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Morphological and molecular systematics of Rocky Mountain alpine *Laccaria*

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Abstract: The alpine zone is comprised of habitats at elevations above treeline, and macromycetes play important ecological roles as decomposers and mycorrhizal symbionts here as elsewhere. *Laccaria* is an important group of ectomycorrhizal basidiomycetes widely used in experimental and applied research. A systematic study of alpine *Laccaria* species using morphological, cultural and molecular (ribosomal DNA internal transcribed spacer) data revealed five taxa in the Rocky Mountain alpine zone: *L. laccata* var. *pallidifolia, L. nobilis* (the first published report for arctic-alpine habitats), *L. pumila, L. montana* and *L. pseudomontana* (a newly described taxon similar to *L. montana* with more ellipsoidal, finely echinulate basidiospores). All occur in the southern Rocky Mountains of Colorado; however, only *L. pumila* and *L. montana* were found on the Beartooth Plateau in the northern Rocky Mountains of Montana and Wyoming. All are associated with dwarf and shrub *Salix* species, with *L. laccata* var. *pallidifolia* also associated with *Dryas octopetala* and *Betula glandulosa.* Maximum-parsimony phylogenetic analysis of rDNA-ITS sequences for 27 *Laccaria* accessions supports the morphological species delineations.

Key words: Agaricales, arctic-alpine macromycetes, internal transcribed spacer (ITS) sequences, macrofungi, molecular phylogenetics, Tricholomataceae

INTRODUCTION

The north-temperate alpine life zone consists of widely dispersed habitats at elevations above treeline in mountainous regions. It is often associated with arctic regions as comprising the arctic-alpine biome, which covers 8% of the earth's terrestrial area (Körner 1999). While the macrofungal mycota of arctic-alpine regions such as Greenland (Borgen et al 2000, Kobayasi et al 1971, Lamoure et al 1982, Lange 1948–1957, Petersen 1977, Watling 1977, 1983), Iceland (Christiansen 1941, Hallgrímsson 1981, 1998), Svalbard (Gulden and Torkelsen 1996, Kobayasi et al 1968, Ohenoja 1971, Watling 1983) the Alps (Eynard 1977, Favre 1955, Graf 1994, Lo Bue et al 1994, Senn-Irlet 1987, 1988) and Alaska (Kobayasi et al 1967, Laursen and Chmielewski 1982, Miller 1982a, b, Miller et al 1982, Saccardo et al 1910) have been the subject of previous investigations, that of the North American alpine is virtually unknown (Cripps and Horak 1999). The results presented in this paper were obtained as part of a National Science Foundation-sponsored biotic inventory of Rocky Mountain alpine macromycetes (Cripps 2002, Cripps and Eddington 2005, Cripps and Horak 1999, Cripps et al 2001, 2002), and represents the first detailed systematic study of *Laccaria* species in the North American alpine zone.

Laccaria Berkeley & Broome (Basidiomycota, Hymenomycetes, Agaricales, Tricholomataceae *sensu* Singer 1986) is a genus commonly reported from arctic-alpine habitats, and it has been noted that the arctic-alpine taxa are in need of revision (Lamoure et al 1982, Watling 1987). A monographic study of North American taxa by Mueller (1992) did not include alpine specimens. Species of *Laccaria* typically form ectomycorrhizae with a variety of tree species. Because of the ability of some *Laccaria* species to grow vegetatively and/or germinate from basidiospores in culture, they are widely used as experimental systems for studies of ectomycorrhizal (EM) basidiomycetes (e.g. Bills et al 1999, Klironomos and Hart 2001, Kropp and Mueller 1999, Lei et al 1991, Podila et al 2002), and alpine species have potential for applied use in high altitude land reclamation (Graf 1997).

Published literature reports of *Laccaria* in arctic-alpine habitats comprise 27 taxa (TABLE I). However, due to synonomy, nomenclatural misapplications and misidentifications common in *Laccaria* taxonomy, it is probable that the number of arctic-alpine taxa is considerably lower in reality. TABLE I presents the most comprehensive published summary of arctic-alpine *Laccaria* to date, providing a starting point for subsequent taxonomic and biogeographic studies.

Because of their high latitudes/altitudes and areas of perennial snow cover, arctic-alpine habitats are

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TABLE I. Previous reports of *Laccaria* species in arctic-alpine habitats

Taxon	Location	References	Comments
L. altaica Singer	Western Alps	Kühner and Lamoure 1986, Trimbach 1978	Later synonym of *L. pumila* Fayod (Mueller 1992; Mueller & Vellinga, 1986). Sivertsen (1993) considered *L. altaica* to be a distinct species. Reported hosts include *Dryas octopetala, Salix herbacea*, and *Salix* sp.
	Russia	Singer 1967	
	Svalbard	Skifte 1979	
	Northwest Territories, Canada	Lahaie 1981	
	Baffin Island, Canada	Lahaie 1981	
	Norway	Sivertsen 1993	
	Sweden	Jacobsson 1984	
	France	Bon 1985	
L. amethystina Cooke	Svalbard	Gulden and Torkelsen 1996, Woldmar 1969	
L. avachaensis Kalamees	Rodygino, Kamchatka	Kalamees and Vaasma 1993	
L. bicolor (Maire) Orton	Kronok Nature Res., Kamchatka	Kalamees and Vaasma 1993	Reported hosts include *Salix herbacea.*
	Radont Valley, Switzerland	Graf 1994	
	Godhavn area, W. Greenland	Lamoure et al. 1982	
	Scotland	Watling 1987, 1992	
	Sweden	Jacobsson 1984	
L. farinacea (Hudson) Singer	Scotland	Watling 1987	Host reported as *Salix herbacea.*
L. laccata (Scop.: Fr.) Cooke	Greenland	Lange 1957, Lamoure et al. 1982, Watling 1983	
	Uzon Caldera, Kamchatka	Kalamees and Vaasma 1993	
	Western Italian Alps	Lo Bue et al. 1994	
	Western Alps	Kühner and Lamoure 1986	
	French Alps	Eynard 1977	
	Swiss Alps	Senn-Irlet 1992, 1993	
	Iceland	Hallgrímsson 1981,1998, Watling 1983	
	Norway	Lange and Skifte 1967	
	Alaska	Linkins and Antibus 1982	
	Svalbard	Gulden and Torkelsen 1996, Ohenoja 1971, Väre et al. 1992	
L. laccata (Scop.: Fr.) Cooke var. *laccata*	Alaska	Saccardo et al. 1910, Miller et al. 1974	Reported hosts include *Salix arctica, Salix glauca, Salix herbacea, Salix* sp., *Arctostaphylos alpina* and *Dryas actopetala.*
	Austria	Murr 1920, Friedrich 1940, Eisfelder 1962	
	Scotland	Watling 1981, 1987, 1992	
	Bulgaria	Hinkova 1958	
	Canada	Polunin 1934	
	France	Costantin 1921, Heim 1924, Lamoure 1982	
	Greenland	Rostrup 1891, 1894, 1904, Ferdinandsen and Winge 1907	
	Iceland	Hallgrimsson and Kristinsson 1965	
	Jan Mayen	Larsen 1923, Hagen 1950	
	Norway	Henning 1885, Gulden and Lange 1971	
	Russia	Singer 1930, Vasilkov 1971, Lebedeva 1927	
	Sweden	Bresinsky 1966, Jacobsson 1984	

