Stipe white, staining yellowish near base. Chemical reactions: Not available.

Micromorphology. Basidiospores, no print obtained, but *R. heterochroa* reported as cream yellow (IIIc) (Ronikier 2008), (8.6–)9.4–10.5–11.6(–13.6) × (6.6–)7.7–8.4–9.2(–9.6) μm, broadly ellipsoid, Q = (1.0–)1.2–1.2–1.3(–1.5); ornamentation of numerous isolated amyloid warts (spines present but rare), 0.5–1 μm high, occasionally fusing, with no reticulation; apiculus truncate and inamyloid; suprahilar plage medium to large,

amyloid. Basidia (53.3–)55.6–62.1–68.5(–73.66) $\times$ (10.2–)11.3–12.1–12.9(–14) μm , clavate-pedicellate, primarily 2-spored, occasionally 1- and 4-spored; basidiola clavate.

Hymenial cystidia (58.4–)70.9–89.7–108.6(–152) $\times$ (10.2–)10.8–12.1–13.5(–15.2) μm , fusiform, occasionally clavate, pedicellate, often mucronate, with 2.5–5.1 μm long appendage; contents granular, gelatinous or absent, no reaction in sulfovanillin.

Pileipellis sharply delimited from underlying context; suprapellis ca. 50–115 μm thick, composed of smooth, tightly interwoven, erect hyphae and embedded pileocystidia, well-defined or gradually transitioning to subpellis; subpellis gelatinized, ca. 125–177 μm thick, composed of hard-to-differentiate horizontally oriented hyphae. Hyphal terminations cylindrical to clavate, thin-walled, ca. 2–4.5 μm wide at apex, apically obtuse or subacute; rarely filled with granular contents. Pileocystidia near pileus margin abundant, with 1–2 septa, clavate to cylindrical, (53.3–)53.5–101.1–148.7(–228.6) $\times$ (3.8–)3.6–5.5–7.5(–14) μm , rarely forking, occasionally diverticulate (with small lateral protrusions); contents lightly granular and gelatinous, blackening in sulfovanillin.

Pileocystidia near center rare, on average longer and thinner, (86.4–)94.7–127.8–161(–190.5) $\times$ (3.8–)3.5–5.1–6.7(–8.9) μm , similar in shape.

Figure 7. *Russula heterochroa* (CLC 1723). Scale bar = 2 cm.

North American Ecology. In alpine zone with *Dryas octopetala* in Colorado. Aug.

Material examined. SVALBARD. Todalen, Adventdalen, Nordensklods Land, with *Salix polaris* and *Dryas octopetala*, 21 Aug 2002, C. Cripps CLC 1918 (MONT); loc. cit., with *Salix polaris* and *Dryas octopetala*, C. Cripps CLC 1919 (MONT). USA. COLORADO. Gunnison/Chaffee Counties, Sawatch Range, Cottonwood Pass, with *Dryas*, 12 Aug 2001, C. Cripps CLC 1723 (MONT).

Observations. *Russula heterochroa* was originally described by Kühner (1975) as an alpine species from the French Alps and Swedish Lapland. Kühner (1975) described three new species, *R. purpureofusca*, *R. heterochroa*, and *R. saliceticola*, and placed all in section *Tenellae* Quélet. *Russula heterochroa* is recognized by a dark purple pileus, white

to cream lamellae, white stipe, large yellow cream spores with primarily isolated warts, and 2-spored basidia (Kühner 1975, Ronikier 2008). Our collections from the Rocky Mountains of Colorado and the Arctic island of Svalbard match the morphology of *R. heterochroa*. No sequences of *R. heterochroa* are currently available in public databases. This species has been previously reported from the French Alps (Kühner 1975), Swedish Lapland (Kühner 1975), and the Carpathians (Ronikier 2008). This is the first report of this species in North America and in Svalbard. Our collections of this species from Svalbard (CLC 1918 and CLC 1919) have diverticulate pileocystidia, similar to the *R. purpureofusca*; these are visible but less abundant in the collection from Colorado (CLC 1723). Similar species morphologically in the Rocky Mountain alpine include *R. laccata*, *R. saliceticola*, and *R. purpureofusca*, which all have predominately purple or magenta pilei. However, the 2-spored basidia and the larger spores (av $10.5 \times 8.4 \mu\text{m}$) are unique to *R. heterochroa*, and all three species can be separated phylogenetically using the ITS region.

Phylogenetically, *R. heterochroa* is located in the *Russula* crown clade. Our three collections (CLC 1723, CLC 1918, and CLC 1919) form a strongly-supported clade sister to *R. cuprea*, which contains one sequence from Germany and another from the United Kingdom. The sequence from Germany (FH12250) lacks host or ecological data; the sequence from the United Kingdom (UDB002420) was found near *Quercus petraea* and *Betula* species.

Russula laccata Huijsman

FIGS. 8, 16C, 18C, 20A

Fungus, Wageningen 24:40 1955

= *Russula norvegica* var. *rubromarginata* Kühner, Bull. trimest. Soc. mycol. Fr.
91(3):389 1975

= *Russula norvegica* D.A. Reid, Fungorum Rariorum Icones Colorate 6:36 1972

= *Russula atrorubens* Quél. *sensu* J.E. Lange, Fl. Agar. Dan.:63 1940 – pro parte.

Macromorphology. Pileus 15–45 mm wide, convex (shallow or broad), almost applanate, or uplifted with slight central depression, occasionally umbonate, deep magenta, dark magenta, and ruby, with a dark, almost black center, but also with a mix of deep magenta, grayish magenta, vivid red, deep red, rarely with yellow brown, typically with dark purple-black center fading to lighter magenta near margin, occasionally darker at margin and lighter over center, aging dark brown, smooth, greasy, viscid, can be shiny, tacky or dry, with occasional debris adhering; margin short or long striate, typically more striate in age, occasionally not striate or indistinctly so, undulating or entire, incurved when young; cuticle separable except at center. Lamellae attached, adnate to adnexed, relatively close to distant, on av. L = 70–110 (n = 8), white, off-white, cream, pale yellow tinge in some, rarely graying, yellow brown near cap margin, rarely deep magenta or ruby near pileus margin, anastomosing or not, occasionally forking near stipe, elastic not brittle, thick to thin; lamellae edge entire or undulate. Lamellulae absent or rare. Stipe 15–50 × 5–15 mm, equal, clavate, sometimes tapering near base, central or slightly eccentric, white, off-white, translucent pale yellowish, grayish cream, base occasionally with pink flush, or red brown or grayish staining, smooth or rarely powdery, fragile, with

indistinct vertical ridges. Context white; stipe spongy, firm or brittle, not hollow but with small to medium cavities. Odor absent, fragrant, or fruity. Taste mildly to strongly acid or burning, immediate or delayed. Exsiccata: Pileus light buff, brown, grayish ruby, deep ruby, grayish magenta, deep magenta, mottled with ocher tones or uniformly one color, usually darker to black in center. Lamellae light golden, ocher, yellow, straw yellow, browning near cap margin, rarely with hints of gray. Stipe white, off-white, yellow, ocher, staining brownish gray, occasionally with magenta or pinkish blush. Chemical reactions: Gum Guaiac = blue green, red brown, brown; ferrous sulfate = pinkish gray, pinkish brown; 2% phenol = pale yellow.

Micromorphology. Basidiospores white in print (Ia-Ib), (6.3–)7.4–8.1–8.9(–11.6) $\times$ (5.1–)5.7–6.2–6.8(–9.6) μm , broadly ellipsoid to ellipsoid, $Q = (1\text{--})1.2\text{--}1.3\text{--}1.4(1.7)$; ornamentation of amyloid ridges forming a complete reticulum connecting raised warts and spines $<0.5 - 1 \mu\text{m}$ high, occasionally with fine line connections, rarely composed of isolated warts or spines that can fuse to form angular elongated structures; ornamentation of abnormally large spores subreticulate with more isolated elements; apiculus truncate or pointed, inamyloid; suprahilar plage small to large, amyloid, occasionally difficult to observe. Basidia (30.5–)38.2–44.9–51.6(–71.1) $\times$ (6–)7.5–8.7–10(–11) μm , clavate-pedicellate, occasionally fusiform, 4-spored, some possibly 2-spored; basidiola clavate. Hymenial cystidia (40.6–)50.7–67.7–84.6(–114.4) $\times$ (6–)7.5–9.3–11.1(–16) μm , fusiform, typically pedicellate, often mucronate, with cylindrical or swollen, occasionally septate, 2.5–5 μm long appendage (rarely up to 10.2 μm); contents granular or gelatinous, immediately blackening in sulfovanillin. Pileipellis gradually transitioning to underlying

context; suprapellis ca. 96–140 μm deep, composed of densely interwoven, erect hyphae, gradually transitioning to subpellis; subpellis gelatinized, ca. 101–152 μm deep, composed of parallel, vertical or horizontally oriented, septate hyphae. Hyphal terminations clavate, thin-walled; ca. 1.5–3.5 μm wide at apex, apically obtuse, and devoid of contents. Pileocystidia near pileus margin abundant, septate, filiform, clavate or cylindrical, pedicellate, (30.6–)43.8–79.6–115.4(–218.4) $\times$ (3–)4.7–6–7.2(–9.6) μm , swollen clavate or acute at apex, occasionally forking near base, occasionally swollen between septa; contents granular and refractive gelatinous, slightly blackening in sulfovanillin. Pileocystidia near the pileus center shorter, similar in shape, contents similar but also crystalline, rarely forking, (30.5–)40–49.8–59.6(–63.5) $\times$ (3.8–)4.4–5.1–5.9(–7.6) μm .

Figure 8. *Russula laccata*. A. with *Salix reticulata*, Beartooth Plateau, Montana (CRN 150). B. with *Salix planifolia* and *S. reticulata*, Niwot Ridge, Colorado (CRN 169). C. with *Salix* species, Beartooth Plateau, Montana (CRN 114). D. with *S. reticulata*, Beartooth Plateau, Montana (CRN 157). E. with *S. reticulata*, Beartooth Plateau (CRN 128). F. with *S. planifolia* from Blue Lake, Colorado. Scale bar = 2 cm.

North American Ecology. In alpine areas of Montana, Wyoming, and Colorado with *Salix planifolia* and *S. reticulata*, often among mosses. Habit: solitary, scattered, or gregarious. Aug.

Material examined. FINLAND. Koillismaa, Kuosamo, Oulanka National Park, with *Salix*, 27 Aug 2017, *J. Vauras JV 23194*. USA. COLORADO. Boulder County, Niwot Ridge, 1 Aug 2005, *C. Cripps CLC 2275* (MONT); loc. cit., with *Salix planifolia* and *S. reticulata*, 20 Aug 2018, *C. Noffsinger CRN 168* (MONT); loc. cit., with *S. planifolia*, 21 Aug 2018, *C. Noffsinger CRN 175* (MONT); Blue Lake, with *S. planifolia*, 24 Aug 2018, *C. Noffsinger CRN 186* (MONT); Clear Creek/Summit Counties, Front Range, Loveland Pass, 9 Aug 2000, *C. Cripps CLC 1487* (MONT); loc. cit., with dwarf *Salix*, 21 Aug 2003, *V. Evenson DBG-F-021608* (DBG); loc. cit., with *Salix*, *R. Brace DBG-F-021511* (DBG); loc. cit., with *S. planifolia*, 19 Aug 2018, *C. Noffsinger CRN 166* (MONT); Pitkin/Lake Counties, Sawatch Range, Independence Pass, 6 Aug 2000, *C. Cripps CLC 1465* (MONT); loc. cit., 6 Aug 2000, *C. Cripps CLC 1467.1* (MONT). MONTANA. Carbon County, Beartooth Plateau, Birch Site, with shrubby *Salix*, 9 Aug 1999, *C. Cripps CLC 1378* (MONT); loc. cit., with *S. planifolia*, 19 Aug 1999, *C. Cripps CLC 1381* (MONT); Highline Trailhead, with *S. reticulata*, 7 Aug 2018, *C. Noffsinger CRN 128* (MONT); loc. cit., with *S. reticulata*, 10 Aug 2018, *C. Noffsinger CRN 157* (MONT). WYOMING. Park County, Beartooth Plateau, Solufluction Terraces, with *Salix* species, 6 Aug 2018, *C. Noffsinger CRN 114* (MONT); Wyoming Creek, 6 Aug 2008, *C. Cripps CLC 2371* (MONT); Billings Fen site, with dwarf *Salix*, 23 Aug 2017, *C. Cripps CLC 3617* (MONT); loc. cit., with *Salix* species, 7 Aug 2018, *C. Noffsinger CRN 133* (MONT).

Observations. *Russula laccata* was originally described from the Netherlands, often in association with *Salix* and *Betula* in swampy habitats with *Sphagnum* (Huijsman

1955). It was thought to be closely related to *R. olivaceoviolascens* Gillet in section *Violaceae* Rom. (Huijsman 1955), or merely a color variant of this species (Romagnesi 1967). Later, *R. norvegica* Reid (and *R. norvegica* var. *norvegica*) was described from alpine habitats in Norway with *Salix herbacea* (Reid 1972), and this name was commonly applied to Arctic and alpine collections fitting this description. Ortega and Esteve-Raventós (2001) examined the type material of *R. laccata* and *R. norvegica* and synonymized the two species giving *R. laccata* priority.

The species is recognized by a dark magenta pileus with black center, white lamellae, white stipe, white reticulate spores, mild to strong acrid taste, and association with *Salix*. In the Rocky Mountain alpine, it can be confused with *R. saliceticola* which has more red coloration in the pileus, lacks a hot taste, has larger yellow spores with mostly isolated warts, and more pink on the stipe; and *R. purpureofusca* which has larger ochre spores with mostly isolated warts and a somewhat hot taste. *Russula nana* and *R. montana* also have whitish spores and a hot taste but are known for bright red pilei without the dark center. In rare cases, *R. laccata* specimens can be pale in the center and thus, can be confused with *R. nana*.

Our North American alpine collections of *R. laccata* fit the morphology of this species and form a strongly-supported phylogenetic clade with collections from Norway (type country of *R. norvegica*), Finland, Canada, and Sweden. Phylogenetically, *R. laccata* is located in the *Russula* core clade and is a sister group of *R. atrorubens*. Molecularly, *R. laccata*, *R. saliceticola*, *R. purpureofusca*, *R. nana*, and *R. montana* can all be separated using the ITS region alone in a phylogenetic analysis.

In the literature, *R. laccata* is well known from Arctic and alpine habitats in Greenland, Iceland, Fennoscandia, the European alps (Watling 1977; 1983; Knudsen and Borgen 1982; Lamoure et al. 1982; Gulden et al. 1985; Graf 1994; Bon and Noguera 1995; Hallgrimsson 1998; Gulden 2005; Borgen et al. 2006), Scotland (Watling 1987), the Netherlands (Huijsman 1955), East Frisian Islands of Germany (Bresinsky 1987), the Pyrenees (Bon and Ballarà 1995), Slovakia (Fellner and Landa 1993b), Japan (Nara et al. 2003), Russia (Knudsen and Muhkin 1998) and Svalbard (Skifte 1989), but these reports have not been molecularly confirmed. *Russula laccata* was also reported in montane habitats with *Salix atrocinerea* Brot. in Spain (Ortega and Esteve-Raventós 2001). It was first reported in North America from Schefferville, Northern Québec (Hutchison et al. 1988) and later reported from the Rocky Mountain alpine zone (Cripps and Horak 2008). This is the first molecularly confirmed report of *R. laccata* in the Rocky Mountain alpine and based on our phylogenetic analysis, this species has an intercontinental distribution in Arctic and alpine habitats including North America and Europe.

There is some debate regarding taxa closely related to *R. laccata* and their synonymy. Kühner (1975) described a variety from alpine habitats, *R. laccata* var. *rubromarginata*, with dwarf willows. Sarnari (1998–2005) recognized *R. fragilis* var. *alpestris* Boudier, *R. norvegica* Reid, and *R. norvegica* var. *rubromarginata* Kühner as synonyms of *R. laccata*. However, some sources synonymize *R. fragilis* var. *alpestris* Boudier with *R. emetica* (Schaeff.) Pers. and Ortega and Esteve-Raventós (2001) only recognized *R. norvegica* D.A. Reid and *R. atrorubens* sensu Lange as synonyms of *R.*

laccata. The collections of *R. atrorubens* included in our phylogeny represent *R. atrorubens* Quél, a valid species that is sister to *R. laccata*.

Russula laevis Kälviäinen, Ruotsalainen & Taipale

FIGS. 9, 16E, 18H, 21A

Fungal Diversity: vol 99:413–414. 2019

Names misapplied:

Russula delicata Fr., Epicr. syst. mycol. (Upsaliae):350 1838 [1836–1838]

Macromorphology. Pileus 40–80 mm wide, concave, shallow convex, depressed in center, infundibuliform, pure white, dingy white, cream, mottled with brownish or orange brown stains in age or when bruised, smooth, greasy, kidskin, or finely tomentose (use hand lens), often with debris adhering to surface; margin strongly incurved or rolled under at first, then turned down, undulating, entire; cuticle can overhang gills. Lamellae attached, adnexed to narrowly-adnate, subdecurrent, occasionally toothed, close, on av. 60–160 (n = 4), sometimes forking, flaking when handled, white to very pale yellowish white, occasionally with slight yellow green, greenish, or greyish cast; edges concolorous. Lamellulae present or absent. Stipe 10–30 × 10–20 mm, equal, short, squared off at base, white, staining ocher, matt, minutely pubescent at apex (use hand lens) and smoother below, can be slightly bumpy. Context white, firm, solid, compact, slightly ocher under cuticle. Odor fruity or sweet, unpleasant in older specimens. Taste hot, acrid, occasionally slowly acrid. Exsiccata: Pileus mottled mostly with brown and orange brown tones, with a few white, buff, ocher, or gray areas. Lamellae ocher, deep orange brown, yellow brown, and light brown. Stipe off white or buff near apex, brown

or dark brown towards base, or mottled white, buff, and brown. Chemical Reactions: Not available.