TABLE I. Continued

Taxon	Location	References	Comments
L. laccata var. *laccata*	Switzerland	Rolland 1889, Boudier and Fischer 1895, Favre 1955	
	Poland	Nespiak 1953, 1961	
	Svalbard	Lindblom 1841, Karsten 1872, Dobbs 1942, Woldmar 1969	
L. laccata var. *montana* Møller	Austria	Horak 1960	= *L. montana* Singer (Mueller 1992)
	Färoes	Møller 1945	
L. laccata var. *proxima* (Boud.) Maire	Alaska	Kobayasi et al. 1967	= *L. proxima* (Boud.) Pat. (Mueller 1992)
	Greenland	Kobayasi et al. 1971	
L. laccata var. *pumila* (Fayod) Favre	France	Remy 1964	
	Sweden	Lange 1946	
	Switzerland	Favre 1955	
L. laccata var. *rosella* (S.F. Gray) Singer	Canada	Linder 1947	Host reported as *Salix polaris.*
L. laccata var. *rosella* f. *pusilla* Larsen	Jan Mayen	Larsen 1923	
L. laccata var. *rufocarnea* Fr.	Austria	Friedrich 1942	= *L. laccata* var. *laccata* (Mueller 1992).
L. laccata var. *subalpina* Singer	Scotland	Watling 1987	= *L. laccata* var. *pallidifolia* (Mueller 1992). Host reported as *Salix herbacea.*
L. laccata var. *tetraspora* Singer	France	Remy 1964	
L. lateritia Malencon	France	Lamoure 1982	
L. maritima (Theodor) Singer	Iceland	Hallgrímsson 1998	
	North Sea coastal	Redhead 1989	
L. montana Singer	Uzon Caldera, Kamchatka	Kalamees and Vaasma 1993	Reported hosts include *Dryas octopetala, Salix herbacea, Salix reticulata* and *Salix* sp.
	Mt. Rae, Alberta, Canada	Kernaghan and Currah 1998	
	Northwest Territories, Canada	Lahaie 1981	
	Ellesmere Island, Canada	Lahaie 1981	
	Baffin Island, Canada	Lahaie 1981	
	Svalbard	Gulden and Torkelsen 1996, Väre et al. 1992, Osmundson (unpub)	
	Iceland	Hallgrímsson 1998	
	Radont Valley, Switzerland	Graf 1994	
	France	Bon 1985, Bon and Cheype 1987	
	Italy	Bon 1987, Mueller 1981, Jamoni 1991	
	Eastern Swiss Alps	Favre 1955	
	Central Swiss Alps	Senn-Irlet 1987	
L. ohiensis (Mont.) Singer	Greenland	Lamoure et al. 1982, Watling 1977	At least some arctic-alpine *L. ohiensis* records are *L. pumila* (Gulden and Torkelsen 1996). Host reported as *Salix arctica*
	Svalbard	Watling and Watling 1988	
L. proxima (Boud.) Pat.	Radont Valley, Switzerland	Graf 1994	Hosts include *Salix pulchra* and *Salix* sp.
	Eastern Swiss Alps	Favre 1955	
	Greenland	Borgen 1993, Lamoure et al. 1982	
	Western Italian Alps	Lo Bue et al. 1994	
	Alaska	Kobayasi et al. 1967, Miller 1982a, 1982b	
	Finnish Lapland	Kallio and Kankainen 1964	
	Norway	Lange and Skifte 1967	

TABLE I. Continued

Taxon	Location	References	Comments
L. proximella Singer	Scotland	Watling 1987, 1992	Arctic-alpine records may represent *L. proxima* (Boud.) Pat. (Mueller, 1992). Host reported as *Salix herbacea*.
	Italy	Jamoni 1991	
L. pumila Fayod	Svalbard	Fellner and Landa 1989, Gulden and Torkelsen 1996, Väre et al. 1992, Osmundson (unpubl)	Reported hosts include *Salix reticulata* and *Salix retusa*.
	Norway	Sivertsen 1993	
	Western Italian Alps	Lo Bue et al. 1994	
	Eastern Swiss Alps	Favre 1955	
	Iceland	Hallgrímsson 1998	
	France	Mueller 1992	
	Switzerland	Senn-Irlet 1988, 1992	
	Alaska	Mueller 1992	
L. striatula (Peck) Peck	Alaska	Laursen and Ammirati 1982, Laursen and Chmielewski 1982, Linkins and Antibus 1982	Host reported as *Salix* sp.
	Svalbard	Reid 1979	
L. tetraspora Singer	Switzerland	Senn-Irlet 1988	Reported hosts include *Betula nana, Dryas octopetala* and *Salix herbacea*. Many arctic-alpine records probably represent *L. montana* (Mueller, 1992).
	Baffin Island	Parmalee 1969	
	Alaska	Kobayasi et al. 1967, Miller 1982b, Miller et al. 1982	
	Svalbard	Ohenoja 1971	
	Greenland	Lange 1957	
L. tortilis (Bolton) Cooke	Greenland	Kobayasi et al. 1971, Lamoure et al. 1982, Lange 1957	Reported hosts include *Betula nana, Salix herbacea, Salix kazbekensis* and *Salix rotundifolia*. Most arctic-alpine records represent *L. pumila* Fayod (Mueller, 1992).
	Western Italian Alps	Lo Bue et al. 1994	
	Alaska	Kobayasi et al. 1967, Laursen and Chmielewski 1982, Miller et al.1982, Miller 1982a	
	Svalbard	Kobayasi et al. 1968, Ohenoja 1971	
	Iceland	Hallgrímsson 1981,1998	
	Kamchatka	Kalamees and Vaasma 1993	
	Spain	Esteve-Raventós et al. 1997	
	Russia	Onipchenko and Kaverina 1989, Vasilkov 1971	
L. trullisata f. *rugulospora* M. Lange	Greenland	Lamoure et al. 1982, Lange 1955, 1957	=*L. maritima* (Theodor) Singer (Mueller, 1992). Host reported as *Salix glauca*.

likely to be sensitive to the effects of large-scale climate change events (Grabherr et al 1995, Smaglik 2000). A better understanding of the composition and ecology of soil communities is critical for assessing and responding to these effects. In addition, biotic surveys of poorly studied regions are important for inferring the biogeography and evolution of taxa (Müller and Magnuson 1987) and for addressing questions regarding the higher-level phylogenetic relationships among the agaricoid fungi (Moncalvo et al 2000).

This study focuses on the alpine component of the North American arctic-alpine mycota assessing the systematics of Rocky Mountain alpine *Laccaria* species with a morphological study of 92 collections from Colorado, Montana and Wyoming and a phylogenetic analysis of ribosomal DNA internal transcribed spacer (rDNA-ITS) sequences from selected collections.

Morphological and molecular characters support the recognition of four known and one previously undescribed species. Rocky Mountain alpine distributions and EM host associations of these taxa are documented.

MATERIALS AND METHODS

Specimen collection.—Specimens were collected at field sites above treeline in the southern and central Rocky Mountains from 1997–2002, with sites surveyed up to nine times during the season when basidiomes are produced (mid-July to early September). Southern Rockies field sites, all located in Colorado, included Independence Pass (elevation 3600–3700 m), Linkins Lake Valley (elev. 3600 m), Cumberland Pass (elev. 3660 m) and Cottonwood Pass (elev. 3700 m) in the Sawatch Range; Cinnamon Pass (elev. 3700–3850 m), Black Bear Pass (elev. 3760 m), Mineral Basin (elev. 3900 m), U.S. Basin (elev. 3660 m) and Horseshoe Lake (elev. 3810 m) in the San Juan Mountains; Loveland Pass (elev. 3700 m) and Haggeman's Pass (elev. 3600 m) in the Front Range and Blue Lake Dam (elev. 3300 m) in the Tenmile Range. North-central Rocky Mountain sites were located on the Beartooth Plateau in southern Montana and northern Wyoming (elev. 2950–3264 m). The Rocky Mountain alpine field sites are characterized by low-statured vegetation with patchy distributions related to topographically influenced microclimates, and by a continental climate resulting in relatively dry average conditions and large differences between summertime and wintertime average temperatures. Ectomycorrhizal fungi are associated with a number of shrubs, woody dwarf plants and herbaceous species; major Rocky Mountain alpine host species include the shrub willows *Salix glauca* L. and *S. planifolia* Pursh, dwarf willows *S. arctica* Pall. and *S. reticulata* L., the recumbant mat plant *Dryas octopetala* L. and the bog birch *Betula glandulosa* Michx. Ectomycorrhizal host plants in proximity to basidiomes were noted for each collection. Basidiospore deposits and/or tissue cultures were maintained on potato dextrose (PDA) or modified Melin-Norkrans (MMN, Marx 1969) media. Basidiomes were preserved by warm air-drying on an electric dryer and deposited in the Montana State University-Bozeman fungal herbarium (MONT) or the herbarium of the Eidgenössiche Technische Hochschule Zürich (ZT). *Laccaria* specimens collected during the course of this study are listed by taxon (TABLE II).

Morphological descriptions.—Macromorphological descriptions were made from fresh basidiomes. Color designations correspond to Kornerup and Wanscher (1967) and are noted as combinations of plate, column and row numbers (e.g. 8A5). Preparation of hand sections for observation of micromorphological characters and use of descriptive terms follow Largent et al (1977). Sections were mounted in 3% KOH for measurement of basidiospores and other micromorphological features and in Melzer's reagent to test for amyloidity. Basidiospore measurements were made with the hilar appendix and ornamentation excluded. Length-width ratios (Q) were calculated for each basidiospore, and a mean calculated for each collection (Q^m). Basidiospore measurements were made from hymenial tissue to maintain consistency between collections. Measurements were made from a random sampling of 10–20 basidiospores and 5–20 basidia and cystidia for each collection, from multiple basidiomes when possible, to represent intracollection variation. Width measurements of basidia and cystidia were made at the widest point. Drawings of micromorphological features were prepared using a drawing tube attached to a Leica DMLS research microscope. Culture morphology was observed for some collections, noting color and relative growth rate on PDA and/or MMN media. Some taxa did not grow in culture, and successful isolation of *L. pumila* was rare.

Scanning electron microscopy.—Lamellar fragments (approx. 1 mm^2) were removed from dried basidiomes, attached to aluminum mounts using double-stick tape and gold-palladium sputter coated at a nominal coating thickness of 15 nm using a Hummer VII sputtering system (Anatech Ltd., Alexandria, Virginia). Basidiospores were examined at 15 kV using a JEOL JSM-6100 scanning electron microscope.

DNA extraction, PCR amplification and DNA sequencing.—DNA was extracted from dried basidiomes using a procedure modified from Edwards et al (1991) and Weiss et al (1998), or using the DNeasy Plant Mini Kit (QIAGEN Inc., Valencia, California). In the former, dried lamellar tissue was ground in an extraction buffer containing 200 mM Tris-HCl pH 7.5, 250 mM NaCl, 25 mM EDTA, and 0.5% SDS, and treated with 1 μg/μl ribonuclease A. DNA was precipitated with 1/10 volume of 3 M sodium acetate (pH 5.2) and two volumes of ethanol, then resuspended in 1× TE buffer (pH 8.0) or sterile ddH_2O.

Preliminary experiments showed that crude extractions of *Laccaria* genomic DNA failed to PCR amplify, therefore, DNA extractions were purified further using a phenol: chloroform extraction following Sambrook et al (1989). An aliquot of the DNA solution was diluted 1 : 25 to 1 : 625 (determined empirically, depending on sample) with sterile ddH_2O prior to PCR amplification.

PCR amplifications of the ribosomal DNA ITS1/5.8S/ITS2 region used the basidiomycete-specific primers ITS-1F and ITS-4B (Gardes and Bruns 1993) in 40 μL mixtures consisting of 8 μL template DNA (approx. 50–100 ng), 8 μL each of forward and reverse primers (20 ng / μl), 4 μL 10× PCR buffer (Fisher Buffer A containing 1.5 mM $MgCl_2$, Fisher Scientific, Pittsburgh, Pennsylvania), 3.2 μL dNTP mixture (2.5 mM each dNTP; Promega Corp., Madison, Wisconsin), 0.3 μl Eppendorf MasterTaq DNA polymerase (Brinkmann Instruments, Westbury, New York), and 8.5 μL sterile ddH_2O. Cycling parameters were as follows: 94 C for 2 min, followed by 30 cycles of 94 C for 30 sec, 55 C for 1 min, and 72 C for 1 min; followed by a final elongation step of 72 C for 5 min. PCR products were purified prior to

TABLE II. Rocky Mountain alpine and reference *Laccaria* specimens examined. An asterisk following collection number denotes specimens used in molecular phylogenetic analysis