Micromorphology. No print obtained, but reported as crème (IIb-d) (Adamčík et al. 2019). Basidiospores $(7.1-7.9-8.7-9.4(-13.3) \times (6.1-6.6-7.2-7.8(-10.2) \mu\text{m}$, subglobose or broadly ellipsoid, $Q = (1.1-1.1-1.2-1.3(-1.4)$; ornamentation composed of numerous or sparse, isolated to subreticulate, amyloid warts and spines, $0.5-1 \mu\text{m}$ high, rarely up to $1.5 \mu\text{m}$, occasionally fusing into large angular masses, occasionally connected by lines or ridges; apiculus truncate, occasionally obtuse, inamyloid; suprahilar plage small to large, weakly amyloid. Basidia $(58.4-61.4-68.7-75.9(-88.9) \times (8.9-9.5-10.5-11.4(-12.7) \mu\text{m}$, fusiform, clavate, constricted in middle, pedicellate, 4-spored, rarely 2-spored; basidiola clavate. Hymenial cystidia $(58.4-70-82.9-95.8(-106.7) \times (5.1-6-7.1-8.1(-8.9) \mu\text{m}$, cylindrical, fusiform, pedicellate, subacute at apex, or swollen, rarely mucronate with swollen or cylindrical $2.5-7.6 \mu\text{m}$ appendage, occasionally forking; contents granular or crystalline, graying in sulfovanillin. Pileipellis sharply delimited from underlying context, not stratified, gelatinized, ca. $88-140 \mu\text{m}$ deep, composed of horizontally oriented hyphae, becoming denser near context. Hyphal terminations cylindrical or clavate, flexuous, thin-walled, occasionally swollen, ca. $3-7 \mu\text{m}$ wide at apex, forking or not, apically obtuse or subacute, devoid of contents. Pileocystida near the pileus margin clavate, fusiform, cylindrical, occasionally forking, with one septa or not, occasionally constricted at septa, $(20.3-21.5-66.7-88.2(-190.5) \times (2.5-3-5-8(-10.2) \mu\text{m}$, apically acute, with one or two ca. $2.5 \mu\text{m}$ long appendages; contents lightly granular, with no reaction in sulfovanillin. Pileocystidia near pileus

center more cylindrical, less granular, rarely forking, occasionally tapering, (30.5–)35.1–67–98.9(–139.7) × (3.7–)3.8–4.3–4.9(–5.1) μm.

Figure 9. *Russula laevis*. A. with *Dryas octopetala*, Cottonwood Pass, Colorado (CLC 1642). B. with *Salix reticulata*, Stony Pass, Colorado (CLC 1690). C. with *D. octopetala*, Cottonwood Pass, Colorado (CLC 1642). D. with *S. arctica* and *S. glauca*, Summit Lake, Mount Evans, Colorado (DBG-F-027685), photo Denver Botanical Garden. Scale bar = 2 cm.

North American Ecology. In alpine areas, often slightly buried in *Salix* or *Dryas octopetala* debris. Aug.

Material examined. SVALBARD. Longyearbyen, with *Salix polaris*, 18 Aug 2002, C. Cripps CLC 1883 (MONT). COLORADO. Boulder County, Niwot Ridge, with dwarf *Salix*, 17 Aug 1997, C. Cripps CLC 1146 (MONT); loc. cit., with *Bistorta vivipara*, 1 Aug 2006, C. Cripps CLC 2271 (MONT); San Juan County, San Juan

Mountains, Stony Pass, with *S. reticulata* and *S. arctica*, 9 Aug 2001, *C. Cripps CLC 1690* (MONT); Pitkin County, Sawatch Range, Independence Pass, with *Dryas octopetala*, 13 Aug 2001, *C. Cripps CLC 1740* (MONT); Chaffee/Gunnison Counties, Sawatch Range, Cottonwood Pass, with *D. octopetala* and *S. glauca*, 4 Aug 2001, *C. Cripps CLC 1642* (MONT); Clear Creek County, Mount Evans, Summit Lake, with *S. arctica* and *B. vivipara*, 12 Aug 2013, *C. Cripps CLC 2981* (MONT); loc. cit., with *S. arctica* and *S. glauca*, 8 Aug 2013, *L. Gillman DBG-F-027685* (DBG).

Similar taxa examined. USA. ALASKA. White Mountains, Eagle Summit, with *Dryas*, 5 Aug 2011, *R. brevipes*, *C. Cripps CLC 2730* (MONT).

Observations. *Russula laevis* was first described by Kälviäinen, Ruotsalainen, and Taipale from a boreal area in Finland with *Betula pubescens*, *B. czerepanovii*, *B. nana*, and various *Salix* species on calcareous soils. Based on a phylogenetic analysis, including sequences from GenBank, *R. laevis* was determined to be a common inhabitant of Arctic and alpine regions in Finland, Norway, Sweden, Europe, Canada, and China (Adamčík et al. 2019).

Russula laevis is in subgenus *Brevipes* along with other whitish, hard-fleshed, concave, and acrid species. These include *R. chloroides* (Krombh.) Bres., *R. brevipes* Peck, and *R. delica* Fr. Previously, reports of Russulas in subgenus *Brevipes* from Arctic and alpine areas with *Salix* and *Dryas* were referred to as *R. delica*, but this species was originally described from temperate habitats with other hosts. Morphological reports of *R. “delica”* from Arctic and alpine habitats include those from Europe (Schmid-Heckel 1985, 1988; Vila et al. 1997; Ballarà 1997; Corriol 2008), Fennoscandia (Gulden 2005;

Lange and Skifte 1967), Greenland (Lange 1957; Kobayasi et al 1971; Peterson 1977; Knudsen and Borgen 1982; Lamoure et al. 1982; Borgen 1993; Borgen et al. 2006), Iceland (Hallgrímsson 1998), the Rocky Mountains (Cripps and Horak 2008), Alaska (Kobayasi et al. 1967), the Canadian Arctic (Ohenoja and Ohenoja 2010) and Svalbard (Kobayasi et al. 1968; Skifte 1989). This work has confirmed that the report of *R. delica* from the Rocky Mountains (Cripps and Horak 2008) actually represents the species *R. laevis* and that this species is also present in Svalbard. It is possible that most other morphological reports of *R. delica* in Arctic and alpine regions actually represent *R. laevis*, but this needs to be confirmed with molecular methods. Previous work matched sequences extracted from ectomycorrhiza in Canada to *R. laevis* (Adamčík et al. 2019), but this is the first work to collect this species in North America.

The Rocky Mountain specimens fall in a strongly supported clade with the holotype of *R. laevis* (only ITS region) along with collections from Norway, Svalbard, and Sweden. This is the first report of *R. laevis* from the Rocky Mountain alpine based on molecular sequence data, although it was previously reported as *R. delica* (Cripps and Horak 2008). Morphologically our specimens fit that of *R. laevis* with a few notable exceptions. The etymology of ‘*laevis*’ refers to the smooth and shiny pileus cuticle of the species (Adamčík et al. 2019); however, pilei of our collections are typically rough, with a matte appearance, a difference that could be due to xeric conditions in the southern Rockies. In addition, our spores are 1 μm smaller ($8.7 \times 7.2 \mu\text{m}$) on average than those of *R. laevis* ($10 \times 8.5 \mu\text{m}$). These differences suggest that further investigation is warranted.

Similar to *R. laevis*, Rocky Mountain specimens were near dwarf and shrubby *Salix*, *Bistorta*, and *Dryas octopetala* in calcareous soil.

There has been considerable taxonomic confusion surrounding the subalpine species *R. chloroides*, *R. brevipes*, and *R. delica* located in *R.* subgenus *Brevipes* (Buyck and Adamčík 2013); however, issues regarding subalpine taxa are beyond the scope of this study. We followed Adamčík et al. (2019) and included a sequence representing the *R. delica* UNITE species hypothesis (UDB025023) and *R. chloroides* UNITE species hypothesis (AF418604) in our phylogenetic analysis. Our phylogenetic analysis confirms that these two species are separate from our Arctic and alpine clade represented by *R. laevis*.

Russula montana Shaffer

FIGS. 10, 16B, 18B, 20C

Beihefte zur Nova Hedwidia 51: 234 (1975)

?= *Russula grisescens* (Bon & Gaugué) Marti, Docums Mycol. 14(no. 53):57

1984

Macromorphology. Pileus (25)35–70 mm wide, pulvinate when young, becoming convex to plano-convex, with a depression in center, primarily bright red, red, light to dark reddish brown with light brown, grayish red, light yellow, yellowish pink, yellow brown areas, occasionally brownish in center and dark pink near margin, sticky; margin with faint striations, 2–5 mm long, turned down; cuticle thin, smooth, viscid, shiny, separable except at center. Lamellae attached, adnexed to narrowly adnate, sometimes rounded in front, 3–6 mm broad, close, on av. L = 100–140 (n = 4), white, tinged grayish yellow, turning dingy yellow, intervenose, rarely forking near stipe, fragile; lamellae

edge entire. Stipe 20–50 × 10–20 mm, flared slightly at apex, otherwise equal or enlarging at base, white, not staining when bruised, dry, smooth, with a few longitudinal grooves, firm, moderately shiny. Context white, occasionally with hints of gray in age, soft or firm, 3–8 mm thick at pileus center, pinkish under cuticle; stipe stuffed. Odor indistinct or absent. Taste moderately to strongly acrid. Exsiccata: Pileus cherry red, dark red, red brown, dark maroon, purple red, purple brown, yellow buff, yellow orange; lamellae light brown or grayish buff; stipe yellow orange, yellow brown, orange brown, brown, occasionally with gray tones. Chemical reactions: Gum guaiac = slowly to quickly moderate green; ferrous sulfate = grayish yellow pink; 2% phenol = grayish red brown.

Micromorphology. Basidiospores white with a yellow tinge, but not as dark as Romagnesi Ib (Shaffer 1975), $(7.1-7.4-8.0-8.6(-9.6) \times (5-5.7-6.3-6.8(-7.1) \mu\text{m}$, broadly ellipsoid to ellipsoid, $Q = (1.1-1.2-1.3-1.4(-1.5)$; ornamentation of numerous, dense or sparse, amyloid, cylindrical or obtuse warts, $<0.5 \mu\text{m}$ high, connected by lines and ridges forming a complete reticulum, with warts merging or rarely isolated; apiculus truncate, inamyloid; suprahilar plage small, weakly to moderately amyloid.

Basidia $(43.2-46.8-53.2-59.5(-63.5) \times (7.6-8.4-9.7-11(-12.7) \mu\text{m}$, subclavate to clavate, usually 4-spored, but 1- and 2-spored possible; basidiola clavate. Hymenial cystidia moderately abundant, $(40.8-51.7-68.8-86(-106.7) \times (5.1-8-9.6-11.3(-15.2) \mu\text{m}$, clavate-pedicellate, fusiform, or almost cylindrical, occasionally subacute at apex, mucronate, with occasionally inflated $2.5-5.1 \mu\text{m}$ appendage; contents granular or crystalline, orange-brown in sulfovanillin. Pileipellis sharply delimited from underlying

context; suprapellis ca. 79–190 μm thick, composed of loosely interwoven hyphae, with occasionally swollen tips, and pileocystidia, well-defined from subpellis; subpellis weakly gelatinized, ca. 73–115 μm thick, composed of tightly interwoven, horizontally oriented hyphae, becoming more dense and darker in color near context. Hyphal terminations cylindrical, occasionally slightly clavate, thin-walled, ca. 1.5–4 μm wide at apex, apically obtuse, lightly granular. Pileocystidia near pileus margin numerous, clavate, occasionally cylindrical, rarely tapering, thin-walled, (45.9–)58.5–91.6–124.6(–180) $\times$ (4–)4.8–5.9–6.9(–8) μm ; contents granular or crystalline, dark gray to black in sulfovanillin. Pileocystidia near pileus center similar in shape and size, (55.9–)64.9–96.5–128.2(–160) $\times$ (5.1–)5.2–6.3–7.4(–8.9) μm , occasionally forking; contents gelatinous or granular.

Figure 10. *Russula montana* (DBG-F-003596), photo Denver Botanical Garden.

North American Ecology. On buried wood or moss in humus under *Psudotsuga menziesii*, *Picea*, *Abies*, and *Pinus contorta*. Aug.

Material examined. FINLAND. Kainuu, Paltamo, Tololanmäki, with *Betula*, *Alnus*, *Picea*, and *Populus*, 30 Aug 2018, *J. Vauras JV 32642F*. USA. COLORADO. Clear Creek County, Arapaho National Forest, Squaw Pass, with spruce and fir, 4 Aug 1998, *V. Evenson DBG-F-019556* (DBG); Gilpin County, Perigo, with *Psudotsuga menziesii* and *Picea*, 10 Aug 1972, *R. L. Shaffer 12231* HOLOTYPE (MICH); loc. cit., 15 Aug 1974, *A. H. Smith DBG-F-003596* (DBG); Park County, Jefferson Lake, with spruce-fir, 13 Aug 1972, *R. L. Shaffer 9654* (MICH) (Shaffer examined this collection when he described the species); Summit County, Blue Lake Dam, with *Betula glandulosa*, 2 Aug 2001, *C. Cripps CLC 1624* (MONT); Sawatch Range, Shrine Pass, in buried wood and moss, 15 Aug 1997, *H. Tuttle DBG-F-019170* (DBG); White River National Forest, Copper Mountain, with Lodgepole Pine and spruce, 14 Aug 1997, *B. Woo DBG-F-019236* (DBG).

Observations. Shaffer (1975) originally described *R. montana* as a gregarious species on duff or rotten wood below *Pseudotsuga menziesii*, *Abies*, and *Picea* from Perigo Colorado, USA. After examining Shaffer's holotype we are confident that our collections from the Rocky Mountains match that of *R. montana*, and all but one were found below treeline with conifers in the vicinity. The closely related *R. nana* is a smaller species that typically has a 12–35 mm wide pileus and is found in Arctic and alpine

habitats with *Salix*; *R. montana* typically has a larger pileus (35–70 mm wide) and occurs with conifers in the subalpine zone. There is also a significant difference in the spore length between *R. montana* and *R. nana* when analyzed using a two sample t-test (p-value = 0.002, based on 100 measurements from each species), but spore width is similar. *Russula montana* spores are on average 0.3 μm longer and have an average Q of 1.3, *R. nana* has an average Q of 1.2.

R. nana forms a strongly-supported clade in a polytomy with sequences of *R. montana* in our phylogenetic analysis. This is not to be confused with some sequences in GenBank and UNITE that are incorrectly labeled *R. nana* (KX579809, UDB016029, and UDB015077) that are in a clade sister to *R. betularum* in our phylogenetic analysis. The *R. montana/nana* clade is sister to *R. aquosa*. A few distinct molecular differences between *R. montana* and *R. nana* are worth noting. There are a few conserved differences in the ITS sequences of *R. montana* that are not found in the closely related *R. nana*. There are two insertions present in the ITS1 region of *R. montana* sequences that are absent in *R. nana*; one is a G at position 184 in our alignment, the second is an ATTT from positions 265–268. There are also two single nucleotide polymorphisms (SNP's) in the ITS2 region (TG at location 602–603) that are conserved throughout all our *R. montana* sequences that differ from that of *R. nana* (CT at these positions). Therefore, we maintain these as two separate species based on morphological and molecular differences as well as habitat.

A species similar to *R. montana* is *R. emetica* var. *grisescens* described by Bon and Guagué in 1975 from France near *Betula*. *Russula grisescens* was raised to species

rank by Marti in 1984. Voitek (2015) recognized that *R. griseascens* (note the error in spelling) forms a species complex with *R. aquosa* and *R. nana* using molecular data, which is similar to our results. Bazzicalupo et al. (2016) investigated the distribution and occurrence of *R. emetica* in Newfoundland and Labrador, Canada, and found that *R. montana* represented the most common species in the region. Their work also indicated that *R. griseascens* and *R. montana* are close morphologically and molecularly. If *R. montana* is the same species as *R. griseascens*, the former has priority because it was described at the species level first in 1975, which was noted by Bazzicalupo et al. (2016). Numerous sequences in our phylogenetic analysis from Finland (JV 9788) and Austria (UDB031192) labeled *R. griseascens* cluster with *R. montana* in the phylogenetic analysis suggesting that these species are synonymous, but this needs to be confirmed by examining the type material of *R. griseascens* (Bazzicalupo et al. 2016). A proposed synonymy with *R. hydrophila* (Reumaux et al. 1996) has been questioned (Bazzicalupo et al. 2016) but should be considered when types can be examined.

Based on morphology, *R. montana* has been reported in Colorado and Utah (Shaffer 1975). Molecularly this species has been confirmed in Newfoundland and Labrador, Canada by Bazzicalupo et al. (2016) and the phylogenetic analysis here include sequences from Colorado USA, Canada, Austria, and Finland, indicating that *R. montana* is intercontinentally distributed. Interestingly, *R. montana* has not been found in Montana, although subalpine Russulas have not been well-sampled.

Russula nana Killerman

FIGS. 11, 16A, 18A, 20B

Denkschr. Bayer. Botan. Ges. In Regnsb. 20: 38 1939

Macromorphology. Pileus 12–35(65) mm wide, hemispheric when young, broadly convex, to applanate, occasionally uplifted, and then slightly depressed in center, candy apple red, strawberry red, deep red, paling to white with ocher tints towards margin in age, smooth, slightly greasy, viscid when wet, occasionally matt, tacky when dry; margin slightly striate when young, more striate in age or not; cuticle separable except at center. Lamellae narrowly attached, adnate or adnexed, widest near pileus margin, close, on av. L = 75–120 (n = 5), white becoming light yellow brown in age or on drying, not anastomosing, occasionally forking near pileus margin, neither fragile nor tough; lamellae edge entire. Lamellulae present and extending 1/3 of the way from pileus margin to stipe. Stipe 6–26 × 5–13 mm, clavate, equal, central to slightly eccentric, white, with greyish or grey brown tints developing first at base, smooth, fragile or not, with faint vertical ridges. Context white, not staining; in stipe not hollow but with soft areas or small cavities near base. Odor indistinct. Taste moderately acrid. Exsiccata: Pileus red pink, cherry red, bleached ocher, tan, occasionally dark maroon near margin. Lamellae gray, ocher gray, yellow brown near pileus margin. Stipe white or grayish, with brown staining near base. Chemical Reactions: Gum Guaiac = blue green or turquoise; ferrous sulfate = very light yellow brown, 2% phenol = no reaction.

Micromorphology. Basidiospores white in print (Ia), (6.1–)7.1–7.7–8.3(–9.6) × (5.1–)5.9–6.3–6.6(–7.6) μm, broadly ellipsoid, Q = (1.1–)1.2–1.2–1.3(–1.6); ornamentation of numerous, amyloid, warts and spines connected by thin lines and ridges

forming a full reticulum, $<0.5\text{--}1\text{ }\mu\text{m}$ high, occasionally subreticulate with isolated cylindrical warts and spines; apiculus truncate or apically tapering, inamyloid; suprahilar plage small to large, amyloid. Basidia $(38.1\text{--})45.7\text{--}50.6\text{--}55.4(63.5) \times (7.62\text{--})8.6\text{--}9.8\text{--}11.1(12.7)\text{ }\mu\text{m}$, clavate-pedicellate, occasionally cylindrical, 4-spored, possibly 2-spored; basidiola clavate. Hymenial cystidia $(55.9\text{--})64.9\text{--}74.9\text{--}85(96.5) \times (7.6\text{--})9\text{--}10.2\text{--}11.4(15.2)\text{ }\mu\text{m}$, clavate-pedicellate, fusiform, rarely forking near apex, mucronate with swollen or cylindrical $2.5\text{--}5.1\text{ }\mu\text{m}$ long appendage or not; contents granular, lipid drops present, blackening in sulfovanillin. Pileipellis sharply delimited from underlying context; suprapellis ca. $100\text{--}150\text{ }\mu\text{m}$ thick, composed of loosely interwoven hyphae and pileocystidia with no direction; subpellis ca. $85\text{--}140\text{ }\mu\text{m}$ thick, composed of tightly interwoven, horizontally oriented hyphae, becoming more dense near context. Hyphal terminations cylindrical, thin walled; terminal cells $16.3\text{--}53 \times 1.5\text{--}4.5\text{ }\mu\text{m}$, apically obtuse, devoid of contents or rarely granular at apex. Pileocystidia near pileus margin abundant, occasionally septate, clavate-pedicellate, becoming thinner as they increase in length, $(30.5\text{--})54.2\text{--}92.3\text{--}130.4(203.2) \times (3.8\text{--})4.7\text{--}5.5\text{--}6.3(7.6)\text{ }\mu\text{m}$, occasionally forking below septa; contents granular or crystalline, blackening in sulfovanillin. Pileocystidia near pileus center scattered to abundant, similar in shape but shorter, occasionally fusiform or swollen, tapering slightly at apex (subacute), $(38.1\text{--})48.6\text{--}71.6\text{--}94.6(137.2) \times (3.8\text{--})4.7\text{--}5.7\text{--}6.6(7.6)\text{ }\mu\text{m}$, occasionally forking; contents similar.