Species/ Collection	Date	State	Range	Location	Elevation (m)	Hosts	GenBank accession
L. amethysteo-occidentalis							
TENN 42526 [**TYPE**]*	3-Oct-81	BC, Canada	—	Alice Lake Provincial Pk.		conifers	DQ149848
L. bicolor							
Osmundson 752 (MONT)*	8-Sep-02	MT	Gallatin	Hyalite Canyon	(subalpine)	conifers	DQ149869
TENN 42529 [**REP. SPEC.**]*		WA	—	Watermain Woods	(subalpine)	conifers	DQ149850
L. laccata var. pallidifolia							
Cripps 1238b (MONT)	13-Aug-98	CO	Sawatch	Independence Pass	3660	*Salix reticulata, S. arctica*	N/A
Cripps 1308 (MONT)	8-Aug-99	CO	Front	Loveland Pass	3050	unknown	N/A
Cripps 1370 (MONT)*	14-Aug-99	CO	Sawatch	Independence Pass	3660	*Dryas octopetala*, dwarf *Salix*	DQ149849
Cripps 1603 (MONT)*	2-Aug-01	CO	Ten Mile	Blue Lake Dam	3300	*Salix reticulata*	DQ149851
Cripps 1633 (MONT)*	3-Aug-01	CO	Ten Mile	Blue Lake Dam	3300	*Betula glandulosa*	DQ149853
Cripps 1648 (MONT)	4-Aug-01	CO	Sawatch	Cumberland Pass	3662	*Salix glauca*	N/A
Cripps 1653 (MONT)	4-Aug-01	CO	Sawatch	Quartz Creek	(subalpine)	*Betula*	N/A
Cripps 1655 (MONT)*	6-Aug-01	CO	San Juan	Horseshoe Lake	3810	*Salix reticulata*	DQ149847
Cripps 1724 (MONT)*	12-Aug-01	CO	Sawatch	Cottonwood Pass	3696	*Dryas* sp.	DQ149857
L. montana							
Cripps 1853 (MONT)	30-Jul-02	CO	San Juan	Mineral Basin	3822–3850	unknown	N/A
DBGH 20424	20-Aug-99	CO	Front	Loveland Pass Lake	3620	*Salix* sp.	N/A
TENN 42877	13-Sep-81	CO	Front	Blue Lake Trail	3048+	unknown	N/A
TENN 42880	15-Sep-81	CO	Front	Cameron Pass	3300	unknown	N/A
Osmundson 264 (MONT)	10-Aug-99	MT	Beartooth	Birch Site	2960–3050	*Salix planifolia*	N/A
Osmundson 319 (MONT)*	1-Aug-00	WY/MT	Beartooth	Highline Trail	3050–3264	unknown	DQ149862
Osmundson 369 (MONT)	14-Jul-01	WY/MT	Beartooth	Highline Trail	3050–3264	*Salix planifolia*	N/A
Osmundson 441 (MONT)	28-Jul-01	MT	Beartooth	Birch Site	2960–3050	*Salix planifolia*	N/A
Osmundson 477 (MONT)	31-Jul-01	WY	Beartooth	Frozen Lake	3111–3233	*Salix arctica*	N/A
Osmundson 504 (MONT)	3-Aug-01	WY/MT	Beartooth	Highline Trail	3050–3264	*Salix glauca*	N/A
Osmundson 505 (MONT)	3-Aug-01	WY/MT	Beartooth	Highline Trail	3050–3264	*Salix glauca*	N/A
Osmundson 512 (MONT)	4-Aug-01	WY	Beartooth	Frozen Lake	3111–3233	*Salix planifolia*	N/A
Osmundson 540 (MONT)	16-Aug-01	WY/MT	Beartooth	Highline Trail	3050–3264	*Salix planifolia*	N/A

TABLE II. Continued

Species/ Collection	Date	State	Range	Location	Elevation (m)	Hosts	GenBank accession
Osmundson 553 (MONT)	17-Aug-01	WY	Beartooth	Frozen Lake	3111–3233	*Salix arctica*	N/A
Osmundson 559 (MONT)	19-Aug-01	WY/MT	Beartooth	Highline Trail	3050–3264	*Salix* cf. *glauca*	N/A
Osmundson 561 (MONT)	19-Aug-01	WY/MT	Beartooth	Highline Trail	3050–3264	*Salix* cf. *glauca*	N/A
Osmundson 591 (MONT)*	1-Sep-01	WY	Beartooth	Frozen Lake	3111–3233	*Salix planifolia*	DQ149865
L. montana							
Osmundson 613 (MONT)	18-Jul-02	WY/MT	Beartooth	Highline Trail	3050–3264	*Salix planifolia*	N/A
Osmundson 710 (MONT)	15-Aug-02	WY/MT	Beartooth	Highline Trail	3050–3264	*Salix* sp.	N/A
TENN 42882*	28-Sep-81	ID	—	Priest Lk. Rd., Keniksu NF	(subalpine)	unknown	DQ149860
TENN 42885*	5-Oct-81	BC, Canada	—	Alice Lk. Provincial Pk.	(subalpine)	unknown	DQ149866
L. nobilis							
Cripps 1304 (MONT)*	6-Aug-99	CO	Front	Loveland Pass	3050	*Salix* shrub	DQ149859
Cripps 1347 (MONT)	11-Aug-99	CO	Sawatch	Independence Pass	3660	*Salix* shrub	N/A
Cripps 1365 (MONT)	13-Aug-99	CO	Sawatch	Independence Pass	3660	*Salix* shrub	N/A
Cripps 1445 (MONT)*	3-Aug-00	CO	San Juan	Black Bear	3761	unknown	DQ149863
Cripps 1469 (MONT)*	6-Aug-00	CO	Sawatch	Independence Pass	3660	*Salix planifolia*	DQ149854
Cripps 1482 (MONT)*	8-Aug-00	CO	Sawatch	Linkins Lake Valley	3597	*Salix planifolia*	DQ149856
Cripps 1656 (MONT)	6-Aug-01	CO	San Juan	Horseshoe Lake	3810	*Salix reticulata*	N/A
Cripps 1672 (MONT)*	7-Aug-01	CO	San Juan	Mineral Basin	3900	*Salix arctica*	DQ149867
Cripps 1709 (MONT)	10-Aug-01	CO	San Juan	Cinnamon Pass	3840	*Salix arctica*	N/A
Cripps 1742 (MONT)	13-Aug-01	CO	Sawatch	Independence Pass	3660–3687	*Salix planifolia*	N/A
Cripps 1825 (MONT)	28-Jul-02	CO	San Juan	Stony Pass	3840	unknown	N/A
DBGH 19109*	6-Sep-97	CO	—	Echo Lake, Arapaho NF	3300	conifers	DQ149858
TENN 42527 [**TYPE**]*	13-Sep-81	CO	—	Blue Lk. Tr., Roosevelt NF	(subalpine)	Pinaceae	DQ149861
ZT 7472	14-Aug-99	CO	Sawatch	Independence Pass	3700	*Salix* spp.	N/A
ZT 7478	10-Aug-99	CO	Sawatch	Independence Pass	3700	*Salix* spp.	N/A
ZT 9048	3-Aug-00	CO	San Juan	Black Bear	3761	*Salix planifolia*	N/A
L. proxima							
Cripps 1595 (MONT)	21-Jul-01	WY	Beartooth	McLaren Mine Tailings	(subalpine)	*Salix, Picea, Pinus*	N/A

TABLE II. Continued

Species/ Collection	Date	State	Range	Location	Elevation (m)	Hosts	GenBank accession
Osmundson 408 (MONT)	21-Jul-01	MT	Beartooth	McLaren Mine Tailings	(subalpine)	*Pinus contorta, Picea engelmanii, Salix* shrub	N/A
Osmundson 495 (MONT)	2-Aug-01	MT	Beartooth	McLaren Mine Tailings	(subalpine)	*Salix* shrub, *Pinus sp.*	N/A
Osmundson 498 (MONT)	2-Aug-01	MT	Beartooth	McLaren Mine Tailings	(subalpine)	*Salix* shrub, *Pinus sp.*	N/A
TENN 42922*	28-Sep-81	ID	—	Priest Lk. Rd, Kaniksu NF	(subalpine)	unknown	DQ149852
L. pumila							
Cripps 1252 (MONT)*	14-Aug-98	CO	Front	Haggeman's Pass	3600	*Salix planifolia*	DQ149864
Cripps 1435 (MONT)	1-Aug-00	CO	San Juan	Cinnamon Pass	3700	*Salix reticulata*	N/A
Cripps 1446 (MONT)	2-Aug-00	CO	San Juan	Black Bear	3761	*Salix arctica, S. planifolia*	N/A
Cripps 1699 (MONT)	10-Aug-01	CO	San Juan	Cinnamon Pass	3840	*Salix arctica*	N/A
Cripps 1819 (MONT)	28-Jul-02	CO	San Juan	Stony Pass	3840	unknown	N/A
Cripps 1835 (MONT)	29-Jul-02	CO	San Juan	Imogene	3850	unknown	N/A
Cripps 1837 (MONT)	29-Jul-02	CO	San Juan	Imogene	3850	unknown	N/A
Cripps 1850 (MONT)	30-Jul-02	CO	San Juan	Mineral Basin	3822–3850	unknown	N/A
Cripps 1851 (MONT)	30-Jul-02	CO	San Juan	Mineral Basin	3822–3850	unknown	N/A
Cripps 1872 (MONT)	31-Jul-02	CO	San Juan	Emma Lake	3688	unknown	N/A
Cripps 1104 (MONT)	27-Jul-97	WY	Beartooth	Frozen Lakes	3111–3233	dwarf *Salix*	N/A
Cripps 1201 (MONT)	7-Aug-98	WY	Beartooth	Highline Trail-head	3050–3264	*Salix* spp.	N/A
Cripps 1404 (MONT)	21-Aug-99	WY	Beartooth	Frozen Lakes	3111–3233	*Salix arctica*	N/A
Cripps 1777 (MONT)	21-Aug-01	WY	Beartooth	Frozen Lake	3100–3250	*Salix planifolia*	N/A
Osmundson 663 (MONT)	31-Jul-02	WY	Beartooth	Solifluction Terraces	3250	*Salix arctica*	N/A
Osmundson 709 (MONT)	15-Aug-02	WY	Beartooth	Highline Trail	3050–3264	*Salix* shrub	N/A
Osmundson 726 (MONT)	28-Aug-02	WY/MT	Beartooth	Highline Trail	3050–3264	*Salix planifolia*	N/A
Osmundson 265 (MONT)	10-Aug-99	MT	Beartooth	Birch Site	2960–3050	*Salix* shrub	N/A
Osmundson 268 (MONT)	10-Aug-99	MT	Beartooth	Birch Site	2960–3050	*Salix planifolia*	N/A
Osmundson 314 (MONT)	31-Jul-00	MT	Beartooth	Birch Site	2960–3050	*Salix planifolia*	N/A
Osmundson 335 (MONT)	21-Aug-00	MT	Beartooth	Birch Site	2960–3050	unknown	N/A
Osmundson 337 (MONT)	21-Aug-00	MT	Beartooth	Birch Site	2960–3050	*Salix planifolia*	N/A

TABLE II. Continued

Species/ Collection	Date	State	Range	Location	Elevation (m)	Hosts	GenBank accession
Osmundson 348 (MONT)	21-Aug-00	MT	Beartooth	Birch Site	2960–3050	*Salix* shrub	N/A
Osmundson 362 (MONT)	12-Jul-01	MT	Beartooth	Clark Fork Picnic Area	(subalpine)	*Salix* shrub, *Picea sp., Pinus contorta*	N/A
Osmundson 374 (MONT)	19-Jul-01	MT	Beartooth	Clark Fork Picnic Area	(subalpine)	*Salix* shrub	N/A
Osmundson 409 (MONT)	21-Jul-01	WY	Beartooth	Top of the World Store	(subalpine)	*Salix* shrub	N/A
Osmundson 411 (MONT)	21-Jul-01	MT	Beartooth	McLaren Mine Tailings	(subalpine)	*Salix* shrub	N/A
Osmundson 442 (MONT)	28-Jul-01	MT	Beartooth	Birch Site	2960–3050	*Salix glauca*	N/A
Osmundson 465 (MONT)	30-Jul-01	MT	Beartooth	Birch Site	2960–3050	*Salix glauca*	N/A
Osmundson 501 (MONT)*	3-Aug-01	WY	Beartooth	Frozen Lake	3111–3233	*Salix planifolia*	DQ149873
Osmundson 520 (MONT)	5-Aug-01	MT	Beartooth	Birch Site	2960–3050	*Salix glauca*	N/A
Osmundson 560 (MONT)	19-Aug-01	WY/MT	Beartooth	Highline Trail	3050–3264	*Salix* cf. *glauca*	N/A
Osmundson 562 (MONT)	19-Aug-01	WY/MT	Beartooth	Highline Trail	3050–3264	*Salix* cf. *glauca*	N/A
Osmundson 589 (MONT)	1-Sep-01	WY	Beartooth	Frozen Lake	3111–3233	unknown	N/A
Osmundson 716 (MONT)	27-Aug-02	MT	Beartooth	Birch Site	2960–3050	*Salix planifolia*	N/A
Osmundson 717 (MONT)	27-Aug-02	MT	Beartooth	Birch Site	2960–3050	*Salix glauca*	N/A
Osmundson 718 (MONT)	27-Aug-02	MT	Beartooth	Birch Site	2960–3050	*Salix* shrub	N/A
Osmundson 730 (MONT)	28-Aug-02	WY/MT	Beartooth	Highline Trail	3050–3264	*Salix* cf. *glauca*	N/A
ZT 6232	30-Jul-97	MT	Beartooth	Highline Trail	3050–3264	*Salix* shrub	N/A
ZT 8068	7-Aug-99	CO	Front	Loveland Pass	3750	*Salix* shrub	N/A
ZT 9049	3-Aug-00	CO	San Juan	Black Bear	3761	*Salix planifolia*	N/A
ZT 9083	8-Aug-00	CO	Sawatch	Independence Pass	3566	*Salix glauca*	N/A
L. pseudomontana							
Cripps 1625 [**TYPE**]*	3-Aug-01	CO	Ten Mile	Blue Lake Dam	3300	*Betula glandulosa, Salix planifolia*	DQ149871
Cripps 1682 (MONT)	8-Aug-01	CO	San Juan	U.S. Basin	3658	*Salix glauca*	N/A
Cripps 1771 (MONT)*	15-Aug-01	CO	Sawatch	Independence Pass	3660–3687	*Salix* shrub	DQ149870
L. trichodermophora							
FMNH 1125225*	9-Oct-98	IL	N/A	Cook Co. Forest Preserve	(non-alpine)	*Quercus*-dominated woodland	DQ149855
TENN 42523 [**TYPE**]*	5-Dec-80	MS	N/A	Harrison Co., DeSoto NF	(non-alpine)	longleaf pine	DQ149868
L. tortilis							
DBGH 20904*	23-Jul-00	CO	—	Boulder Co., near Hwy. 72	(subalpine)	*Salix* sp., *Alnus* sp.	DQ149872