Figure 11. *Russula nana*. A. with *Salix reticulata*, Beartooth Plateau, Montana (CLC 3619). B. with *S. arctica*, Cinnamon Pass, Colorado (CLC 1812). Scale bar = 2 cm.

North American Ecology. In alpine areas of Colorado, Montana, and Wyoming with *Salix reticulata* and *S. planifolia* in wet soil with moss. Jul and Aug.

Material examined. ITALY. Belluno, with *Salix reticulata* and *S. retusa*, 7 Aug 2011, *E. Campo EC 17.08.2011*. USA. COLORADO. Boulder County, Niwot Ridge, with *Salix* species, 23 Aug 2018, *C. Noffsinger CRN 177* (MONT); Pitkin County, Sawatch Range, Independence Pass, with dwarf *Salix*, 6 Aug 2003, *V. Evenson DBG-F-021359* (DBG); San Juan County, San Juan Range, Cinnamon Pass, with *S. planifolia* and *S. reticulata*, 1 Aug 2000, *C. Cripps CLC 1440* (MONT); loc. cit., *Salix arctica*, 27 Jul 2002, *C. Cripps CLC 1812* (MONT); Black Bear Pass, 3 Aug 2000, *C. Cripps CLC 1450* (MONT). MONTANA. Carbon County, Hellroaring Plateau, 14 Aug 2008, *C. Cripps CLC 2330* (MONT). WYOMING. Park County, Beartooth Plateau, Frozen Lake, with *Salix reticulata*, 23 Aug 2017, *C. Cripps CLC 3619* (MONT); loc. cit., *S. reticulata*, 17 Aug 2017, *C. Cripps CLC 3575B* (MONT); Billings Fen site, with *S. planifolia*, 7 Aug 2018, *C. Noffsinger CRN 135* (MONT).

Similar taxa examined. GREENLAND. Sisimiut, with *Salix herbacea*, 20 Aug 2000, *C. Cripps CLC 1544* (MONT).

Observations. Killerman described *R. nana* in 1936 based on a collection he found at 2700 meters in Tirol, Austria. The original description mentions a small specimen with a blood-red, flat pileus, white lamellae, and very hot taste; he did not specify the date or where the type was deposited. Kühner (1975) then reported *R. nana* as a common species in Arctic and alpine habitats of Europe near dwarf willow and occasionally *Polygonum*

viviparum (*Bistorta vivipara*). Bresinsky et al. (1980) examined the type material of Killerman's and confirmed that *R. nana* represented a common Arctic-alpine species as Kühner (1975) had recognized. They also synonymized the name *R. alpina* (Blytt) Møller and Schäffer with *R. nana* Killerman. Sarnari (1998–2005) claimed that the type material examined by Bresinsky et al. (1980) was unusable because it lacks a collection date. Killerman's original illustration consists of only a small, black and white drawing of two fruiting bodies and a single spore, which was also not sufficient. Therefore, Sarnari designated an epitype from the alpine region of Monta Rosa, Italy near *Dryas* (n° 97/800, in Herb. IB).

Russula nana is one of the most iconic Arctic-alpine species of *Russula* and is considered common in regions of Europe where it has been reported in the Alps, Pyrenees, or Carpathians (Favre 1955; Horak 1960; Kühner 1975; Lamoure 1982; Bon 1985; Kühner and Lamoure 1986; Bon 1987; Bon and Cheype 1987; Senn-Irlet 1987; Schmid-Heckel 1988; Tondl 1988; Bon 1991; Fellner and Landa 1991; Fellner and Landa 1993b; Jamoni 1995; Adamčík 1998; Peintner 1998; Sarnari 1998–2005; Bon 2000; Bresinsky et al. 2000; Moreau 2002; Corriol 2008; Jamoni 2008; Ronikier 2008; Gyosheva and Dimitrova 2011), Faroe Islands (Vesterholt 1998), Fennoscandia (Gulden and Lange 1971; Kühner 1975; Gulden et al. 1985; Graf 1994; Sarnari 1998–2005; Ohenoja 2000; Gulden 2005), Netherlands (Geml et al. 2014), Poland (Ronikier and Adamčík 2009), Russia (Knudsen and Mukhin 1998; Niezdoiminogo 2003), Scotland (Watling 1987), Iceland (Hallgrímsson 1998), and Svalbard (Gulden et al. 1985; Skifte 1989; Gulden and Torkelsen 1996). In North America, *R. nana* has been reported from Alaska (Miller

1982a), Canada (Ohenoja and Ohenoja 2010), Greenland (Watling 1977; Knudsen and Borgen 1982; Lamoure et al. 1982; Borgen 1993; Borgen et al. 2006), and the Rocky Mountains (Moser and McKnight 1987; Cripps and Horak 2008). The species has also likely been reported under the names *R. nana* var. *alpina* in the European Alps (Bon and Ballarà 1996) and as *R. alpina* in Fennoscandia (Lange and Skifte 1967), Greenland (Lange 1957; Kobayasi et al. 1971; Peterson 1977; Watling 1977; Lamoure et al. 1982; Watling 1983), Iceland (Christiansen 1941), and Svalbard (Kobayasi et al. 1968). None of these reports have been molecularly confirmed.

This is the first research to perform an in-depth systematic analysis of *R. nana* that includes molecular data. Our phylogenetic analysis includes Rocky Mountain alpine collections from Colorado, Wyoming, and Montana as well as reference sequences from Italy (near epitype locality), Scotland, and Switzerland. *Russula nana* forms a strongly-supported clade that forms a polytomy with several collections of *R. montana* (FIG. 4), including the *R. montana* holotype. *Russula nana* and *R. montana* are morphologically similar, but differ in a few important characteristics. *Russula nana* is a small species (pileus usually 12–35 mm wide) found in Arctic and alpine habitats with *Salix*. Whereas, *R. montana* has a larger pileus (usually 35–70 mm wide) and occurs with conifers in the subalpine zone. This ecological distinction is true with the exception of one collection originally identified as *R. nana* (F-127873); this collection was found near *Salix herbacea* in an alpine region of Norway and was resolved with *R. montana*. Sarnari (1998–2005) also noted a few small morphological differences between *R. nana* and the closely related *R. grisescens*, the latter being a possible synonym of *R. montana* (see observations under

R. montana). *Russula montana* spores are significantly longer than those of *R. nana* when analyzed using a two-sample t-test (p-value = 0.002, based on 100 measurements from each species). There are also few conserved differences in the ITS sequences of *R. montana* that are not shared with the closely related *R. nana* (see observations under *R. montana*). Based on this evidence we maintain *R. nana* and *R. montana* as two separate species. This is the first molecularly confirmed report of *R. nana* in the Rocky Mountain alpine zone; however, Geml et al. (2010) reported it in Alaska base on 97% sequence similarity, which may not be sufficient for *Russula* species delineation. This is the first work to molecularly confirm that this common Arctic and alpine species is indeed intercontinentally distributed, confirming earlier morphological studies in Alaska and the Rocky Mountain alpine (Miller et al. 1973; Miller 1982a; Moser and McKnight 1987; Cripps and Horak 2008).

Several species and varieties have been synonymized with *R. nana*; however, none of these names have been verified using molecular methods and there are inconsistencies between sources. Kühner (1975) synonymized only *R. emetica* var. *alpina* Blytt & Rostr. with *R. nana*. Whereas, Sarnari (1998–2005) synonymized eight names with *R. nana*. He stated that two names, *Russula emetica* var. *alpina* A. Blytt & Rostr. and *R. fragilis* var. *alpestris* Boud., were generally believed to be synonymous with *R. nana* Killerman because *R. nana* was first described at the species level. He also synonymized *R. alpina* (A. Blytt & Rostr.) F.H. Møller & Jul. Schäff., *R. alpestris* (Boudier) Singer, *R. emetica* ssp. *alpestris* (Boudier) Singer, *R. emetica* var. *alpestris* Singer, *R. nana* var. *alpina* (Blytt & Rostrup) Bon and cited some concerns about the

synonymy of *R. nigrodisca* Peck (Singer 1943; Shaffer 1975) with *R. nana*. However, many of these names have now been synonymized under *R. emetica* (Shaeff.) Pers. by others. Therefore, at this time we have not included these proposed synonyms of *R. nana* until further analysis of type specimens and the corresponding molecular work can be completed.

There is some confusion in the literature regarding the correct phylogenetic placement of *R. nana*. Several studies have resolved *R. nana* as a closely related species to *R. betularum* (Miller and Buyck 2002; Li et al. 2015; Bazzicalupo et al. 2016). This work that used morphological and molecular data from European and North America collections determined that *R. nana* is closely related to *R. montana*. Multiple sequences in Genbank and UNITE labeled *R. nana* form a sister clade to *R. betularum* in our analysis (UDB015077, UDB016029, and KX579809) that are distantly related to our *R. nana* clade. We also have collections of *Russula* from Alaska that fall into this imposter clade (CLC 3821 and CLC 3822B), which we are calling *R. cf. alpigenes* based on the description produced by Bon (1993). Based on our collections this species does not represent the common Arctic and alpine fungus described by Killerman. *Russula* cf. *alpigenes* and closely related taxa can be distinguished from *R. nana* in the field, by the pileus color that is carmine red with a dark center (not cherry red fading to white as in *R. nana*) and by the longer stipe that can have pink tints, (absent in *R. nana*). Of particular note is that the stipe dried bright pink in most of our collections tentatively identified as *R. cf. alpigenes*, this character has not been reported in *R. nana*. Also, the odor can be slightly sweet, and spores are smaller in *R. nana* (av $7.7 \times 6.3 \mu\text{m}$) compared to *R. cf.*

alpigenes ($8.9 \times 7 \mu\text{m}$). There have been sequences generated prior to this study of the true *R. nana*; however, they are not publicly available. Caution is advised when using *R. nana* sequences available in public databases.

Russula cf. pascua (F.H. Møller & Jul. Schäff.) Kühner

FIGS. 12, 17C, 18G, 19A

Bulletin de la Société Mycologique de France 91(3):331 1975

Macromorphology. Pileus 25–35 mm wide, convex, irregular convex, becoming applanate, with or without slight depression in center, deep magenta, red, dark red, candy apple red, ocher, rarely with small hints of green, lighter or darker at margin, smooth, dry, coarsely cracking or not, debris adhering to cap; margin striate for short distance or not, undulating in some; pileus cuticle separable except at center. Lamellae attached, adnate to adnexed, relatively close, on av 100–104 L (n = 2), light straw yellow, yellow brown, browning near pileus margin in age, rarely anastomosing or forking, elastic not brittle. Lamellula absent or rare. Stipe 15–20 × 8–20 mm, clavate or strongly clavate, central, white or off-white, with brownish yellow stains near base or covering stipe, slightly pink on drying, smooth with indistinct vertical ridges. Context in stipe hard or soft, not hollow but with small cavities near base. Odor fishy. Taste radish hot, weakly acrid, or mild. Exsiccata: Pileus dark maroon, red, or ocher. Lamellae ocher, browning at pileus margin. Stipe white to ocher, usually darker near base. Chemical reactions: Gum Guaiac = brownish green; Ferrous sulfate = grayish green; 2% phenol = light brown to dark brown with a green hue.

Micromorphology. Basidiospores white to light cream in mass (Ib-IIa), (7.6–)8.4–9.1–9.8(–10.6) $\times$ (5.5–)6.5–7–7.5(–8.2) μm , broadly ellipsoid to ellipsoid, $Q = (1.1–)1.2–1.3–1.4(–1.5)$; ornamentation of isolated, amyloid warts and spines, 0.5–1 μm high that are typically round or elongated at base and occasionally connected by thin lines, clustered to subreticulate; apiculus truncate, inamyloid; suprahilar plage large, amyloid. Basidia (45.7–)50.2–56.2–62.3(–66.3) $\times$ (7.6–)9.3–10.4–11.5(–12.2) μm , clavate or fusiform, 4-spored; basidiola clavate. Hymenial cystidia (53.9–)58.6–66.8–75.1(–81.3) $\times$ (6–)7.5–8.7–10(–10.2) μm , fusiform, pedicellate, often mucronate, with swollen ca. 3.8–12.7 μm long appendage; contents granular or refractive, possibly banded, slightly browning in sulfovanillin. Pileipellis sharply delimited from underlying context; not stratified, ca. 114–331 μm thick, composed of highly variable, parallel, horizontally or vertically oriented, loosely or tightly interwoven, septate hyphae. Hyphal terminations near the pileus margin often attenuated, occasionally cylindrical, rarely inflated, thin-walled, (19.4–)24.7–30.7–36.7(–41.8) $\times$ (2.5–)3–3.5–4.1(–4.5) μm ; contents lightly granular. Hyphal terminations near the pileus center cylindrical or attenuated, occasionally inflated, thin-walled, (24.8–)26.7–31.5–36.4(–40.8) $\times$ (3.1–)3.2–3.7–4.2(–5.1) μm ; contents lightly granular. Pileocystidia near the pileus margin rare, clavate, septate, (25.5–)32.9–58.2–83.5(–106.7) $\times$ (4.1–)4.5–5.8–7.1(–8.9) μm ; contents lightly granular, no reaction in sulfovanillin. Pileocystidia near pileus center similar in shape and size, tapering at apex (subacute), or fusiform, (27.9–)37.2–53.6–70(–88.9) $\times$ 4.7–5.8–6.9(–7.6) μm ; contents lightly granular or refractive gelatinous.

Figure 12. *Russula* cf. *pascua* (CRN 138) growing with *Salix reticulata*, Beartooth Plateau, Montana. Scale bar = 2 cm.

North American Ecology. Occurring in the alpine with *Salix reticulata* in Montana, Wyoming, and Colorado. Aug.

Material examined. USA. COLORADO. Boulder County, Niwot Ridge, 1 Aug 2006, *C. Cripps* CLC 2274 (MONT). WYOMING. Park County, Beartooth Plateau, Frozen Lakes, with *Salix reticulata*, 8 Aug 2018, *C. Noffsinger* CRN 138 (MONT); loc. cit., with *S. reticulata*, 8 Aug 2018, *C. Noffsinger* CRN 146 (MONT).

Similar taxa examined. USA. MONTANA. Boulder County, Niwot Ridge, 8 Aug 1998, *C. Cripps* CLC 1220 (MONT).

Observations. One species from the Rocky Mountain alpine is phylogenetically located in *R.* subsection *Xerampelinae*, whose members are known for having red-brown colors in the pileus, a strong fishy odor, and a green reaction in the context when exposed to ferrous sulfate (Adamčík and Knudsen 2004); the well-known *R. xerampelina* is in this subsection. When encountering this species in the field, a few collections were initially identified as *R. nana* because of the bright red color, until a fishy odor was noticed. In the phylogenetic analysis, collections from the Rocky Mountain alpine zone form a polytomy with members of the closely related *R. clavipes* complex (Adamčík et al. 2016b). The *R. clavipes* complex contains *R. pascua* (F.H. Møller & Jul. Schäff.) Kühner, *R. clavipes* Velen., and *R. nuoljae* Kühner. *Russula nuoljae* is morphologically and molecularly distinct; however, *R. pascua* and *R. clavipes* are believed to be similar morphologically and do not separate with strong support in phylogenetic analyses (Adamčík et al. 2016b). However, others think of *R. clavipes* as a bigger subalpine species with *Betula* (Læssøe and Peterson 2019). Adamčík et al. (2016b) separated the three species in the *R. clavipes* based on morphological characters, mainly those present in the pileipellis and the habitat. When considering the important characters for species delineation in Adamčík et al.'s (2016b) key, our species has pileocystidia near the pileus margin that are barely less than 6 μm wide on average, attenuated terminal cells that are barely longer than 30 μm wide on average, and is reported with dwarf and shrubby *Salix* from Arctic-alpine habitats. When using these characters to delineate the European taxa studied in Adamčík et al. (2016b) our taxon from the Rocky Mountain alpine does not clearly fit the description of *R. pascua*. However, our species matches many other morphological characters of *R.*

pascua (Adamčík and Knudsen 2004) and is found in the same habitat. Another similar species based on morphology and ecology is *R. amoenipes* Romagn. f. *kuehneriana* *ad int.* (Bon 2000). *Russula amoenipes* f. *kuehneriana* is characterized by a pileus around 30–50 mm in diameter with a matte red color, yellow basidiospores $9 \times 7 \mu\text{m}$ with warts $0.6\text{--}1 \mu\text{m}$ high, and pileocystidia $4\text{--}7 \mu\text{m}$ wide that do not blacken in sulfovanillin. All of the above characteristics closely match that of our species.

Of the three species reported by Adamčík et al. (2016b), *Russula pascua* is the one most commonly reported in Arctic and alpine areas, and these include Europe (Adamčík and Knudsen 2004; Adamčík et al. 2016b; Fellner and Landa 1993b; Graf 1994; Ronikier and Adamčík 2009; Schmid-Heckel 1988), Fennoscandia (Gulden 2005), Faroe Islands (Adamčík and Knudsen 2004), Greenland (Adamčík and Knudsen 2004; Borgen et al. 2006), Poland (Adamčík and Knudsen 2004; Adamčík et al. 2016b; 59), Russia, and Scotland (Watling 1987). The reports in Europe and Poland have been molecularly confirmed (Adamčík et al. 2016b).

Due to the similarity of our species to *R. pascua*, the large distribution reported for *R. pascua* in Arctic and alpine habitats, and the lack of reference material available for *Russula amoenipes* f. *kuehneriana* we elect to call our species *R. cf. pascua* at this time. However, our species shared similarities with *Russula amoenipes* f. *kuehneriana* and this will continue to be investigated.