DBGH = Denver Botanical Garden Herbarium; FMNH = The Field Museum Herbarium; TENN = University of Tennessee Herbarium (coll. G.M. Mueller); ZT = Geobotanic Institute, Zurich, Switzerland (coll. E. Horak).

sequencing using the QIAquick PCR purification kit (QIAGEN Inc., Valencia, California).

PCR products were direct sequenced on both strands using the primers ITS-1F or ITS-4B. DNA sequencing reactions were performed using ABI Prism BigDye Terminator chemistry and analyzed using an ABI PRISM 377 automated DNA sequencer (Applied Biosystems, Foster City, California). Initial multiple sequence alignments were performed using ClustalX software (Thompson et al 1997) and edited manually using BioEdit (http://www.mbio.ncsu.edu/BioEdit/bioedit.html). Ambiguously aligned sequence regions were unequivocally coded and step matrices were generated for each of these regions using INAASE 2.3b (Lutzoni et al 2000, Miadlikowska et al 2002, software available for download from http://www.lutzonilab.net). For unequally weighted parsimony analyses, symmetric step matrices were constructed for the unambiguously aligned regions using the program STMatrix 2.2 (F. Lutzoni and S. Zoller, Duke Univ.; software available at http://www.lutzonilab.net) as described by Miadlikowska et al (2002). Sequence data are available in GenBank (see TABLE II for accession numbers), and the phylogenetic data matrix in TreeBase (study accession number S1355; matrix accession number M2395).

Phylogenetic analyses.—Phylogenetic analyses were performed using PAUP* 4.0b10 (Swofford 2001), using maximum parsimony as the optimality criterion. Outgroup taxa were *Tricholoma unifactum* (GenBank accession number AF241514) and *Tricholoma portentosum* (GenBank accession number AF349686). Outgroups were selected based on shared family classification (Family Tricholomataceae in Singer's 1986 classification) and trophic type (ectomycorrhizal) with *Laccaria*. To clarify the identity of specimens within the *L. bicolor* complex and examine the relationship of the Rocky Mountain alpine collections to subalpine material, the analysis included the type specimens of *L. trichodermophora* G.M. Mueller, *L. nobilis* G.M. Mueller, *L. amethysteo-occidentalis* G.M. Mueller, a designated ''representative specimen'' (Mueller 1992) of *L. bicolor* (Maire) Orton and non-alpine collections of *L. bicolor*, *L. montana* Singer, *L. nobilis*, *L. proxima* (Boudier) Patouillard, *L. tortilis* (Bolton) Cooke, and *L. trichodermophora* (TABLE II).

A primary analysis was performed on the full data set consisting of the unambiguously aligned positions and INAASE characters. All characters were specified as unordered and equally weighted, with gaps treated as missing data. A branch-and-bound search was performed using 1000 random-addition sequences with one tree held at each step, tree bisection-reconnection branch swapping, Multrees option enabled, and branches collapsed when maximum branch length equaled zero. Parsimony-uninformative characters were excluded. Branch confidence was assessed using 1000 bootstrap replicates with full heuristic searches, one random addition sequence per bootstrap replicate, and saving one tree per random addition sequence. In order to assess the effect on tree topology of weighting nucleotide changes and transitions between INAASE character states unevenly, two additional analyses were conducted. In the first, the unambiguously aligned regions were treated as equally weighted and the INAASE characters were treated as unequally weighted (using step matrices generated by INAASE). For the second, a weighted parsimony analysis was conducted using the full data matrix (unambiguously aligned regions + INAASE characters), using step matrices constructed in STMatrix 2.2 and INAASE 2.3b, respectively.

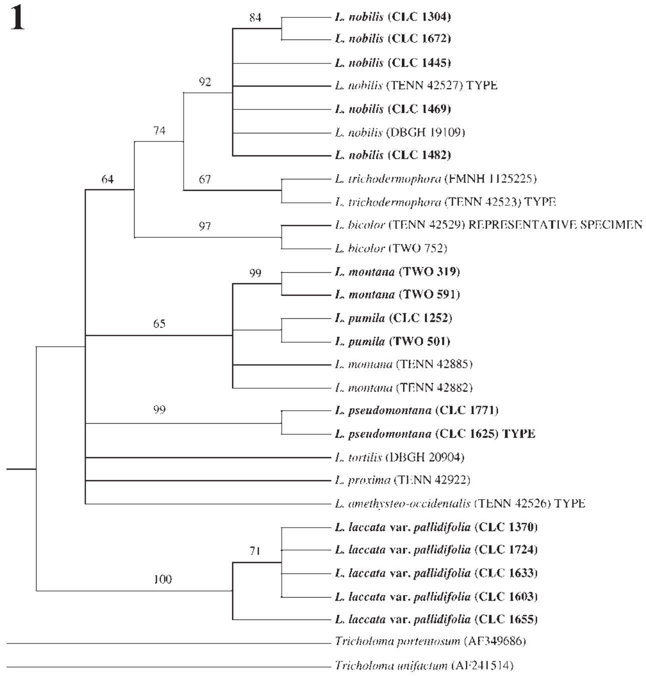
RESULTS

The primary data matrix included 27 ingroup sequences consisting of 477 unambiguously aligned sites and 11 INAASE characters. Of these 488 characters, 61 were parsimony-informative. The analysis yielded 364 equally most parsimonious trees of 151 steps (FIGS. 1, 2). The strict consensus tree from this analysis shows several well-supported clades corresponding to morphological species described in the Taxonomy section: *L. laccata* var. *pallidifolia* (100% bootstrap support), *L. nobilis* (92%) and a previously undescribed taxon, described here as *L. pseudomontana* (99%). The two other species, *L. montana* and *L. pumila*, group together with moderate bootstrap support (65%), but relationships within this clade are unresolved. Due to this lack of phylogenetic resolution as well as the observed consistency in the number of spores per basidia (the primary character used to delimit the two species) within collections (Mueller 1992), *L. montana* and *L. pumila* are maintained as distinct taxa in this study. The two additional analyses yielded an identical consensus tree topology to that produced in the primary analyses (data not shown).