Russula pascua was originally described as *R. xerampelina* var. *pascua* F.H. Møller & Jul. Schäff. and its species status was confirmed by Kühner (1975). Sarnari (1998–2005) incorrectly designated a neotype for *R. pascua* that also fell into the

subrubens clade (Adamčík et al. 2016b). We used sequences from Adamčík et al. (2016b) to build our phylogeny to investigate Rocky Mountain alpine members of the *R. clavipes* complex. Based on their work, *R. pascua* has been molecularly confirmed in Italy, Poland, Slovakia, Austria, and Romania.

A BLAST search in the UNITE database revealed numerous highly similar sequences. However, species in the *R. clavipes* complex are so molecularly similar that even BLAST matches that share 99.6% sequence similarity do not fall into our Rocky Mountain clade. If Adamčík et al.'s (2016) circumscription of the *R. clavipes* complex reflects reality, speciation in this group may occur with as little as 0.3% variation in the ITS region.

Russula purpureofusca Kühner

FIGS. 13, 18H, 19D

Bull. Trimmest. Soc. Mycol. Fr. 91(3):389. 1975

= *Russula cupreola* Sarnari, Boll. Assoc. Micol. Ecol. Romana 7 (20–21):64.

1990

Macromorphology. Pileus 20–45 mm wide, convex when young, becoming applanate with a slight depression, fully maturing to a funnel-shape, deep red, reddish brown, deep magenta, light yellowish green, yellow brown, darker over disk in age, smooth, viscid, with debris adhering; margin not striate or striate in age, occasionally undulating; cuticle separable except at center. Lamellae attached, adnate, close, on av. 70–104 L (n = 3), light yellow, cream, dark yellow cream, brownish yellow, darker near margin, anastomosis rare, no forking, entire, elastic not brittle. Lamellulae rare. Stipe 10–35 x 5–15 mm, clavate or equal, central, white, off-white, light yellow, graying, with

yellow-brown stains near base, yellow-brown when bruised, smooth. Context hard or soft, white or watery gray, with large cavity near base in some collections. Odor absent, fungoid, or sweet. Taste strongly acrid (after 20–30 seconds), mild in one collection. Exsiccata: Pileus dark violet brown, darker brown to black over disk, sometimes olive green near margin. Lamellae brownish orange, ocher, dark yellow, dull. Stipe white, yellow brown, with hints of gray. Chemical reactions: Gum Guaiac = dark olive brown; ferrous sulfate = faintly pink or pinkish gray brown; 2% phenol = no reaction.

Micromorphology. Basidiospores dark yellow in print (IIIb – IIIc), (7.5–)8.0–8.5–9.0(–9.6) $\times$ (6.1–)6.6–7.0–7.4(–8.2) μm , subglobose to broadly ellipsoid, $Q = (1.1\text{--})1.1\text{--}1.2\text{--}1.3(1.4)$; ornamentation of numerous, isolated, amyloid, warts, 0.5–1 μm high and ca. 1 μm in diameter at base, with some warts fusing or occasionally connected by fine lines or ridges, not forming a reticulum; apiculus truncate or pointed, inamyloid; suprahilar plage medium to large, amyloid. Basidia (43.2–)48.9–54.2–59.4(–63.5) $\times$ (10.2–)10.3–11.1–11.8(–12.7) μm , clavate-pedicellate, 4-spored; basidiola clavate. Hymenial cystidia (71.1–)74.2–85.5–96.8(–119.4) $\times$ (7.6–)8.9–11.2–13.5(–15.2) μm , fusiform or clavate, often mucronate, with 2.5–7.6 μm long appendage; contents granular, gelatinous, or crystalline, graying to slightly blackening in sulfovanillin. Pileipellis sharply delimited from underlying context; suprapellis ca. 114–152 μm thick, composed of erect, forking, septate, hyphae, well-defined or gradually transitioning to subpellis; subpellis gelatinized, ca. 127–203 μm thick, composed of difficult to differentiate horizontal hyphae. Hyphal terminations cylindrical or clavate, flexuous, thin-walled, ca. 5–6 μm wide at apex, apically obtuse or occasionally subacute,

occasionally with granular contents. Pileocystidia near pileus margin 1–2 septate, clavate or cylindrical, thin-walled, $(53.3\text{--})70.6\text{--}102.9\text{--}135.2(-177.8) \times (5\text{--})5\text{--}6\text{--}7(-7.6) \mu\text{m}$, apically obtuse or subacute, occasionally forking, with small lateral protrusions present (lateral diverticulate); contents granular or gelatinous, occasionally banded, dark black in sulfovanillin. Pileocystidia near pileus center often shorter, strongly clavate, and not forking, $(50.8\text{--})60.1\text{--}83.1\text{--}106(-127) \times (3.8\text{--})5\text{--}6.4\text{--}7.8(-8.9) \mu\text{m}$; contents similar.

Figure 13. *Russula purpureofusca*. A. with *Salix* and *Dryas*, near Girdwood, Alaska (CLC 3820), photo Noah Siegel. B. with *S. planifolia*, Loveland Pass, Colorado (CRN 165). Scale bar = 2 cm.

North American Ecology. In the alpine zone with *Salix planifolia* and other *Salix* species in Alaska and Colorado. Aug.

Material examined. NORWAY. Nord-Trøndelag, Levanger, 21 Aug 1998, G. Gulden F-60573 (O). SWEDEN. with *Salix* and *Dryas*, 22 Aug 2019, J. Vauras JV 32876F. USA. ALASKA. Anchorage County, Girdwood, with *Salix* and *Dryas* species, 22 Aug 2018, C. Cripps CLC 3820 (MONT). COLORADO. Summit County, Loveland Pass, with *Salix planifolia*, 19 Aug 2018, C. Noffsinger CRN 164 (MONT); loc. cit., with *S. planifolia*, 19 Aug 2018, C. Noffsinger CRN 165 (MONT).

Observations. *Russula purpureofusca* was originally described by Kühner in 1973 as a small brownish-red alpine species with a light-yellow spore print (IIc), an acrid taste, and $8\text{--}8.7 \times 6.7\text{--}7.5$ μm basidiospores, occurring near *Salix reticulata* (Ruotsalainen and Huhtinen 2015). In 1990, Sarnari described a similar species from the alpine zone of Europe that he called *R. cupreola*. This species was also collected with *S. reticulata* but differed from Kühner's species by the darker yellow spore print (IVc). After examining the holotypes of both *R. purpureofusca* and *R. cupreola*, Ruotsalainen and Huhtinen (2015) synonymized the two species and gave the older name, *R. purpureofusca*, priority. They determined that differences in spore color were due to the maturity of the specimens collected by Kühner compared to the specimens examined by Sarnari. They also found that the holotypes of *R. purpureofusca* and *R. cupreola* had identical spore morphology and pileocystidia with abundant lateral diverticulae, which appears to be a distinguishing feature. A BLAST search for sequences similar to CLC 3820 in the UNITE database revealed 98.2% sequence similarity of the ITS region with *R. cupreola* type (UDB032344), but this sequence is locked and unavailable.

This is the first report of *R. purpureofusca* from North America. Our phylogenetic analysis produced a strongly-supported clade containing North American collections and reference material from Norway and Sweden, including a collection examined by Ruotsalainen and Huhtinen (2015) labeled *R. purpureofusca* (H6042234). Our North American collections from Colorado have a yellow-green pileus; whereas, the pileus in our Alaskan collection is reddish-brown to magenta, colors normally associated with this species. However, Sarnari (1998–2005) mentioned an olive-ocher coloration in his description of *R. cupreola*. Significant intraspecific color variation has been observed in the pileus of other species of *Russula* (Bazzicalupo et al. 2017). All our collections matched *R. purpureofusca* in spore dimensions and all had lateral protrusions (lateral diverticulae) on the pileocystidia. There are only three base pairs difference between the Alaska collection and the two collections from Colorado.

Morphologically and to some degree molecularly, Ruotsalainen and Huhtinen (2015) confirmed *R. purpureofusca* to occur in Finland, Norway, and Switzerland, although their molecular data were not published. Morphologically, Sarnari (1998–2005) reported *R. cupreola* from Finland and Fellner and Landa (1993) reported it in alpine areas of Slovakia. Therefore, it is likely that *R. purpureofusca* has an intercontinental distribution in Arctic and alpine habitats of North America, Fennoscandia, and the European Alps.

Russula purpureofusca can be confused with *R. laccata* and *R. saliceticola*, which also have a deep magenta to ruby pileus and occur in alpine and Arctic areas with *Salix*. However, *R. laccata* has white lamellae and white spores that are smaller ($8.1 \times 6.2 \mu\text{m}$)

and reticulate. *Russula saliceticola* is mild tasting, often with pink tones on the stipe, and the spore print is usually a lighter yellow color. Of the three species, only *R.*

purpureofusca has lateral protrusions on the pileocystidia and all can be separated phylogenetically using the ITS region (FIG. 3).

***Russula saliceticola* (Singer) Kühner ex Knudsen & T. Borgen** FIGS. 14, 17A, 18E, 19C

Arctic and Alpine Mycology, 1980 (Seattle):224 1982

= *Russula saliceticola* var. *gaviae* Bincol., Giac. & Ostellari, Riv. Micol. 54(1):30
2011

= *Russula sphagnophila* subsp. *saliceticola* Singer, Annls mycol. 34(6):425 1936

Macromorphology. Pileus 10–55 mm in wide, convex, conic, applanate, occasionally depressed in center, deep red, grayish ruby, almost black in center, red to dark red closer to margin, occasionally with ocher or tan areas, occasionally lighter in center or uniform in color, glabrous, greasy or dry, matte or shiny, with debris adhering; margin smooth to faintly sulcate-striate, more striate in age, inrolled or not, entire or undulate; cap cuticle separable except at center. Lamellae attached, adnate to adnexed, subdistant or close, on av. L = 64–84 (n = 5), white, light yellow, cream, warm yellow, occasionally white near stipe and more straw yellow near pileus margin, occasionally magenta near cap margin, anastomosing or not, forking near margin or not, elastic not brittle; browning near margin in age, entire or undulate. Lamellulae present or absent. Stipe 15–60 × 5–25 mm, clavate or equal, central, pure white, off-white, buff yellow, cream, occasionally becoming tan brown in age, smooth, pruinose near base (maybe due to frost), with or without purple or pinkish tint, that becomes more pronounced after

collecting, with greyish brown and brownish red stains near base, with indistinct vertical ridges. Context watery white, flesh tinted red under cuticle; in stipe spongy but firm, neither hard nor fragile, not hollow but occasionally with a few cavities. Odor usually absent, rarely sweet. Taste mild, occasionally weakly acrid. Exsiccata: Pileus grayish ruby to dark ruby, almost black near center, with red, brown, ocher, or buff. Lamellae light buff or brown, ocher gray yellow, grayish orange, egg yolk yellow, staining darker brown in areas. Stipe off-white, yellow brown, light tan brown, brown black, with pinkish purple stains that became more pronounced on drying, gray stains also present. Chemical reactions: Gum Guaiac = bluish green, grayish brown, green brown, brown; ferrous sulfate = ranging from yellow brown, dark pink, to red brown, rarely with green hue; 2% phenol = no reaction or occasionally light brown or brown.

Micromorphology. Basidiospores white, light yellow cream, or warm yellow cream in print (Ia-IIId), $(7.1-8.1-8.9-9.8(-11.6) \times (5.1-6.3-7-7.6(-9.6) \mu\text{m}$, broadly ellipsoid to ellipsoid, $Q = (1.1-1.2-1.3-1.4(-1.5)$; ornamentation of dense, amyloid, isolated warts, $0.5-1 \mu\text{m}$ high, with cylindrical, oval, or angular bases, that fuse, and are occasionally connected by thin lines and/or ridges forming a subreticulum; apiculus truncate or pointed, inamyloid; suprahilar plage small to large, amyloid, occasionally difficult to observe. Basidia $(38.1-43.9-51-58.1(-66) \times (7.6-9.5-11-12.5(-14.3) \mu\text{m}$, clavate-pedicellate, subacute at apex, 4-spored, occasionally 2-spored; basidiola clavate. Hymenial cystidia rare, $(55.9-62.9-78.8-94.7(-147.3) \times (6-7.8-9.6-11.4(-12.7) \mu\text{m}$, fusiform, cylindrical, occasionally pedicellate, often mucronate, with $1-4 \mu\text{m}$ long appendage; contents granular, crystalline, amorphous, or absent, occasionally with lipid

drops, slightly graying, with orangish-brown reaction in sulfovanillin. Pileipellis sharply delimited from underlying context; suprapellis weakly gelatinized, ca. 63–100 μm deep, composed of tightly or loosely interwoven, erect, septate hyphae, hard to differentiate, gradually passing to subpellis; subpellis, strongly gelatinized ca. 63–102 μm deep, composed of hard to differentiate, densely interwoven, septate, horizontally oriented hyphae. Hyphal terminations slightly clavate, thin-walled, ca. 2–4 μm wide at apex, apically obtuse and swollen; rarely with lightly granular contents, difficult to observe. Pileocystidia near the pileus margin usually with one septa, cylindrical, pedicellate, hyphal like, $(58.4\text{--})81\text{--}110.4\text{--}139.7\text{--}(221) \times (3.8\text{--})4.2\text{--}5.1\text{--}6\text{--}(7.6) \mu\text{m}$; contents granular or crystalline, occasionally with small lipid drops, blackening in sulfovanillin. Pileocystidia near the pileus center similar in shape but shorter and with 1–2 septa, occasionally deformed; heavily filled with granular contents $(48.3\text{--})51.6\text{--}77.2\text{--}102.9\text{--}152.4) \times (3.8\text{--})4.7\text{--}5.9\text{--}7.1\text{--}(7.6) \mu\text{m}$.

Figure 14. *Russula saliceticola*. A. with *Salix planifolia*, Niwot Ridge, Colorado (CRN 173). B. with *S. planifolia*, Beartooth Plateau, Montana (CRN 155). Scale bar = 2 cm.

North American Ecology. In alpine areas of Montana, Wyoming, and Colorado with *Salix reticulata* and *Salix planifolia*. Jul and Aug.

Material examined. SWEDEN. Lycksele lappland, Arjeplog, with *Salix* and *Betula*, 13 Aug 2018, *J. Vauras JV 32515F*. USA. COLORADO. Boulder County, Blue Lake, with *Salix planifolia*, 24 Aug 2018, *C. Noffsinger CRN 184* (MONT); Niwot Ridge, with *S. planifolia*, 20 Aug 2018, *C. Noffsinger CRN 173* (MONT). MONTANA. Carbon County, Beartooth Plateau, Birch site, with *S. planifolia*, 20 Aug 2017, *C. Cripps CLC 3575C* (MONT); borrow pit, with dwarf *Salix*, 29 Jul 1997, *C. Cripps CLC 1137* (MONT); Highline Trailhead, with *S. planifolia*, 10 Aug 2018, *C. Noffsinger CRN 155* (MONT). WYOMING. Park County, Beartooth Plateau, Billings Fen site, with *S. reticulata*, 23 Aug 2017, *C. Cripps CLC 3616* (MONT); loc. cit., with *Salix* species, 7 Aug 2018, *C. Noffsinger CRN 134* (MONT); Frozen Lake, *S. planifolia*, 8 Aug 2018, *C. Noffsinger CRN 140* (MONT); loc. cit., with *Salix* species, 8 Aug 2018, *C. Noffsinger CRN 143* (MONT); loc. cit., with *S. planifolia*, 8 Aug 2018, *C. Noffsinger CRN 144* (MONT). Wyoming creek, 6 Aug 2008, *C. Cripps CLC 2370* (MONT).

Observations. Singer originally described *R. nitida* var. *saliceticola* Sing. in 1936 from the Altai Mountains near *Salix herbacea* (Romagnesi 1967; Schmid-Heckel 1985) and Kühner (1975) raised the variety to species rank. However, Kühner did not validly publish the species and Knudsen and Borgen (1982) re-described *R. saliceticola* in 1982. This species is recognized by a deep-red to ruby pileus that is almost black in the center, light yellow to cream lamellae, whitish stipe often with a pink tint, yellow spores with primarily isolated warts, and a mild taste. In the Rocky Mountain alpine, *R. saliceticola*

can be confused with *R. laccata*, which has more magenta in the pileus, a hotter taste, white reticulate spores, and a completely white stipe; and with *R. purpureofusca*, which has deeper magenta and yellow tones in the pileus, and darker yellow spores.

Molecularly, *R. saliceticola*, *R. laccata*, and *R. purpureofusca* can all be separated using the ITS region.

In the Rocky Mountains, this species is commonly found with *Salix planifolia* and *S. reticulata* in alpine habitats during July and August. Our description matches the morphology of *R. saliceticola* as described by Kühner (1975) and our Rocky Mountain alpine collections form a moderately-supported clade that includes reference sequences from Norway, Sweden, and Switzerland. The *R. saliceticola* clade forms a polytomy with the the species *R. nitida* and *R. sphagnophila*. *Russula nitida*, *R. sphagnophila*, and *R. saliceticola* are all morphologically similar with magenta in the pileus, cream-yellowish lamellae, whitish stipe, often with a pink tint, weak odor, and mild taste, although *R. saliceticola* has a typically darker, less striate pileus. *Russula nitida* and *R. sphagnophila* are both associated with *Betula* (Knudsen and Borgen 1982), and *R. saliceticola* occurs with *Salix*, primarily in Arctic-alpine habitats. *Russula sphagnophila* is often in sphagnum moss and appears to be comparatively more fragile, with more of a slight lavender tint at the apex of the stipe and more reticulated spores. *Russula nitida* has spores with primarily isolated warts.

Morphologically, *R. saliceticola* has been reported in Arctic and alpine areas of the European alps (Favre 1955; Kühner 1975; Schmid-Heckel 1985, 1988; Bon 1991), Fennoscandia (Kühner 1975; Hansen and Knudsen 1992; Gulden 2005), Western

Carpathians in Slovakia (Fellner and Landa 1993; Knudsen and Ronikier 2003), Romania (Ronikier 2008), Faroe Islands (Vesterhot 1998), Greenland (Knudsen and Borgen 1982; Lamoure et al. 1982; Borgen et al. 2006), Iceland (Hallgrimsson 1998), and Svalbard (Skifte 1989). Knudsen and Borgen (1982) also claim that this species was described from the alps as *R. brunneoviolacea* Crawshay (Singer 1936; Favre 1955). This is the first report of *R. saliceticola* from the Rocky Mountains.

Russula subrubens (J.E. Lange) Bon

FIGS. 15, 17B, 18F, 19B

Docums. Mycol. 2(5):33 1972

= *Russula chamiteae* Kühner, Bull. trimest. Soc. mycol. Fr. 91(3):389 1975

= *Russula chamiteae* var. *microsperma* Kühner, Bull. trimest. Soc. mycol. Fr. 91(3):389 1975

= *Russula graveolens* var. *subrubens* J.E. Lange, Fl. Agaric. Danic. 5 (Taxon. Consp.):VIII 1940

Macromorphology. Pileus 10–80 mm wide, convex (shallow or broad), becoming applanate, or slightly dished, rarely umbonate, primarily mottled with some combination of reddish, reddish brown, reddish orange, orange brown, yellowish brown, ocher, or light brown, also with brownish violet, pale maroon, olive, pale orange, pinkish ocher, and cream tones, lighter in age, smooth or roughened, matt, dry, greasy, or sticky, cracking in age; margin not striate, indistinctly striate, or slightly tuberculate-striate, turned under at first, entire, undulating or not; cap cuticle separable except at center. Lamellae narrowly attached, adnexed, adnate, slightly sinuate or dished, crowded, becoming broad, on av. L = 90–200 (n = 8), white, cream, pale ocher, dark cream,

yellowish, pale golden yellow, straw yellow, staining brownish near pileus margin, rarely anastomosing, forking or not, fragile or elastic; edges concolorous, occasionally dark brown. Lamellulae rare. Stipe 10–60 × 10–30 mm, equal to strongly clavate, central to slightly eccentric, white, cream, yellow, ocher, dark cream, orange, yellow, yellow brown, or pinkish ocher, occasionally lighter near apex and darker near base, grooved, rarely with bumps, hoary or smooth, greasy, matt; not staining when bruised. Context white, cream, dark cream, buff, pinkish ocher under cuticle; in stipe hard, spongy, or fragile, slightly watery grey in base, staining slightly brown, not hollow but a few cavities near base. Odor slightly to strongly fishy, especially in older specimens or when dried, but can be absent. Taste mild, bitter, slightly astringent (acidic or bitter), or absent.

Exsiccata: Pileus mottled with light and dark brown, grayish magenta, red brown, ocher, shiny. Lamellae light straw yellow to yellowish brown, yellow orange, yellow gray, gray brown, more brownish near pileus margin. Stipe whitish, off-white, yellow brown, or gray brown, with yellow brown and brown stains. Chemical reactions: Gum guaiac = blue green, brown green, brown, or brown gray; ferrous sulfate = strongly to moderately gray green; 2% phenol = slowly pinkish or brownish.

Micromorphology. Basidiospores yellow to yellow cream in print (IIId-IIIa), (7.1–7.8–8.5–9.2(–12.2) × (5.6–)6.2–6.7–7.3(–9.6) µm, broadly ellipsoid to ellipsoid, Q = (1.1–)1.2–1.3–1.3(–1.6); ornamentation of dense, isolated, amyloid, warts and spines, 0.5–1 µm high, with circular, angular bases ca. 1–1.5 µm in diameter, with some warts and spines fusing but individually recognizable, occasionally connected by fine lines and ridges, occasionally forming a subreticulum, rarely forming a complete reticulum;

apiculus truncate, rounded, or pointed, inamyloid; suprahilar plage medium to large, amyloid. Basidia (43.2–)49.9–59.9–70(–101.6) $\times$ (7.6–)9.1–10–10.9(–12) μm , clavate, subacute, occasionally asymmetric, 4-spored, some possibly 2-spored; basidiola clavate. Hymenial cystidia scattered, (61–)70.9–82.4–93.9(–114.3) $\times$ (7.4–)8.5–9.9–11.3(–12.7) μm , turbinate (spindle shaped), fusiform, rarely cylindrical, pedicellate, often mucronate with occasionally swollen or irregular 1–7 μm long appendage, thin-walled; contents granular, amorphous, crystalline, or absent, orange-brown in sulfovanillin. Pileipellis sharply delimited from underlying context; suprapellis weakly gelatinized, ca. 68–78 μm thick, composed of loosely to tightly interwoven, erect, septate hyphae, gradually transitioning to subpellis; subpellis, strongly gelatinized, ca. 50–76 μm thick, composed of densely interwoven, horizontally oriented hyphae with slightly swollen tips. Hyphal terminations cylindrical, clavate, or swollen, ca. 2.5–4.5 μm wide at apex, apically obtuse, occasionally forking, difficult to differentiate; contents lightly granular or absent. Pileocystidia near the pileus margin abundant 1–2 septate, clavate, cylindrical, fusiform, occasionally irregular, (81.3–)97.2–117.9–138.6(–165.1) $\times$ (2.3–)4.1–5.2–6.4(–9) μm , occasionally forking, appearing to arise from deep within the suprapellis; contents granular, gelatinous, or crystalline, no reaction or slightly graying in sulfovanillin. Pileocystidia near the pileus center sparse, shorter, usually lightly granular or devoid of contents, (53.3–)58.6–73.8–88.9(–101.6) $\times$ (3.8–)4.4–5.4–6.5(–7.6) μm .

Figure 15. *Russula subrubens*. A. with dwarf *Salix*, Loveland Pass, Colorado (DBG-F - 020848), photo Denver Botanical Garden. B. with *S. planifolia* and *S. glauca*, Beartooth Plateau, Wyoming (CLC 3597). C. with *S. reticulata* and *S. planifolia*, Beartooth Plateau, Montana (CLC 3588). D. with *S. reticulata*, Beartooth Plateau, Montana (CRN 139). E. with *S. planifolia*, Blue Lake, Colorado (CRN 187). F. with *S. glauca* on the Beartooth Plateau, Montana (CLC 3550). Scale bar = 2 cm.

North American Ecology. In the alpine zone in open, mesic, meadows with shrubby and dwarf willows including *Salix glauca*, *S. arctica*, and *S. planifolia*. Jul and Aug.

Material examined. USA. COLORADO. Boulder County, Blue Lake, with *Salix planifolia*, 24 Aug 2018, *C. Noffsinger CRN 185* (MONT); loc. cit., with *Salix planifolia*, 24 Aug 2018, *C. Noffsinger CRN 187* (MONT); Niwot Ridge, with *S. planifolia*, 20 Aug 2018, *C. Noffsinger CRN 174* (MONT); Clear Creek/Summit Counties, Front Range, Loveland Pass, 9 Aug 2000, *C. Cripps CLC 1488* (MONT); Pitkin/Lake Counties, Sawatch Range, Independence Pass, with dwarf *Salix*, 3 Aug 2000, *V. Evenson DBG-F-020848* (DBG); loc. cit., with *S. planifolia*, 6 Aug 2000, *C. Cripps CLC 1464* (MONT); loc. cit., with *S. planifolia* and *S. glauca*, 6 Aug 2000, *C. Cripps CLC 1466* (MONT); loc. cit., with shrubby and dwarf *Salix*, 6 Aug 2006, *V. Evenson DBG-F-023519* (DBG); San Juan County, San Juan Range, Black Bear Pass, with *S. arctica*, 11 Aug 2001, *C. Cripps CLC 1719* (MONT); Cinnamon Pass, with *S. arctica*, 27 July 2002, *C. Cripps CLC 1808* (MONT); Mineral Basin, with *S. arctica*, 7 Aug 2001, *C. Cripps CLC 1666* (MONT).

MONTANA. Carbon County, Beartooth Plateau, Highline Trailhead, with *S. reticulata* and *S. planifolia*, 8 Aug 2017, *C. Cripps CLC 3588* (MONT); Birch Site, with *S. glauca*, 17 Aug 2017, *C. Cripps CLC 3550* (MONT); loc. cit., with shrubby *Salix*, 19 Aug 1999, *C. Cripps CLC 1382* (MONT); WYOMING. Park County, Beartooth Plateau, Billings Fen site, with *Salix* species, 7 Aug 2018, *C. Noffsinger CRN 137* (MONT); Highline trailhead, with dwarf *Salix*, 8 Aug 1998, *C. Cripps CLC 1218* (MONT); loc. cit., 8 Aug 1998, *C. Cripps CLC 1219* (MONT); loc. cit., with *S. planifolia* and *S. reticulata*, 10 Aug 2018, *C. Noffsinger CRN 156* (MONT); Frozen lakes, with *S. planifolia* and *S. glauca*, 22 Aug 2017, *C. Cripps CLC 3597* (MONT); loc. cit., with *S. planifolia*, 22 Aug 2017, *C.*

Cripps CLC 3601 (MONT); loc. cit., with *S. reticulata*, 8 Aug 2018, *C. Noffsinger CRN 139* (MONT).

Observations. *Russula subrubens* is located in subsection *Xerampelina*, along with the well-known edible, *R. xerampelina*; species in this group are recognized by a red-brown pileus, strong fishy odor, and green reaction of the context to ferrous sulfate (Adamčík and Knudsen 2004). *Russula subrubens* was originally described as *Russula graveolens* var. *subrubens* from Elsehoved, Denmark and validated by Lange (1938, 1940); the variety was later raised to the species rank (Bon 1972). It was later reported from subalpine habitats with *Alnus* and *Salix* (Bon 1972, 1988). The similar *R. chamiteae*, was described from alpine regions of the Western European Alps (Kühner 1975), and this name became common in Arctic and alpine literature. The two species were synonymized (Knudsen and Stordal 1992) and *R. subrubens* is now considered to occur in both temperate and alpine habitats. Adamčík and Knudsen (2004) agreed with the synonymy based on morphology and noted that the association with *Salix* species appears to override habitat or elevation. They designated an epitype for *R. subrubens* from Western Jutland (Denmark) because the holotype consisted of only a spore print. Later, Adamčík et al. (2016b) examined subsection *Xerampelinae* and confirmed earlier conclusions using ITS sequence data because the holotype of *R. chamiteae* Kühner fell into the *R. subrubens* clade (ITS2 only). The presence of *R. subrubens* in Italy, Norway, France, Denmark, and Austria was molecularly confirmed. Our phylogenetic analysis produced a strongly supported clade that included sequences from western Jutland,

Denmark, the epitype locality of *R. subrubens* (Adamčík et al. 2016b), and several sequences from the Rocky Mountain alpine zone.

In the central and southern Rocky Mountains, *R. subrubens* is recognized by the features described for the subsection, plus an association primarily with shrubby *Salix* in open mesic meadows. However, the pileus color and diameter are highly variable in our collections; large specimens were adjacent to small ones (FIG. 15). Occasionally, the fishy odor is absent in fresh collections, but usually becomes apparent on drying. All our collections are from alpine habitats. The similar, *R. cf. pascua* also occurs in alpine habitats of the central and southern Rockies. The pileus of this species is dominated more by red and magenta colors, the spores are significantly longer and wider (av $9.1 \times 7 \mu\text{m}$) according to a two sample t-test (length p-value = < 0.001 , width p-value = < 0.001 based on 80 measurements from each species), the pileus is usually smaller, and it occurs more with dwarf willow, specifically *S. reticulata*. *Russula subrubens* can be separated from the closely related *R. pasuca*, which has inflated terminal cells of hyphae in the pileipellis near the pileus center that are lacking in *R. subrubens* (Adamčík et al. 2016b). Inflated terminal cells of the pileipellis near the pileus center were also absent in our collections. Phylogenetically *R. subrubens* is closely related to, but distinct from, our *R. cf. pascua* in the *Xerampelinae* clade (FIG. 3). The two species appear to overlap in habitat, but their host associations indicate that *R. subrubens* may be found more in open mesic meadows with *S. planifolia*; whereas, *R. cf. pascua* is usually found with *S. reticulata*. Kühner (1975) originally separated *R. chamiteae* (now synonymous with *R. subrubens*) from *R.*

pascua based on a weak reaction in sulfovanillin for the former and no reaction in the latter (Kühner 1975), which is consistent with our observations of these species.

Based on morphology, *R. subrubens* has been reported in Arctic and alpine areas of Denmark (Adamčík et al. 2016b), the Alps, Pyrenees, Carpathians (Adamčík and Knudsen 2004; Ronikier and Adamčík 2009; Adamčík et al. 2016b), Fennoscandia (Adamčík and Knudsen 2004; Adamčík et al. 2016b), Greenland (Adamčík and Knudsen 2004; Borgen et al. 2006), Slovakia (Adamčík 2001), and Poland (Adamčík and Knudsen 2004; Ronikier and Adamčík 2009), this does not include reports of *R. chamiteae*. This is the first report of *R. subrubens* under this name in the Rocky Mountains where it appears to be quite common in alpine regions of Colorado, Montana, and Wyoming. It has been reported under the name *R. cf. pascua* in the Rocky Mountains (Cripps and Horak 2008) and has likely been reported under other names (i.e. *R. chamiteae*). It is now confirmed to have an intercontinental distribution in Arctic and alpine habitats of North America and Europe.

Figure 16. Scanning electron microscope photographs of basidiospores from species in the *Russula* core clade and *Brevipes* clade. A. *Russula nana* (CLC 3619). B. *R. montana* holotype (MICH 12231). C. *R. laccata* (CLC 3617). D. *R. altaica* (CLC 1618). E. *R. laevis* (CLC 1690). Scale bar = 10 μ m.

Figure 17. Scanning electron microscope photographs of basidiospores from species in the *Russula* crown clade. A. *Russula saliceticola* (CLC 3616). B. *R. subrubens* (CLC 3550). C. *R. cf. pascua* (CLC 2274). D. *R. heterochroa* (CLC 1723). Scale bar = 10 μm .

Figure 18. Compound microscope photographs of basidiospores. A. *Russula nana* (CLC 3619). B. *R. montana* (MICH 12231). C. *R. laccata* (CLC 3617). D. *R. altaica* (CLC 1618). E. *R. saliceticola* (CRN 184). F. *R. subrubens* (CRN 156). G. *R. cf. pascua* (CRN 146). H. *R. purpureofusca* (CLC 3820). I. *R. heterochroa* (CLC 1723). H. *R. laevis* (CLC 1883). Scale bar = 10 μ m.

Figure 19. Maps of *Russula* species distributions Set 1. Collection locations confirmed in the phylogenetic analyses are indicated by a red dot. Longitude (lon) and latitude (lat) are indicated on the X and Y axes, respectively. A. *Russula cf. pascua*. B. *R. subrubens*. C. *R. saliceticola*. D. *R. purpureofusca*.

Figure 20. Maps of *Russula* species distributions Set 2. Collection locations confirmed in the phylogenetic analyses are indicated by a red dot. Longitude (lon) and latitude (lat) are indicated on the X and Y axes, respectively. A. *Russula laccata*. B. *R. nana*. C. *R. montana*. D. *R. altaica*.

Figure 21. Maps of *Russula* species distributions Set 3. Collection locations confirmed in the phylogenetic analyses are indicated by a red dot. Longitude (lon) and latitude (lat) are indicated on the X and Y axes, respectively. A. *Russula laevis*. B. *R. heterochroa*.

Key 1. *Russula* in the central and southern
Rocky Mountain alpine zone with *Salix*, *Dryas*,
and *Bistorta* (one subalpine with conifers)

1 Flesh dense. Pileus 40–80 mm, depressed with inrolled margin at first, dingy cream-colored or whitish, buff, rough; lamellae decurrent, dark cream at maturity; stipe short, dingy cream, solid; odor fruity; taste acrid; spores av $8.7 \times 7.2 \mu\text{m}$; primarily with *Dryas*.....***R. laevis***

1' Flesh fragile. Pileus convex, applanate, or indented, more highly colored; lamellae attached not decurrent.....2

2 Spore print white (possibly tinged yellowish). Lamellae primarily whitish at maturity or slightly yellow; odor faint, not distinctive; taste slightly to distinctly hot; spores fully reticulate or subreticulate.....3

2' Not with the above combination of features; spore print yellow; lamellae yellow at maturity; taste mild or slightly hot; spores with isolated warts, occasionally subreticulate.....5

3 Pileus 15–45 mm, dark magenta, maroon, purplish with almost blackish center; lamellae white at maturity; stipe white; odor faint; taste strongly acrid; spores av $8.1 \times 6.2 \mu\text{m}$; with dwarf *Salix* or other willows***R. laccata***

3' Pileus more red without dark center, fading to white or ocher in areas; with *Salix* or conifers.....4

4 With dwarf *Salix* in alpine areas. Pileus 12–35 mm, cherry red fading to white in areas; lamellae white at maturity; stipe white, 6–26 $\times$ 5–13 mm; odor indistinct; taste slightly to distinctly hot; spores av $7.7 \times 6.3 \mu\text{m}$***R. nana***

4' With conifers near treeline. Pileus larger, 35–70 mm, cherry red with ocher areas; lamellae white or with slight yellow tinge at maturity; stipe white, 20–50 $\times$ 10–20 mm; odor indistinct; taste hot; spores av $8.0 \times 6.3 \mu\text{m}$ ***R. montana***

5 Odor fishy; taste mild, rarely hot; bluish green reaction in FeSO_4 ; spores subreticulate, rarely fully reticulate.....6

5' Odor not fishy; taste mild to slightly hot; lacking a reaction to FeSO_4 ; spores mostly with isolated warts that can cluster or form branches, rarely subreticulate.....7

6 Pileus 10–80 mm, reddish brown, mottled with brown, red, copper, ocher, and hints of green possible, matt; lamellae cream to ocher; stipe white, cream, or yellow, occasionally with brown or pinkish areas, 10–60 $\times$ 10–30 mm; odor fishy; taste mild; spores av $8.5 \times 6.7 \mu\text{m}$; usually near *Salix planifolia*, reported elsewhere at or below treeline with *Salix*.....***R. subrubens***

6' Pileus 25–35 mm, with more red, dark red, and magenta colors, occasionally with hints of green; lamellae yellow to yellow brown; stipe white or off-white, with brownish yellow stains near base, slightly pink upon drying, 15–20 $\times$ 8–20 mm; odor fishy; taste

- mild or hot; spores av $9.1 \times 7 \mu\text{m}$; in alpine habitats, usually near *Salix reticulata*.....***R. cf. pascua***
- 7 Primarily with *Betula*, near treeline;** pileus 10–40 mm, primarily magenta, mottled with green, yellow, and pink; lamellae white, occasionally graying; stipe white, with or without pink blush, $20\text{--}30 \times 5\text{--}15 \text{ mm}$; odor indistinct; taste mild or bitter; spores composed completely of isolated warts, av $7.9 \times 6.1 \mu\text{m}$***R. altaica***
- 7' Primarily with *Salix* or *Dryas* in alpine habitats; taste mild or slowly acrid;** pileus deep magenta, dark reddish, occasionally yellow brown.....8
- 8 Odor lacking or indistinct. Stipe often with pink tint. Spores primarily with isolated warts, but fine lines and ridges possible.** Pileus 10–55 mm, deep red, grayish ruby, almost black in center; lamellae cream to pale yellowish, edge occasionally reddish near cap margin; stipe white, often with pink tint, $15\text{--}60 \times 5\text{--}25 \text{ mm}$; taste mild; spores av $8.9 \times 7 \mu\text{m}$; pileocystidia lacking lateral protrusions; with *Salix* species.....***R. saliceticola***
- 8' Odor fruity or of geraniums. Stipe lacking pink tints. Spores with isolated warts or spines;** pileocystidia with abundant lateral protrusions9
- 9 Spores on average $8.5 \times 7 \mu\text{m}$;** pileus 20–45 mm, reddish brown, deep magenta, or occasionally yellow-brown; lamellae cream to dark yellow-cream; stipe white, off-white, or yellow; odor indistinct or of geraniums; taste slowly hot; with *Salix* species.....***R. purpureofusca***
- 9' Spores larger, on average $10.5 \times 8.4 \mu\text{m}$;** pileus 20–40 mm, variable, magenta, ruby, reddish brown, ocher brown; lamellae white to yellow cream, thick; stipe white; odor fruity or faintly fishy; taste mild; with *Dryas octopetala*.....***R. heterochroa***

Discussion

This research confirmed eight species of *Russula* in the alpine zone, one from the alpine-subalpine transition zone and one from subalpine habitats in the Rocky Mountains from Montana to Colorado. Five of the *Russula* species from the Rocky Mountain alpine (*R. nana*, *R. cf. pascua*, *R. saliceticola*, *R. heterochroa*, and *R. purpureofusca*) can be referred to as primarily Arctic and alpine species because they have been collected only in these habitats near shrubby and dwarf *Salix* species or *Dryas* in the northern hemisphere. Three species, *R. laccata*, *R. laevis*, and *R. subrubens* were collected only in

alpine areas of the Rocky Mountains, mostly with *Salix*, in this study; however, all have been reported above and below treeline in Europe (Ortega and Esteve-Raventós 2001; Adamčík and Knudsen 2004; Adamčík et al. 2016b, 2019). Even in subalpine habitats, *R. subrubens* is believed to be strictly associated with *Salix* (Adamčík et al. 2016b); this may also be the case for *R. laccata*, which has been reported with *S. atrocinerea* below treeline (Ortega and Esteve-Raventós 2001). It is possible that *R. laccata*, *R. laevis*, and *R. subrubens* are also present in subalpine habitats in the Rockies, but none have been reported below treeline. *Russula* cf. *pascua* is a potential North American endemic, but more research is necessary to confirm this. *Russula altaica* is reported from the transition zone between alpine and subalpine habitats where it was associated with *Betula*; it was only collected at Blue Lake, Colorado. *Russula montana* was the only species identified that was first described from North America (Perigo Colorado, USA) (Shaffer 1975). In our analysis, *R. montana* was shown to have an intercontinental distribution in subalpine habitats where it associates with conifers. Most matching collections from Europe were originally identified as *R. grisescens*, which may be a synonym. This research adds first reports of six species (*R. altaica*, *R. heterochroa*, *R. purpureofusca*, *R. saliceticola*, and *R. subrubens*) for the Rocky Mountain alpine and two species (*R. heterochroa* and *R. purpureofusca*) for North America.