KEY TO ROCKY MOUNTAIN ALPINE *LACCARIA* SPECIES

1. Basidia two-spored; basidiomes small (pileus generally five to 15, but in rare instances up to 35 mm in diam), pale orange-brown to nearly red-brown; basidiospores (8–) 9–13.5 (–15) × (6.8–) 7.5–10.5 (–14.5) µm; subglobose to broadly ellipsoidal (Q^m = 1.08–1.18), with moderately coarse echinulae (=1.5 (–2) µm in length, 0.4–1 (–1.2) µm wide at base) . *Laccaria pumila* Fayod
1. Basidia 4-spored 2
2. Basidiomes small to medium-sized (pileus 5–35 mm in diam); pileus translucent-striate or nonstriate, glabrous to indistinctly fibrillose, pale orange to dark orange-brown or red-brown; stipe +/− equal, glabrous to minutely fibrillose . . . 3
2. Basidiomes medium to large in size (pileus 15–70 mm in diam); pileus distinctly finely fibrillose, pale pinkish-orange to dark orange-brown or red-brown; stipe robust, basally enlarged to clavate, distinctly fibrous-striate. 5

1



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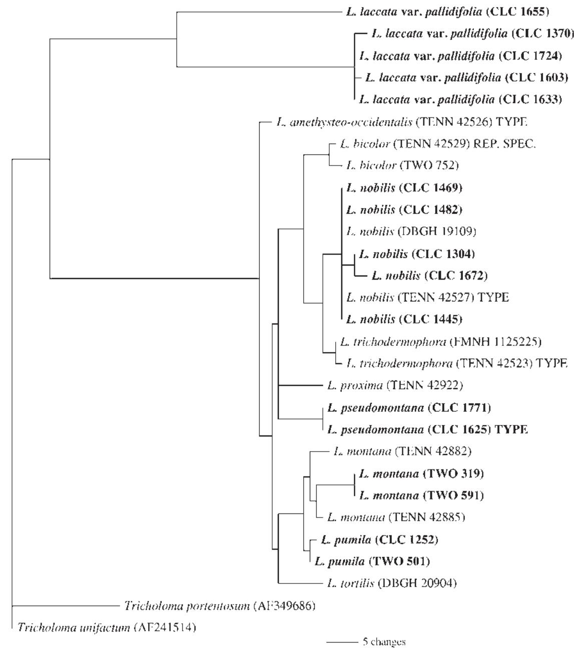
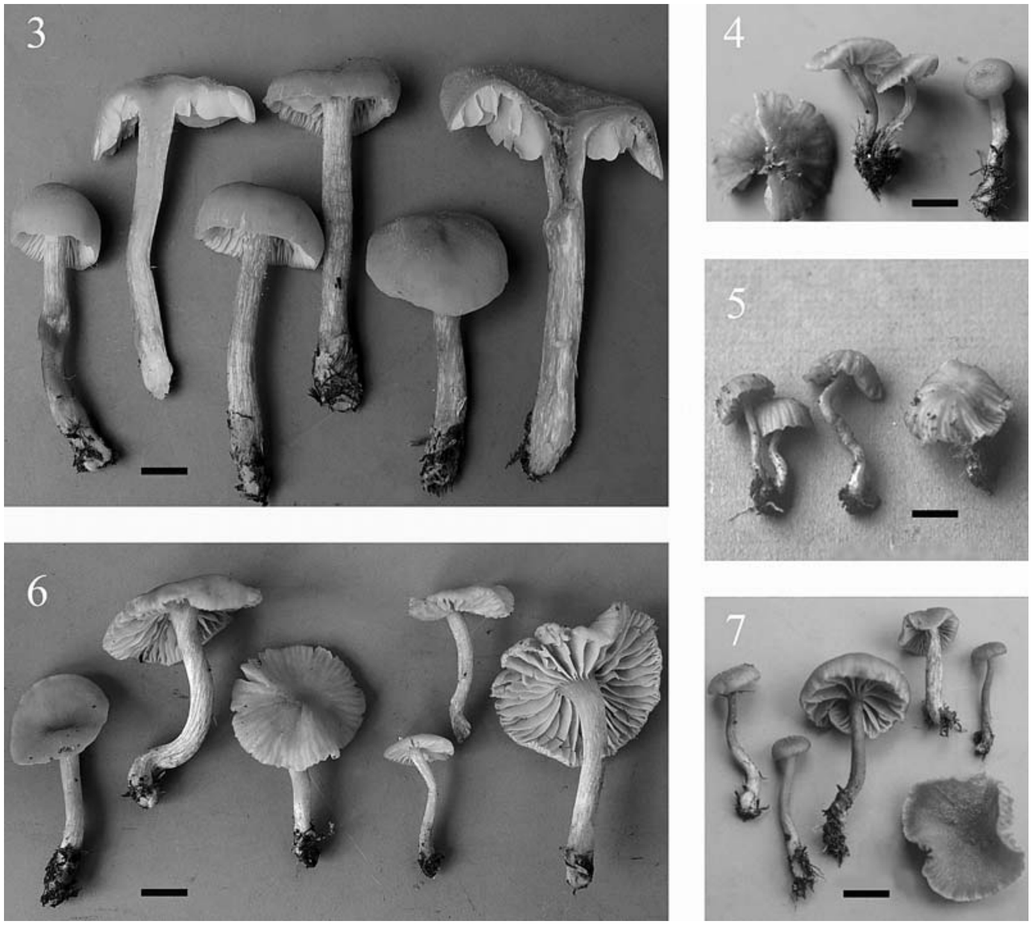


FIGS. 1 and 2. Phylogenetic relationships of Rocky Mountain alpine *Laccaria* species and non-alpine reference specimens inferred from rDNA ITS1/5.8S/ITS2 sequences. 1. Strict consensus of 364 most-parsimonious trees for the primary phylogenetic analysis. Rocky Mountain alpine *Laccaria* specimens shown in bold type. The most-parsimonious trees were 151 steps in length, with CI = 0.8278, RI = 0.9110 and RC = 0.7541. Bootstrap values >50% shown above branches. 2. Phylogram of one of the 364 most-parsimonious trees, showing branch lengths. Rocky Mountain alpine accessions shown in bold type.