Our first hypothesis stated that the *Russula* species reported from the Rocky Mountain alpine will be the same as those reported in Arctic and alpine habitats of Europe, Asia, and Arctic Islands, based on molecular and morphological data, even though these would be disjunct populations. Our results indicate that all the species we

report from the Rocky Mountain alpine were originally described from Europe or Asia with one exception. *Russula* cf. *pascua* formed a strongly-supported monophyletic clade containing only collections from the Rocky Mountain alpine; therefore, it may be endemic to this region. However, if this species is found to be conspecific with *R. pascua*, then it too would have been originally described from Europe. In addition, we report *Russula montana*, which was originally described from Colorado where it is a known subalpine species with conifers (Shaffer 1975).

The second hypothesis stated that the *Russula* species present in the Rocky Mountain alpine will have large, intercontinental distributions similar to the Arctic and boreal species studied molecularly in Europe (Adamčík et al. 2019; Caboň et al. 2019). Our results confirmed that seven species of *Russula* have intercontinental distributions in Arctic and alpine habitats of North America and Europe or Asia, which confirms conclusions from earlier studies based on morphology (Lamoure et al. 1982; Knudsen and Borgen 1982; Borgen 1993; Elborne and Knudsen 1990; Adamčík and Knudsen 2004). Species molecularly confirmed to have large, intercontinental distributions in Arctic and alpine habitats are *R. nana*, *R. laccata*, *R. subrubens*, *R. saliceticola*, *R. purpureofusca*, and *R. laevis*. *Russula heterochroa* was identified based on morphological evidence alone due to the lack of availability of type or reference sequences for this species; but the collections studied formed a strongly-supported, monophyletic clade containing collections from Colorado, USA and Svalbard, indicating that it too has an intercontinental distribution. The collections identified as *R. cf. pascua* form a strongly-supported clade containing only collections from the Rocky Mountain

alpine; if this species is found to be conspecific with *R. pascua* it would also have an intercontinental distribution in Arctic and alpine habitats; if not it may be endemic to the Rocky Mountain alpine. The subalpine species *R. montana/grisescens* also appears to have an intercontinental distribution in subalpine and boreal habitats of North America and Europe. Collections were molecularly matched to the type for *R. montana* which has precedence (Shaffer 1975; Bazzicalupo et al. 2016). However, the type for *R. grisescens* was not available, so synonymy cannot be absolutely confirmed. North American collections of *R. altaica*, a transitional zone species that occurs with *Betula*, were matched to Singer's collection from the Altai Mountains (Singer originally described the species) (Singer 1951). Intercontinental distributions have also been confirmed for 44 other alpine species, in four ectomycorrhizal genera, found in the central and southern Rockies, even though these are disjunct populations. This includes 15 species of *Hebeloma* (Beker et al. 2010; Cripps et al. 2019), one *Cortinarius* (Peintner 2008), 23 species of *Inocybe* (Cripps et al. 2010; Larsson et al. 2014; Larsson et al. 2018; Cripps et al. 2019), and five species *Lactarius* (Barge et al. 2016; Cripps and Barge 2016). Therefore, large intercontinental distributions appear to be a trend in Arctic and alpine ectomycorrhizal genera and implies that species maintain large, intercontinental populations. This is in contrast with data from other habitats that show most ectomycorrhizal fungi have small geographic distributions (Bazzicalupo et al. 2019) and that spore dispersal from basidiocarps appears limited (Fischer et al. 2010). Although we do not have data to explain the large, intercontinental distributions found here for alpine species of *Russula* in the Rocky Mountains, we believe that one of the most parsimonious

explanation is that Arctic and alpine fungi are following their primary host, dwarf and shrubby species of *Salix*. This seems plausible considering that *Russula* species have the ability to follow their host in response to changes in climate (Looney et al. 2019, 2020). Other possible factors that could help explain intercontinental distributions of Arctic and alpine fungi include historical changes in glaciation that influence ectomycorrhizal communities and their host (Timling et al. 2012; Barge et al. 2016) or long-distance, transoceanic dispersal as maintaining large populations (Geml et al. 2012; Timling et al. 2014).

Our third hypothesis stated that the *Russula* species in the Rocky Mountains have independently colonized alpine habitats and do not form a monophyletic group. This research has confirmed that the *Russula* species in the Rocky Mountain alpine are in two distinct clades, seven in the *Russula* clade (*R. subgenus Russula*) and one in the *Brevipes* clade (*R. subgenus Brevipes*). Within *R. subgenus Russula*, no two species form a sister group. Therefore, the data suggest that *Russula* species in the Rocky Mountain alpine do not share a most recent common ancestor that is unique to this group. The molecular, morphological, and ecological data presented here indicate that the *Russula* species present in the Rocky Mountain alpine have distinct evolutionary backgrounds and colonization of alpine habitats appears to have happened independently in multiple *Russula* lineages. This result implies that the potential of *Russula* species to colonize alpine habitats is present in multiple lineages. Most of the Rocky Mountain alpine species have phylogenetically closely related relatives found in subalpine or boreal habitats. It is possible that the transition from subalpine to alpine habitats involved a host switch from

conifers to the hosts commonly found in alpine habitats (*Salix*, *Betula*, and *Dryas*) and the ability to survive in the harsh abiotic environmental conditions present in the alpine (colder temperatures, poor soil composition, etc.). Research has shown that host switching from Pinaceae to angiosperms is about 15 times more likely than in the opposite direction for *Russula* species and that host switching may drive species diversification (Looney et al. 2016), which indicates that certain *Russula* species could overcome this barrier. Looney et al. (2016) proposed orogenesis events as a possible mechanism to explain host switching from Pinaceae to angiosperms, which could lead to species diversification. This conclusion is fitting in the context of this study, which is concerned with alpine fungi whose evolutionary history was also likely shaped by orogenesis events. Another possibility is that alpine fungi and their close relatives were already associated with angiosperm hosts like *Salix* in subalpine and boreal zones and did not need to switch hosts to colonize alpine habitats, which may be the case for *R. subrubens* and *R. laccata* (Ortega and Esteve-Raventós 2001; Adamčík and Knudsen 2004; Adamčík et al. 2016b, 2019). Subalpine fungi are often reported to be associated with conifers even when *Salix* is present. Researchers need to report ectomycorrhizal plant hosts as accurately as possible and find creative ways to confirm host associations; however, this will be difficult in diverse temperate zones where many potential hosts exist.

Russula species are known to be one of the most abundant ectomycorrhizal associates of Arctic and alpine *Betula* (Deslippe and Simard 2011). *Russula* species have been reported to form ectomycorrhizal associations with *Betula nana* L., *B. glandulosa*,

and *B. pubescens* Ehrh. in Alaska, Canada, Fennoscandia, and Greenland (Miller et al. 1973; Miller et al. 1982b; De Groot et al. 1973; Elborne and Knudsen 1990; Deslippe et al. 2011; Deslippe and Simard 2011). *Betula* is rare in the Rocky Mountain alpine zone, and this study found only *R. altaica* with *Betula* shrubs at treeline. It is likely that there are more species of *Russula* that occur with *Betula* in the Rocky Mountain alpine zone that await discovery. Several species of *Russula* from treeline habitats in Alaska were found in association with *Betula*, including *R. cf. alpigenes*, *R. cf. sphagnophila*, *R. intermedia*, and *R. aff. vinosa*. It is likely that these species extend into the alpine where *Betula* occurs. These species were only collected a few times and are included in the phylogenetic trees produced in this study (FIGS. 2, 3, 4). A key to these red-capped *Russula* from Alaska, mostly with *Betula* at treeline, is included in the Addendum along with descriptions of each species.

Even though identification of *Russulas* to species can be difficult without molecular data, this work has confirmed some morphological trends in the genus that aid in identification. *Russula subrubens* and *R. cf. pascua* are in *R.* subsection *Xerampelinae* and have features consistent with this group (Adamčík and Knudsen 2004), including yellow spores, a fishy odor, a green reaction of the context to ferrous sulfate, and a mild taste. This combination of features is unique to the subsection and can be used for identification at this level; however, identification to species can be complex (see Adamčík et al. 2016b).

Rocky Mountain alpine species *R. nana* and *R. laccata* have reddish to maroon pilei, white reticulate spores, and an acrid taste, which is specific to these taxa when only

considering the species examined in this study. However, many other species with these features occur in the subalpine zone that are not fully understood. One, *R. montana*, was confirmed in this study; this species also has a reddish to maroon pileus, white reticulate spores, and an acrid taste. The well-known *R. emetica* that can also occur near treeline shares these features, and care is needed to delineate this species and other look-alikes in the transition zone (see Bazzicalupo et al. 2016).

Two species in the Rocky Mountain alpine zone, *R. saliceticola* and *R. purpureofusca*, typically have deep magenta pilei and a yellow spore print (although some collections of *R. purpureofusca* can have an olive-yellow pileus), and a non-fishy odor; these characters can be used to aid in identification, and these two species are separated based on microscopic characteristics (see species observations or key for identification to species).

One species, *R. laevis* in *R. subg. Brevipes*, occurs in the Rocky Mountain alpine and has a unique morphology compared to the other species studied. *Russula laevis* has a white to brown concave pileus, compact flesh, a white spore print, and an acrid taste, which together are diagnostic for *R. laevis* in the Rocky Mountain alpine. However, in the subalpine zone, many species in *R. subgenus Brevipes* including *R. brevipes*, *R. chloroides*, and *R. delica* also share these characteristics, although fruiting bodies are typically larger. However, one collection of small fruiting bodies from a treeline habitat in Alaska, turned out not to be *R. laevis*, highlighting that size is not always reliable. *Russula* subsection *Lactarioideae*, which contains these species, has been morphologically examined but has not been subjected to rigorous molecular phylogenetic

analysis (Buyck and Adamčík 2013). In our analysis of *R. subg. Brevipes* (FIG. 5) sequences representing the UNITE species hypotheses for *R. chloroides* (AF418605) and *R. delica* (UDB025023) were distinct from the Rocky Mountain alpine species *R. laevis*, as has been previously shown (Adamčík et al. 2019). The sequence representing the UNITE species hypothesis *R. delica* forms a clade by itself and BLAST search for similar sequences found only uncultured Russulaceae isolates that matched with a high Max Score. This is concerning, and warrants investigation due to the prevalence of sequences in public databases labeled *R. delica* that do not match the UNITE species hypothesis. *Russula delica* is known to encompass a “wide species concept” because 11 varieties have been described and there is some confusion regarding the interpretation of Fries’s (1838) original description of the species (Buyck and Adamčík 2013). The *R. chloroides* complex contains two strongly-supported clades with numerous collections labeled *R. chloroides*, *R. brevipes*, and *R. delica* from public databases (FIG. 5). Buyck and Adamčík (2013) indicated that the American *R. brevipes* is similar to the European *R. chloroides* based on morphology; however, any potential synonymy needs to be verified using type material. This research indicates that the *R. chloroides* complex, as defined here, contains two strongly-supported clades, both of which show intercontinental distributions. The distribution of these *Russula* species needs to be re-evaluated and results could cast doubt on the hypothesis suggesting that subalpine ectomycorrhizal species lack large, transatlantic distributions (Buyck and Hofstetter 2011).

There were a few trends that emerged in the spore morphology of *Russula* species in the Rocky Mountains. The three closely related species *R. montana*, *R. nana*, and *R.*

laccata all have spores with fully reticulated ornamentation (FIGS. 16, 18). *Russula subrubens* and *R. cf. pascua* in *Russula* subsection *Xerampelinae* both have partially reticulated spores with some isolated warts (FIGS. 17, 18). The same spore morphology is also present in *R. saliceticola*, which is found in the clade sister to *R.* subsection *Xerampelinae*. The remaining species (*R. altaica*, *R. heterochroa*, *R. laevis*, and *R. purpureofusca*) all have spores with primarily isolated warts (FIGS. 16, 17, 18) and these species are found in various other clades. The observed trends in spore ornamentation for closely related species indicate that spore ornamentation may be connected to species evolutionary history, at least at small scales. However, connecting the two would require ancestral character state reconstruction of a detailed, multi-locus, phylogenetic dataset including species from all major clades and habitats along with careful observations of spore morphology.

Identification of *Russula* species in western North America is challenging due to a lack of reliable information and expertise (Buyck 2007; Buyck et al. 2015). This research approached the genus *Russula* from an ecological perspective by focusing on species occurring above treeline with alpine host plants such as *Salix* and *Dryas*. This approach helped to mitigate some of the broader taxonomic issues, but other problems arose that are inherent to alpine research in the Rockies. The Rocky Mountain alpine is remote and difficult to access, making sampling challenging. In addition, the fruiting season is short, and basidiocarps are extremely small, making them difficult to find. Also, a dry, continental climate means potential for droughts and smoke from lower elevation fires, which can make collecting difficult. In some years, alpine fungi are virtually absent. The

high elevations are also prone to lightning storms and snow at any time of year. These issues make thorough sampling of alpine fungi in the Rocky Mountains an arduous task. Fortunately, this study had access to collections of *Russula* and other alpine fungi collected in the Rockies over the last 20 years. Another problem is that much of the literature published on Arctic and alpine *Russula* is written in a variety of languages including French (Favre 1955; Romagnesi 1967; Kühner 1975; Bon 1993, 2000), Catalan (Bon and Ballarà 1996), Italian (Jamoni 1995; Sarnari 1998–2005), and Danish (Borgen 1993). This literature can be easily translated using online resources, but these iterations are not perfect, and taxonomists rely on small differences among taxa that can be lost in translation.

On a broader scale, the diversity of *Russula* has not been adequately addressed in western North America. This research adds first reports of six species (*R. altaica*, *R. heterochroa*, *R. purpureofusca*, *R. saliceticola*, and *R. subrubens*) for the Rocky Mountain alpine, two of which (*R. heterochroa* and *R. purpureofusca*) are also first reports for North America. Much remains to be discovered for *Russula* in the conifer and deciduous forests at lower elevations. The genus *Russula* has been found to be most diverse in temperate regions (Looney et al. 2016), and these regions have not been adequately sampled, particularly in western North America. We produced the broad phylogeny (FIG. 2) in order to understand the placement of Rocky Mountain alpine species in the larger infrageneric classification of *Russula*. However, a more thorough sampling of *Russula* species diversity in temperate regions will influence our understanding of ecological, biogeographical, and evolutionary trends in the genus,

which would likely extend to alpine species. It is worth noting that five of the species we found in the Rocky Mountain alpine are located in the *Russula* crown clade, which also contains the highest species diversity in the genus, including many tropical taxa (Looney et al. 2016).

Research has indicated that morphological studies alone often fail to recognize the true diversity of *Russula* in a region (Buyck 2007), which also appears to be the case for *Russula* in the Rocky Mountain alpine. Previous morphological research discovered four species of *Russula* in the Rocky Mountain alpine (Moser and McKnight 1987; Cripps and Horak 2008), while this research doubled the number of species known in the region. Results emphasize the importance of detailed systematic studies that combine morphological, molecular, and ecological data. Fortunately, this approach is already being used for *Russula* (Adamčík et al. 2016b, 2019; Buyck et al. 2018; Caboň et al. 2019; Buyck et al. 2020) and is further supported by recent research that found a loose connection between morphological character states and species boundaries within *Russula* (Bazzicalupo et al. 2017).

Some general trends in this study also emerged when comparing our molecular and phylogenetic data to other studies and public databases. Based on our phylogenetic analyses the ITS region alone was sufficient at separating and supporting the species studied here and no major changes in species clades were observed when adding the *RPB2* gene region to the analysis, although the support and topology of internal nodes varied slightly. The *RBP2* gene region was also more difficult to successfully sequence in the *Russula* studied here. All collections for which the ITS region were successfully

sequenced, the *RPB2* region was also attempted, but 55 *RPB2* sequences could not be obtained (40% less than for the ITS). The ITS-*RPB2* gene combination was not sufficient for resolving deep phylogenetic relationships in the broad phylogenetic analysis of *Russula* (FIG. 2), mainly at the subgeneric level, even when several reference sequences contained additional loci (LSU and *RPB1*). This result is also evident in earlier studies using only one or a few gene regions where support is lacking for deep nodes (Miller and Buyck 2002; Buyck et al. 2008), stressing the importance of complete, multi-locus phylogenies when studying the evolutionary relationships within *Russula*, as was done in Looney et al. (2016). Our work uncovered some misidentifications in public databases such as GenBank and UNITE, most notably with *R. nana* (see observations for *R. nana*), but many other errors were found that could not be included here. Given that the morphology in *Russula* is complex (Romagnesi 1967; Singer 1986; Sarnari 1998–2005), some types are difficult or impossible to obtain, and sequence-based identification is known to be insufficient and difficult (Hofstetter et al. 2019), identification based on sequences in public databases is unlikely to provide confident results until the quality of these databases can be improved. Therefore, we stress the recommendations outlined in (Hofstetter et al. 2019), which focus on the importance of proper sequence annotation during submission, to increase the value of sequence-based identification, especially within the genus *Russula*.

Many of the species of *Russula* found in the Rocky Mountain alpine are morphologically and molecularly similar, with many closely related species being more than 97% similar in ITS sequences. For example, when comparing ITS sequence

similarity for the species included in our phylogenetic analysis, *R. nana* and *R. montana* are approximately 98.6% similar, but have consistent molecular differences; *R. laccata* and *R. atrorubens* are approximately 98.3% similar; *R. altaica* is approximately 98.2% similar to *R. gracillima*; *R. saliceticola* is approximately 98.2% similar to *R. nitida*; *R. laevis* is approximately 98.9% similar to *R. cf. brevipes*; and species in the *R. clavipes* complex range from 98.9–99.4% in similarity. The other three species studied here (*R. heterochroa*, *R. purpureofusca*, and *R. subrubens*) are all 97% similar or less in the ITS region when compared to closely related species included in our phylogenetic analyses. The low genetic variation found here is similar to what was observed in closely related alpine species of *Lactarius* from the Rocky Mountain alpine (Barge et al. 2016) and casts doubt on the effectiveness of 97% sequence similarity cutoffs for species delineation in environmental studies (e.g. Geml et al. 2012; Timling et al. 2012, 2014), especially for alpine members of the Russulaceae.

Environments like the Arctic and alpine are seeing some of the most severe negative impacts of climate change. As shrub expansion into these cold-dominated habitats continues in conjunction with changes in climate, the composition of ectomycorrhizal fungal communities will begin to shift. The functioning of individual ectomycorrhizal species is not redundant, with various species, even within the same genus, showing preferences for different forms of nitrogen (Antibus et al. 2018), indicating that the shift of individual species could have impacts on overall ecosystem function. These conclusions emphasize the importance of continuing research aimed at understanding the diversity and function of Arctic and alpine ectomycorrhizal fungi prior

to large environmental shifts. A deeper taxonomic understanding of Arctic and alpine fungi will increase the value of models aimed at understanding the evolution of Arctic and alpine communities (Gardes and Dahlberg 1996). This research increased our knowledge of *Russula* diversity in alpine habitats of the Rocky Mountains, adding value to models that use members of the Russulaceae to understand ecosystem function and diversification of ectomycorrhizal fungi in all habitats (Looney et. al. 2018).

Addendum – Alaskan species of *Russula*

Several collections in the phylogenetic analyses are from subalpine, treeline, and alpine regions of Alaska (TABLE 5; FIGS 2, 3, 4). Initially, we believed that our *Russula* collections from Alaska would extend the distribution of some species described from the central and southern Rocky Mountains, and thus would be included in the main study. Other research has reported *R. xerampelina* var. *pascua* (*R. pascua*) and *Russula emetica* var. *alpestris* (possibly synonymous with *R. nana*) based on morphology in Arctic areas of Alaska with *Salix* (Miller et al. 1973). These are species we report from Colorado, Montana, and Wyoming. It seems highly likely that some of the *Russula* species from alpine areas of the central and southern Rockies would also occur in alpine areas of Alaska. However, our research confirmed only *R. purpureofusca* in alpine areas of both Colorado and Alaska where it occurs with *Salix* and *Dryas*.

Our other collections from Alaska were morphologically and molecularly distinct from those in the central and southern Rocky Mountains. This is likely due to minimal and biased sampling in Alaska. *Russula* cf. *alpigenes*, which is found near *Salix* and *Dryas*, is reported from Alaska but not Colorado, Montana, or Wyoming. If confirmed, this would be the first report of this rare species for North America. We report two collections of *R. intermedia*, and one each of *R. cf. sphagnophila* and *R. aff. vinosa* with *Betula* at treeline in Alaska. *Betula* is rare in our main collecting areas, and only *R. altaica* is reported with *Betula* from one area of Colorado. Thus, *Russula* associated with *Betula* are under-sampled, but they are included here, because they should be considered when collecting near *Betula* in the central and southern Rockies.

All of these species' clades were resolved as monophyletic and with strong-support in both phylogenetic analyses (FIGS. 2, 3, 4). There is some taxonomic confusion regarding *R. cf. alpigenes*, which clusters phylogenetically with sequences previously identified by others as *R. nana* and is sister to *R. betularum* (FIG. 4); we believe these sequences are incorrectly identified (see observations under *R. nana*). All of the species from Alaska were consistently resolved in *R.* subgenus *Russula* in the phylogenetic analyses (FIG. 2). Four species were consistently resolved in the *Russula* crown clade (FIG. 3) and one species, *R. cf. alpigenes*, was consistently resolved in the *Russula* core clade (FIG. 4).

Previous research on *Russula* suggests the genus is diverse in Alaska (Geml et al. 2010; Geml and Taylor 2013) and is dominant in moist tussock and dry tundra in Arctic Alaska (Morgado et al. 2015). However, *Russula* is seriously under-sampled and its diversity is poorly known in Alaska. The species described here provide morphological and molecular information regarding just a few of the undoubtedly numerous *Russula* in the region. A key is provided for their identification, mainly including *Russula* with *Betula* near treeline, and descriptions are provided for each species.

Key 2. Red-capped *Russula* from Alaska,
mostly with *Betula* at treeline

- 1 Spore print white;** Pileus ruby red, depressed in center or not; lamellae white at maturity; stipe white with pinkish tints, especially after drying; odor fruity; taste mild to acid; spores on average $8.9 \times 7 \mu\text{m}$, reticulate; with *Salix* and *Dryas* in the low alpine.....*R. cf. alpigenes*
- 1' Not with the above combination of features; spore print light to dark yellow;** lamellae yellow at maturity, rarely white; taste mild or slightly hot; spores with isolated warts; with *Betula* or other hosts, one species with *Salix*.....2

- 2 Taste strongly acrid, occasionally delayed; with *Salix*;** pileus reddish brown, deep magenta, or occasionally yellow-brown; lamellae cream to dark yellow-cream; stipe white, off-white, or yellow; odor indistinct or of geraniums; taste slowly hot; spores on average $8.5 \times 7 \mu\text{m}$***R. purpureofusca*** (see Chapter 2)
- 2' Taste usually mild**.....3
- 3** Pileus reddish maroon, edges paling to whitish, dished in center, striate almost to center, fragile, thin-fleshed; lamellae white to cream with a pink tinge; stipe clavate, white, with pinkish rosy tint at apex, especially in age; odor absent; spores on average $8.7 \times 6.8 \mu\text{m}$, with *Betula nana*, hemlock, and spruce.....***R. cf. sphagnophila***
- 3'** Pileus more brown, orange, or deep red, more thick-fleshed, robust, less striate.....4
- 4 Spores usually $< 8.5 \mu\text{m}$ long, on average $8.0 \times 6.9 \mu\text{m}$;** Pileus red, reddish orange, salmon, mottled; lamellae white then cream or golden; stipe clavate, robust; odor absent or fruity; taste bitter; primarily with *Betula* but occasionally near *Dryas* and *Salix* in subalpine habitats.....***R. intermedia***
- 4' Spores usually $> 8.5 \mu\text{m}$ long;** primarily with deciduous hosts including *Betula nana*, also with hemlock and spruce; Pileus bright red with center fading to ocher then gray; lamellae white, a bit cream in age; stipe long ($50\text{--}60 \times 15\text{--}20 \text{ mm}$), white and gray; spores on average $8.7 \times 7.1 \mu\text{m}$ ***R. aff. vinosa***

Taxonomy of Alaskan Species

Russula cf. alpigenes (Bon) Bon

FIG. 22

Bull. trimest. Féd. Mycol. Dauphiné-Savoie 32(no. 128):20 1993

Macromorphology. Pileus 20–60 mm wide, shallow convex almost flat, some dished in center, deep ruby red to almost black in center, smooth, greasy (viscid), not striate; margin turned down, entire. Lamellae narrow adnate, narrow to broad, crowded, L = 100 (n = 1), white, then cream, edges concolorous, staining pink near pileus margin or not. Lamellulae absent. Stipe 25–60 $\times$ 8–18 mm, long clavate, clavate, but narrower in middle, white, but with a few pinkish stains in age, smooth. Context white, solid; pink under cap cuticle. Odor fruity-sweet or absent. Taste slightly acrid or not, bitter, or mild. Chemical reactions: not available.

Micromorphology. Basidiospores no spore print obtained, but reported as white in print (Bon 1993), $(7.6-8.3-8.9-9.5(-10.6) \times (6.1-6.6-7-7.4(-8.2) \mu\text{m}$, broadly ellipsoid to ellipsoid, $Q = (1.1-1.2-1.3-1.4(-1.5)$; ornamentation of amyloid warts and spines, $<0.5-0.5 \mu\text{m}$ high, occasionally fusing, connected by thin line connections and occasionally ridges forming a reticulum, rarely isolated, clustered, branched or subreticulate; apiculus truncate, inamyloid; suprahilar plage small to medium, weakly amyloid, difficult to observe. Basidia $(45.7-49.2-53.7-58.3(-63.5) \times (8.9-9.8-10.5-11.2(-11.4) \mu\text{m}$, clavate-pedicellate, 4-spored, sterigma swollen and finger-like; contents gelatinous and granular, lipid drops occasionally present, no reaction in sulfovanillin; basidiola clavate, granular, often filled with lipid drops. Hymenial cystidia $(48.3-53.7-66.5-79.4(-101.6) \times (7.6-7.6-8.5-9.5(-10.2) \mu\text{m}$, fusiform, cylindrical, pedicellate, rarely lanceolate, often mucronate, with $1.3-7.6 \mu\text{m}$ long appendage; contents gelatinous, granular, and crystalline, staining dark red-brown to black in sulfovanillin. Pilepellis sharply delimited from underlying context; weakly gelatinized, ca. $63.5-114 \mu\text{m}$ deep suprapellis composed of loosely intertangled, erect, hyphae and pileocystidia, well differentiated from subpellis; strongly gelatinized ca. $38.1-101.6 \mu\text{m}$ deep subpellis composed of densely intertangled, horizontally oriented, hard to differentiate hyphae. Hyphal terminations cylindrical, thin-walled, septate, occasionally tapering at apex, occasionally forking, terminal cells ca. $2-7.6 \mu\text{m}$ wide, apically obtuse; devoid of contents or lightly granular. Pileocystidia near the pileus margin abundant, cylindrical or clavate, $(53.3-68-108.6-149.1(-203.2) \times (5.1-5.1-5.9-6.8(-7.6) \mu\text{m}$, occasionally forking; contents granular, blackening in sulfovanillin. Pileocystidia near the pileus

center shorter, occasionally moniliform, more septate, occasionally tapering near apex but still apically obtuse, (63.5–)74.9–91.9–109(–114.3) × (5.1–)5.4–6.6–7.8(–8.9) μm; contents similar.

Figure 22. *Russula cf. alpigenes*. A. with *Salix* and *Dryas*, Girdwood, Alaska (CLC 3822B). B. with *Salix*, Girdwood, Alaska (CLC 3821). Photos by Noah Siegel. Scale bars = 2 cm.

North American Ecology. Found in the transition zone between subalpine and alpine habitats in Alaska with *Dryas* and mixed *Salix*. Aug.

Material examined. USA. ALASKA. Anchorage County, Girdwood, with *Salix*, 22 Aug 2018, *C. Cripps CLC 3821* (MONT); loc. cit., with *Salix* and *Dryas*, 22 Aug 2018, *C. Cripps CLC 3822B* (MONT).

Observations. *Russula fragilis* var. *alpigenes* was originally described by Bon in 1990 from the European Alps with *Salix herbacea*, shortly after he raised *R. alpigenes* to the species rank (Bon 1993). Our species matches Bon's (1993) description. Our collections form a strongly-supported clade with three accessions incorrectly labeled *R. nana* (UDB015077, UDB016029, and KX579809, FIG. 4) see observations under *R. nana* and discussion in Chapter 2. This clade is sister to *R. betularum*.

***Russula intermedia* P. Karst.**

FIG. 23

Meddelanden af Societas pro Fauna et Flora Fennica 16:38 1888

= *Russula intermedia* f. *mesospora* (Singer) Bidaud, Moënné-Locc. & Reumaux, in Reumaux, Bidaud & Moënné-Loccoz, Russules Rares ou Méconnues (Marlioz):285 1996

= *Russula lundellii* Singer, Lilloa 22:719 1951 (1949)

= *Russula mesospora* Singer, Bull. trimest. Soc. mycol. Fr. 54:161 1938

= *Russula pulcherrima* S. Lundell & Jul. Schäff., Annls mycol. 36(4):31 1938

= *Russula aurantiolutea* Kauffman Rep. Michigan Acad. Sci. 11:81. 1909

Macromorphology. Pileus 30–65 mm wide, convex to shallow convex, deep red, reddish brown, orange brown, but also mottled with pink, ocher, cream, and yellow tones, smooth, greasy, viscid, or sticky; margin not striate, turning down, entire; cuticle thick, hardly peeling near margin. Lamellae narrowly attached, adnate, crowded, $L=100$ ($n = 2$), white then cream, golden yellow, with mostly concolorous edges, but slightly grayish in one collection, occasionally forking. Stipe $20\text{--}50 \times 10\text{--}20$ mm at apex, $10\text{--}25$ mm at base, clavate, white, smooth, matt, without graying. Context white and solid. Odor absent or fruity. Taste mild, but bitter. Exsiccata: Pileus uniformly violet brown or mottled with violet brown, yellow, orange, and brown, ocher in center. Lamellae light yellow brown, ocher-yellow, lighter yellow near gill margin with occasional hints of gray. Stipe white, yellow brown, light brown, brown, with more brown stains near base. Chemical reactions: Not available.

Micromorphology. Basidiospores no print obtained (see observations), $(7.1\text{--})7.5\text{--}8.0\text{--}8.5(-9.2) \times (6.1\text{--})6.4\text{--}6.9\text{--}7.3(-7.6)$ μm , subglobose to broadly ellipsoid, $Q = (1.1\text{--})1.1\text{--}1.2\text{--}1.2(-1.3)$; ornamentation of medium to high density, primarily of isolated, amyloid warts, <0.5 μm high, warts often fusing but still individually recognized, occasionally branched or subreticulate; apiculus inamyloid, truncate; suprhilar plage small to large, amyloid. Basidia $(45.7\text{--})51.5\text{--}59.4\text{--}67.4(-81.3) \times (8.9\text{--})9.6\text{--}10.4\text{--}11.2(-12.2)$ μm , clavate-pedicellate, 4-spored, some possibly 2-spored; contents granular, gelatinous, or absent, lipid drops present, vibrant light yellow orange to bright red in sulfovanillin, contents not staining; basidiola clavate, usually occasionally filled with lipid drops and granular contents. Hymenial cystidia $(58.4\text{--})66.7\text{--}84.3\text{--}102(-122) \times (6.4\text{--})$

)8.2–10.1–12.0(–12.7) μm , fusiform, clavate, or irregular, rarely with tiers gradually decreasing in size near apex, typically pedicellate, often mucronate, with 2.5–15.2 μm long appendage; contents granular, gelatinous, and crystalline, staining black in sulfovanillin. Pileipellis sharply delimited from the underlying context; suprapellis well-defined, weakly gelatinized, ca. 50–76 μm deep, composed of interwoven and erect hyphae and pileocystidia; subpellis gelatinized, ca. 127–500 μm deep, composed of tightly interwoven, hard to differentiate, horizontally oriented hyphae. Hyphal terminations swollen, forking, or deformed, flexuous, septate; terminal cells ca. 3 μm wide, apically obtuse or subacute. Pileocystidia near the pileus margin with 0–3 septa, cylindrical, slightly or strongly clavate, or tapering, occasionally with visible cell wall 1–2 μm thick, rarely forking, similar to hyphae but containing contents, (68.6–)85.6–139–192.4(–254) $\times$ (2.5–)4–5.1–6.3(–8.9) μm ; contents amorphous, granular, irregular, and gelatinous, or absent, difficult to measure, granular contents staining red-brown in sulfovanillin. Pileocystidia near pileus center similar in shape to those at margin, but thinner, with more septa (2–4), and possibly less abundant, (73.7–)103.3–130.1–157(–170.2) $\times$ (3.8–)3.9–4.7–5.4(–6.4).

Figure 23. *Russula cf. intermedia*. A. with *Dryas*, Girdwood, Alaska (CLC 3822). B. with *Dryas* and *Salix*, Girdwood, Alaska (CLC 3784). Photos Noah Siegel. Scale bar = 2 cm.

North American Ecology. Found in the transition zone between subalpine and alpine habitats in Alaska with *Betula*, *Dryas*, and *Salix*. Aug.

Material examined. USA. ALASKA. Anchorage County, Girdwood, Crow Pass, with *Dryas* and *Salix*, 9 Aug 2011, C. Cripps CLC 2759 (MONT); with *Dryas*, 22 Aug 2018, C. Cripps CLC 3822 (MONT); Municipality of Anchorage, Flattop Mountain, with *Dryas* and *Salix*, 20 Aug 2018, C. Cripps CLC 3784 (MONT).

Observations. *Russula intermedia* Karsten was originally described from Finland (Karsten 1888); Karsten's second collection, from a forested area near birch, was later designated as a neotype (Ruotsalainen and Vauras 1994). The species is common in forests of Finland where it occurs with *Betula* and *Picea abies* but is rare in northern areas. It is also reported from Denmark, Sweden, and Norway with *Betula*. Ruotsalainen and Vauras (1994) found the well-established species *R. lundellii* Singer (Singer 1951) to be the same taxon and synonymized the names, although Sarnari (1998–2005) does not agree with this synonymy. Under the name *R. lundellii*, the species also has been reported from Germany, France, Spain, Belgium, Estonia and Iceland. Ruotsalainen and Vauras (1994) also synonymized the North American species *R. aurantiolutea* Kauffman (Shaffer 1970) with *R. intermedia*, after examining MICH collections. The species has been reported from Eastern and Western U.S. and Canada under this name. Thus, *R. intermedia* in the broad sense appears to have a wide intercontinental range, primarily in montane to subalpine habitats with *Betula*.

Our *R. intermedia* collections are all from Alaska, and are characterized by a red, red-brown, or orange-brown pileus mottled with pink, ocher, and yellow tones, a hardly

peeling cuticle, yellow lamellae and spores, a white stipe, fruity odor, mild but bitter taste, subglobose to broadly ellipsoid spores with isolated warts ($8.0 \times 6.9 \mu\text{m}$), commonly with thin, cylindrical pileocystidia, and in association with *Betula* or *Dryas*. Our description matches that for *R. intermedia* (Ruotsalainen and Vauras 1994) and that for *R. lundellii* (Sarnari 1998–2005). The pileus color is noted as variable, ranging from red, reddish orange, orange yellow, to yellow brown in various descriptions that could explain some of the taxonomic confusion. A pink tint on the stipe is sometimes noted but was absent in our collections. Also, an acrid taste was not reported in our specimens, but they were bitter and perhaps not chewed long enough for acrid flavors to develop. The Alaskan collections were from just below or just above treeline with *Betula*, *Dryas*, and *Salix* in the vicinity.

Phylogenetically our three collections form a strongly-supported clade with an *R. intermedia* collection from Norway (KU928147, FIG. 3), the type country, and one from Finland (JV 32189F) morphologically identified as *R. intermedia* by Jukka Vauras. Phylogenetic analyses produced by Adamčík et al. (2016a) also grouped this reference collection with two other collections from Estonia (UDB011296 and UDB015997).

Russula cf. sphagnophila Kauffman

FIG. 24

Report Mich. Acad. Sci. 11:86 1909

Macromorphology. Pileus 20–35 mm wide, applanate uplifted or slightly infundibuliform, reddish maroon with blackish center, much lighter red toward margin, bit viscid or just wet, striate almost to center, evenly pleated, edge paling to whitish; margin a bit crenate. Lamellae narrow attached, a bit separated, L = 30–40 (n = 1), white

to cream, tinged pinkish in age. Stipe 35–50 × 4–5 mm at apex to 13 mm at base, clavate, white, smooth with pinkish rosy tinge at apex, especially in age. Odor absent. Exsiccata: Pileus dark magenta, almost black in center, much lighter toward margin; lamellae light yellow browning in age; stipe ranging from light brown going toward dark brown in age, with tints of magenta. Chemical reactions: Not available.

Micromorphology. Basidiospores no spore print obtained, reported as cream (Woo 1989), (7.6–)7.9–8.7–9.5(–11.2) × (6.1–)6.4–6.8–7.2(–7.6) μm, broadly ellipsoid to ellipsoid, $Q = (1.2–)1.2–1.3–1.4(–1.5)$; ornamentation of prominent, cylindrical, amyloid warts, ca. 1 μm high, some warts merging forming larger obscure warts, not forming a reticulum, but with a few thin lines connecting elements; apiculus tapering to a truncate end, inamyloid; suprahilar plage relatively large, weakly to moderately amyloid. Basidia (35.6–)35.9–41.7–47.4(–55.9) × (10.2–)10.2–11.1–11.9(–12.7) μm, clavate, some very swollen, 4-spored; basidiola clavate. Hymenial cystidia (53.3–)60.1–67.6–75.1(–76.2) × (5.1–)7–8.9–10.8(–11.4) μm, fusiform, pedicellate, mucronate, with long, ca. 10.2–12.7 μm appendage with raised granular or crystalline structures; filled with lipid drops, contents granular or crystalline. Pileocystidia near pileus margin clavate, occasionally septate, forking below a septa, (43.2–)47.9–72.9–98(–114.3) × (3.8–)4.8–5.8–6.7 μm; contents granular, crystalline, or amorphous.

Figure 24. *Russula* cf. *sphagnophila* with *Betula nana*, Girdwood, Alaska (CLC 3779), photo Noah Siegel. Scale bar = 2 cm.

North American Ecology. Found in the transition zone between subalpine and alpine habitats in Alaska with *Betula nana*, near *Tsuga* and *Picea*. Aug.

Material examined. USA. ALASKA. Anchorage County, Girdwood, Crow Pass Road, with *Betula nana*, *Tsuga*, and *Picea*, 19 Aug 2018, C. Cripps CLC 3779 (MONT).

Observations. *Russula sphagnophila* was originally described by Kauffman in 1909 from Cold Spring Harbor, Michigan. Kauffman described it as a fragile species with a 20–45 mm wide, rosy-purple to olive-brown pileus, with a raised margin; white to buff lamellae; and a 40–50 × 7–12 mm, fragile, stipe. Phylogenetically our collection forms a strongly-supported clade with a collection identified as *R. sphagnophila* by Singer from

Russia (MICH 256930, FIG. 3). This clade forms a polytomy with a collection of *R. nitida* (KU205269) and the weakly-supported *R. saliceticola* clade. At this time, we elect to call our collection *R. cf. sphagnophila* because it clusters phylogenetically with Singers collection and its morphology matches that of Kauffman's original description, with the exception of olive-brown coloration in the pileus.

Russula aff. vinosa Lindblad

FIG. 25

Svampbok: 67 1901

Macromorphology. Pileus 50–60 mm wide, shallow convex, almost flat, sunken in center, bright cherry red, center paling first ocher then grayish, white, smooth, bit viscid, sticky; margin down, faintly striate. Lamellae narrowly attached, narrowly crowded, L = 120 (n = 1), white, maybe a bit cream in age. Lamellulae absent. Stipe 50–60 × 15–20 mm, slightly enlarged at base, white, bit graying, smooth, greasy-dry. Odor a bit fruity. Taste not hot or with a tiny tingle. Exsiccata: Pileus maroon, red brown, red, orange brown, occasionally ocher in center. Lamellae cream, ocher, with grayish and brown tints. Stipe white with slight yellow, brown, or gray tints. Chemical reactions: Not available.

Micromorphology. Basidiospores no spore print obtained, (8.2–)8.3–8.7–9.1(–9.2) × (6.6–)6.9–7.1–7.4(–7.6) μm, broadly ellipsoid, Q = (1.1–)1.2–1.2–1.3(–1.3); ornamentation of dense, isolated warts, occasionally merging, with no reticulation; apiculus truncate, inamyloid; suprahilar plage small to large, amyloid. Basidia (48.3–)49.7–52.8–56(–56) × (10.2–)10.5–11.5–12.5(–12.7) μm, clavate, pedicellate, 4-spored;

basidiola clavate. Hymenial cystidia (71.1–)75–81–87.2(–88.9) $\times$ (8.9–)9–9.7–10.3 μm , clavate, weakly fusiform, rarely mucronate, with small, ca. 2.5 μm long appendage; contents granular and crystalline. Pileocystidia near pileus margin abundant, cylindrical, flexuous, septate, forking often, sometimes multiple times, (53.3–)59.2–89.4–119.6(–152.4) $\times$ (2.5–)2.6–3.4–4.3(–5) μm ; devoid of contents.

Figure 25. *Russula* aff. *vinosa* with *Betula nana*, Girdwood, Alaska (CLC 3778), photo Noah Siegel. Scale bar = 2 cm.

North American Ecology. Found in the transition zone between subalpine and alpine habitats in Alaska with *Betula nana*, near *Tsuga* and *Picea*. Aug.

Material examined. USA. ALASKA. Anchorage County, Girdwood, Crow Pass Road, with *Betula nana*, *Tsuga*, and *Picea*, 19 Aug 2018, C. Cripps CLC 3778 (MONT).

Observations. *Russula vinosa* was originally described by Lindblad in 1901. Our collection forms a strongly-supported clade with another collection identified as *R. vinosa* (AY061724, FIG. 3) by Miller and Buyck (2002). Our collections match the habitat and general morphology of this species; therefore, we elect to call our species *R. aff. vinosa*.

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APPENDICES

APPENDIX A

C-TAB EXTRACTION PROTOCOL, WITH LAB NOTES

CTAB DNA Extraction Protocol from Nguyen et al. (2013)

Grind tissue in liquid N with a pinch of fine beads (glass beads 50–100 microns) using a mortar and pestle. Harvest the powder into 2 ml screw cap tubes.

1. Add **500 µl 2% CTAB** extraction buffer, a dash of **2% PVP-40**, and **2.5 µl β-mercaptoethanol** to freshly ground tissue. Mix well.

2x CTAB buffer and 2% PVP-40 can be mixed in advance and stored at room temperature. Upon using, mix with appropriate amount of β-mercaptoethanol. Add β-mercaptoethanol under a fume hood.

2. Incubate at 65 °C for 30 minutes, shake sample every 10 minutes.

For difficult or poorly preserved samples, incubate for at least 1 hour.

3. Add **500 µl isoamyl-chloroform**, shake well and shake on the Nutator for 20 minutes, invert tube occasionally.

Phenol-isoamyl-chloroform can also be used at this step.

4. Spin down at max speed for 5 minutes.

5. Transfer the top phase to a fresh tube and repeat steps 3 and 4 if the top phase is disturbed.

6. Add **15 µl 5M sodium acetate** and **500 µl ice-cold isopropanol**. Gently mix the sample.

Any acetate salt can be used for this step. Cold incubation from -20°C to -80°C for 10 minutes is optional. You can store in -80°C overnight to increase yield. This step causes the negatively charged DNA to clump at the bottom of the tube.

7. Spin down 3 minutes at max speed. Discard isopropanol by pipetting it out of the tube, being careful not to lose the pellet.

Adding acetate salt usually causes the pellet to be goopy.

8. Wash the pellet with **500 µl ice-cold 70% ethanol** by filling the same tube, make sure the pellet is loose and has been washed throughout. Incubate at room temperature for at least 5 minutes. If pellet is thick, dislodge the pellet from the side of the tube and flatten it out to allow ethanol to permeate.

9. Spin down for 1 minute and discard solution by pipetting it out of the tube.

10. Wash the pellet with **500 µl 95% ice-cold ethanol**.

11. Spin down for 1 minute and discard solution by pipetting it out of the tube.

12. Completely dry the pellet at 65 °C, either with a dry heater or vacuum centrifuge.

You can also dry the pellet by pipetting out all of the ethanol and placing the tube on a clean paper towel in a positive pressure flow hood to air dry.

13. Reconstitute with **30–50 µl TE buffer or ddH₂O**.

14. The sample is now ready for PCR preparation or can be stored at -80°C.

Additional Information

1M Tris (1L pH=8.0); milipore
before bottling

Tris-HCl	88.75g
Tris base	53g
dH ₂ O	to 1L

EDTA	1L .25M pH=8	.5M pH=8
Ethylenedinitrilo-tetracetic acid, dissodium salt	93.05g	186g
NaOH pellets	10g	10g
dH ₂ O	800ml	to 1L

****Stir solution vigorously on magnetic stirrer (heated) until EDTA crystals dissolve.**
Adjust pH to 8 with NaOH pellets. Fill to 1 or L, millipore filter and bottle

2% CTAB

Ingredients for 200 ml:

2 % CTAB (4.0 g)
100 mM Tris pH 8 (20 ml of 1.0 M sol)
20 mM EDTA (16 ml of 0.25 M sol)
1.4 M NaCl (16.4 g)

1-2 % PVP polyvinylpyrrolidone 40 (4.0 g) – relieves the effects of PCR inhibitors
0.2 % Beta mercaptoethanol Add just before use (20 µl per 10 ml solution)

Notes:

CTAB is Hexadecyltrimethylammonium bromide. Dissolve it before adding NaCl, with stirring and a little warmth, if necessary.

When the NaCl is dissolved, lots of tiny bubbles come out of solution; they rise to the surface very slowly, simulating undissolved material.

PVP of 40,000 average molecular weight makes the solution slightly translucent, but no large particles should be present after dissolving.

Beta-mercaptoethanol should be kept in the refrigerator in a dry box.

APPENDIX B

PREPERATION OF PRIMERS ORDERED FROM INTEGRATED DNA
TECHNOLOGIES (IDT)

Preparing Primers from IDT (Integrated DNA technologies)**Created by Ed Barge,**

Ordering from IDT: go to "order custom DNA oligos", enter # of items (number of primers you are ordering), enter sequence for each primer, enter name for each primer. That's it. You don't need to mess with anything else. Once the primers arrive, briefly spin down in centrifuge to make sure all of the primer powder is at bottom of tube (you won't see anything though, as there is such a small amount of material), and then dilute to 100 μM with molecular grade water. To do this, add a volume of molecular grade water equal to 10 times the number of nanomoles (nm) of primer (nm is noted on the side of the primer tube from IDT). This is your stock solution, which should be frozen. To make the 10 μM working solution, dilute from the above stock 1:10 in molecular grade water.

APPENDIX C

SEQTRACE PROTOCOL

SeqTrace Protocol**Created by Ed Barge, updated by Chance Noffsinger****Program downloadable at <https://code.google.com/archive/p/seqtrace/downloads>**

1. Click "File"
 - a. Select "New project"
 - i. Choose Location of Trace Files
 - ii. Set Forward to "F_"
 - iii. Set Reverse to "R_"
 - iv. Add Forward and Reverse Primers sequences
 - v. Select "OK"
2. Click on the Large Blue Plus Sign
 - a. Select all files
 - b. Click "Add"
3. Select pair of forward and reverse sequences
 - a. Click "Traces"
 - i. Select "Group selected Forward/Reverse files"
 1. Name Sample and hit "OK"
 2. Repeat for all Forward and Reverse files
4. Select Group
 - a. Click "Traces"
 - i. Select "View selected trace files"
 1. Edit
 2. Save the working sequence to project by clicking the Blue floppy disk or file -> "Save working sequence to project"
 3. Repeat for all Groups
5. After all are edited
 - a. Click "Sequences"
 - i. Select "Export Sequences"
 - ii. Click either "From all trace files.." or "From selected trace files"
6. Name the file
 - a. Select Location
 - b. Save as FASTA
 - c. Will open in notepad with clean sequences

APPENDIX D

CODE REQUIRED TO RUN THE DESKTOP VERSION OF MUSCLE ON
WINDOWS

Download Muscle from <https://www.drive5.com/muscle/downloads.htm>. Copy and paste the command prompt into the folder containing the muscle.exe file. Open command prompt from this folder and enter the following commands. Replace “file_name” with the actual file name.

```
muscle -in file_name.txt -fastaout file_name_aln.fas  
muscle -in file_name_aln.fas -out file_name_refine.fas -refine  
muscle -in file_name_refine.fas -out file_name_refine_2.fas -refine  
muscle -in file_name_refine_2.fas -out file_name_refine_3.fas -refine  
muscle -in file_name_refine_3.fas -out file_name_refine_4.fas -refine
```


APPENDIX E

MAXIMUM LIKELIHOOD PHYLOGENIES PRODUCED

Maximum likelihood phylogeny of the genus *Russula* produced using select sequences from the multi-locus dataset produced by Looney et al. (2016) in addition to ITS and *RPB2* sequences generated in this study. Thickened branches lead to clades receiving $\geq 75\%$ bootstrap support (BS). AA = Arctic-alpine habitats.

Maximum likelihood phylogeny of the *Russula* crown clade combining ITS and *RPB2* data. Thickened branches lead to clades receiving $\geq 75\%$ bootstrap support (BS). AA = Arctic-alpine habitats.

Maximum likelihood phylogeny of the *Russula* core clade combining ITS and *RPB2* data. Thickened branches lead to clades receiving $\geq 75\%$ bootstrap support (BS). AA = Arctic-alpine habitats.

Maximum likelihood phylogeny of the *Brevipes* clade combining ITS and *RPB2* data. Thickened branches lead to clades receiving $\geq 75\%$ bootstrap support (BS). AA = Arctic-alpine habitats.

APPENDIX F

BEAST PROTOCOL

Some alignment files were additionally analyzed in BEAST (Bouckaert et al. 2019) following these instructions. In BEAUti all data partitions were selected, and the Tree models and Clock models were linked for all partitions. Under the site models tab, the Gamma category count was set to 4, the shape parameter was set to 1.0, and the Proportion Invariant sites was set to 0.2. The boxes for Proportion Invariant, Substitution Rate, and for Shape parameter were all checked, and the Subst Model was set to RB. The settings for the first site model was then cloned for all other partitions. A Relaxed Clock Log Normal and the Birth Death models were selected. The chain length was set to 50 million with Pre-Burnin set to zero. Trees were logged every 50,000 chains. The xml file was then run in BEAST.

APPENDIX G

BEST-FITTING SUBSTITUTION MODELS DETERMINED BY PARTITION
FINDER FOR BAYESIAN ANALYSES

Best-fitting substitution models determined by Partition Finder for Bayesian analysis of the Broad *Russula* phylogeny.

Partition	Substitution Model
ITS	GTR+I+G
<i>RPB1</i> 1 st Codon	HKY+G
<i>RPB1</i> 2 nd Codon	K80+I
<i>RPB1</i> 3 rd Codon	K80+I
<i>RPB2</i> 1 st Codon	GTR+I+G
<i>RPB2</i> 2 nd Codon	HKY+I+G
<i>RPB2</i> 3 rd Codon	GTR+G
LSU	GTR+I+G

Best-fitting substitution models determined by Partition Finder for Bayesian analysis of the *Russula* core clade.

Partition	Substitution Model
ITS	SYM+I+G
<i>RPB2</i> 1 st Codon	GTR+I
<i>RPB2</i> 2 nd Codon	HKY+G
<i>RPB2</i> 3 rd Codon	SYM+G

Best-fitting substitution models determined by Partition Finder for Bayesian analysis of the *Russula* crown clade.

Partition	Substitution Model
ITS	GTR+I+G
<i>RPB2</i> 1 st Codon	GTR+I+G
<i>RPB2</i> 2 nd Codon	GTR+I+G
<i>RPB2</i> 3 rd Codon	HKY+G

Best-fitting substitution models determined by Partition Finder for Bayesian analysis of the *Brevipes* clade.

Partition	Substitution Model
ITS	GTR+G
<i>RPB2</i> 1 st Codon	GTR+G
<i>RPB2</i> 2 nd Codon	HKY+G
<i>RPB2</i> 3 rd Codon	SYM+G

APPENDIX H

R CODE FOR MAPS OF *RUSSULA* SPECIES DISTRIBUTIONS

```

## install necessary packages
library(ggplot2)
library(ggmap)
library(maps)
library(mapdata)

## Latitude and longitude for Russula subrubens collections, W is negative, South is
negative
lon <- c(-109.40645, -105.5816675, -107.5378, -106.5640, 9.5018, -105.6200, -105.8792,
-106.3992)
lat <- c(45.00593, 40.0605419, 37.9339, 39.1086, 56.2639, 40.0892, 39.6636, 38.7606)
species_loc <- c("Beartooth Plateau", "Niwt Ridge", "Cinnamon Pass", "Independence
Pass", "Denmark", "Blue lake", "Loveland Pass", "Mineral Basin")
species_cor <- data.frame(species_loc, lon, lat)
species_cor

## f is the boarder surrounding the points I have included in my matrix, larger the
## number, bigger the map
species_bbox <- make_bbox(lon = species_cor$lon, lat = species_cor$lat, f = .4)
species_bbox

## zoom - low numbers (3 = world level) easy for R to load, higher numbers hard to load
## (20 = house level), play with to get good resolution
species_map <- get_map(location = species_bbox, maptype = "terrain", source =
"google", zoom = 4)

## map, can add labels to points with geom_text(data = species_cor, aes(label = paste(" ",
## as.character(species_loc), sep="")), angle = 60, hjust = 0, color = "black")
ggmap(species_map) +
  geom_point(data = species_cor, color = "red", size = 2.5) +
  ggtitle("Russula subrubens")

```