3. Basidiomes small to medium (pileus 10–35 mm in diam, stipe 15–50 mm long), glabrous, indistinctly striate to nonstriate; pale orange; basidiospores globose to subglobose (Q^m = 1–1.07) and small to moderate in size (mean = 6.8–8.8 × 6–8.8 µm with moderately coarse echinulae (=1.5 (–2) µm in length, 0.4–1.0 µm wide at base) . . . . *Laccaria laccata* var. *pallidifolia* (Peck) Peck
3. Basidiomes small (pileus 5–20 (–35) mm in diam, stipe generally =30 mm long), usually translucent-striate; orange brown to red-brown; basidiospores subglobose to broadly ellipsoidal (Q^m = 1.04–1.18) and moderately long (mean length = 8–10 µm), with fine to moderately coarse echinulae 4
4. Basidiospores subglobose to broadly ellipsoidal (Q^m = 1.04–1.16), moderately large (mean = 9.0–10.0 × 8.6–9.0 µm) with moderately coarse echinulae (=1.8 (–2.5) µm in length, 0.–1.0 µm wide at base) . . . . *Laccaria montana* Singer
4. Basidiospores broadly ellipsoidal (Q^m = 1.16–1.18), mean = 8.0–9.8 × 6.8–8.4 µm, with fine echinulae (=1 (–1.8 at basidiospore apex) µm in length, 0.4–0.6 µm wide at base) . . . . *Laccaria pseudomontana* Osmundson, Cripps et G.M. Mueller, sp. nov.
5. Basidiomes pale pinkish-orange to dark orange-brown, medium to large (pileus in mature specimens 20–70 mm in diam); basal tomentum white to violet; mycelium on PDA bright violet, fading to red-brown, pale violet or nearly white; basidiospores subglobose to broadly ellipsoidal (Q^m = 1.06–1.15) with moderately coarse echinulae (=1.5 (–2.5) µm in length, 0.4–1.2 µm wide at base), associated with shrub *Salix* species. . . . . . *Laccaria nobilis* Smith *apud* G.M. Mueller (NOTE: Large specimens of *L. laccata* var. *pallidifolia* may key out here due to pileus diam and can be distinguished by having less clavate, glabrous to indistinctly fibrillose stipes and white mycelium in culture on PDA).
5. Basidiomes dark orange-brown to red-brown, medium to large (pileus in mature specimens 15–55 mm in diam); basal tomentum white; mycelium white in culture on PDA; basidiospores ellipsoidal (Q^m = 1.36–1.51) and finely echinulate (echinulae =1 µm in length with occasional long echinulae (1–1.8 µm long) at apex; echinulae 0.2–0.8 µm wide at base); subalpine; commonly on mine tailings and disturbed sites . . . .*Laccaria proxima* (Boud.) Pat.

Though not found in alpine habitats during the course of the present study, *L. proxima* (Boud.) Pat. is



FIGS. 3–7. Basidiomes of Rocky Mountain alpine *Laccaria* species. 3. *L. nobilis* (CLC 1672). 4. *L. pseudomontana* (CLC 1625). 5. *L. montana* (TWO 504). 6. *L. laccata* var. *pallidifolia* (CLC 1655). 7. *L. pumila* (CLC 1446). Bar = 1 cm for all figures.

included in the key because this species was found in Beartooth subalpine areas in mixed EM plant communities that included *Salix* shrubs, and because its apparent affinity for disturbed sites and mine tailings makes it likely to be found in such sites above treeline.

TAXONOMY

Laccaria laccata var. *pallidifolia* (Peck) Peck, Annual Rep. New York State Botanist 43: 274. 1890.
Basionym: *Clitocybe laccata* var. *pallidifolia* Peck
FIGS. 6, 10, 21–22

Type: USA, New York, Selkirk, October, *C. H. Peck s.n.* (NYS).

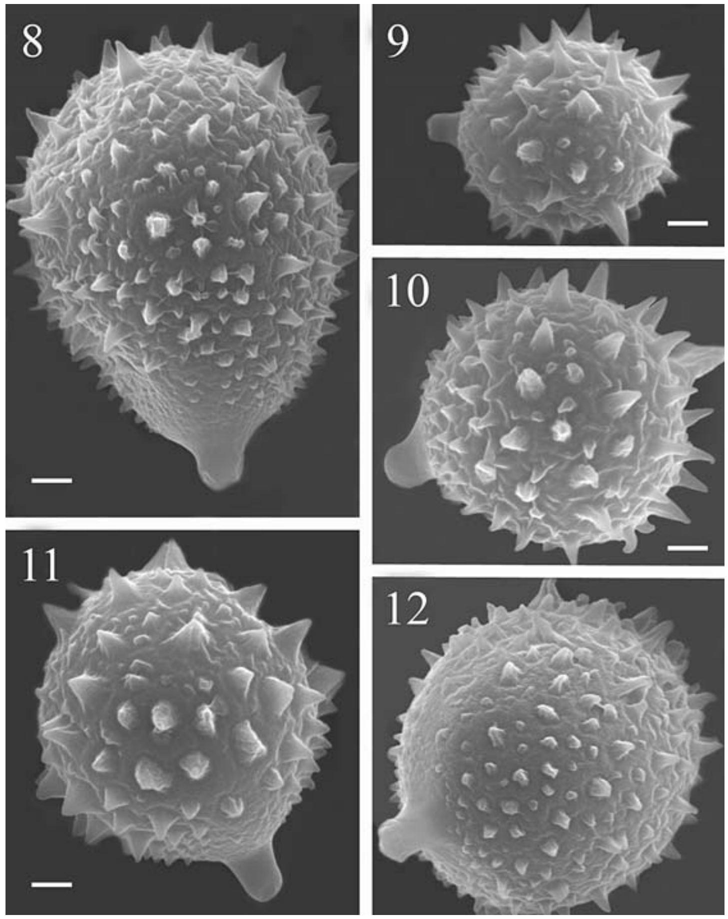
For complete descriptions of this species, see Mueller (1992) and Osmundson (2003). Diagnostic features for the Rocky Mountain alpine collections examined are described below.

Pileus (5–) 10–20 (–30) mm in diam, convex, shallow convex or nearly omphaloid, glabrous, occasionally lubricous, indistinctly translucent-striate or nonstriate; pale orange (5A8 to darker), hygrophanous, drying to paler orange (5B6); margin equal, uneven or crenulate, rimulose in age. *Lamellae* adnate to subdecurrent or rarely decurrent, broadly attached, adnate, subdistant, thick, pale orange or pink. *Stipe* 15–50 × 2–5 mm, equal to slightly enlarged toward base, generally appearing long and thin, straight to undulating, glabrous, minutely fibrillose, or finely longitudinally striate, occasionally tough, rubbery; pale orange. Basal tomentum white. *Context* white or pale orange.

Basidia four-spored. *Basidiospores* (5–) 6.2–10 (–11) × (4–) 5.6–9.8 (–10.8) μm (mean = 6.8–8.8 × 6–8.8 μm), Q = 1–1.22 (–1.32) (Q^m = 1–1.07 (–1.18), subglobose or broadly ellipsoidal, hyaline, echinulate; echinulae =1.5 (–2) μm in length, 0.4–1 μm wide at base.

Culture morphology. Culture not obtained.

Rocky Mountain alpine habitat and distribution. Solitary to scattered, occurring in alpine habitats in the Sawatch Range, 10-mile Range, Front Range and San Juan Mountains in Colorado. Associated



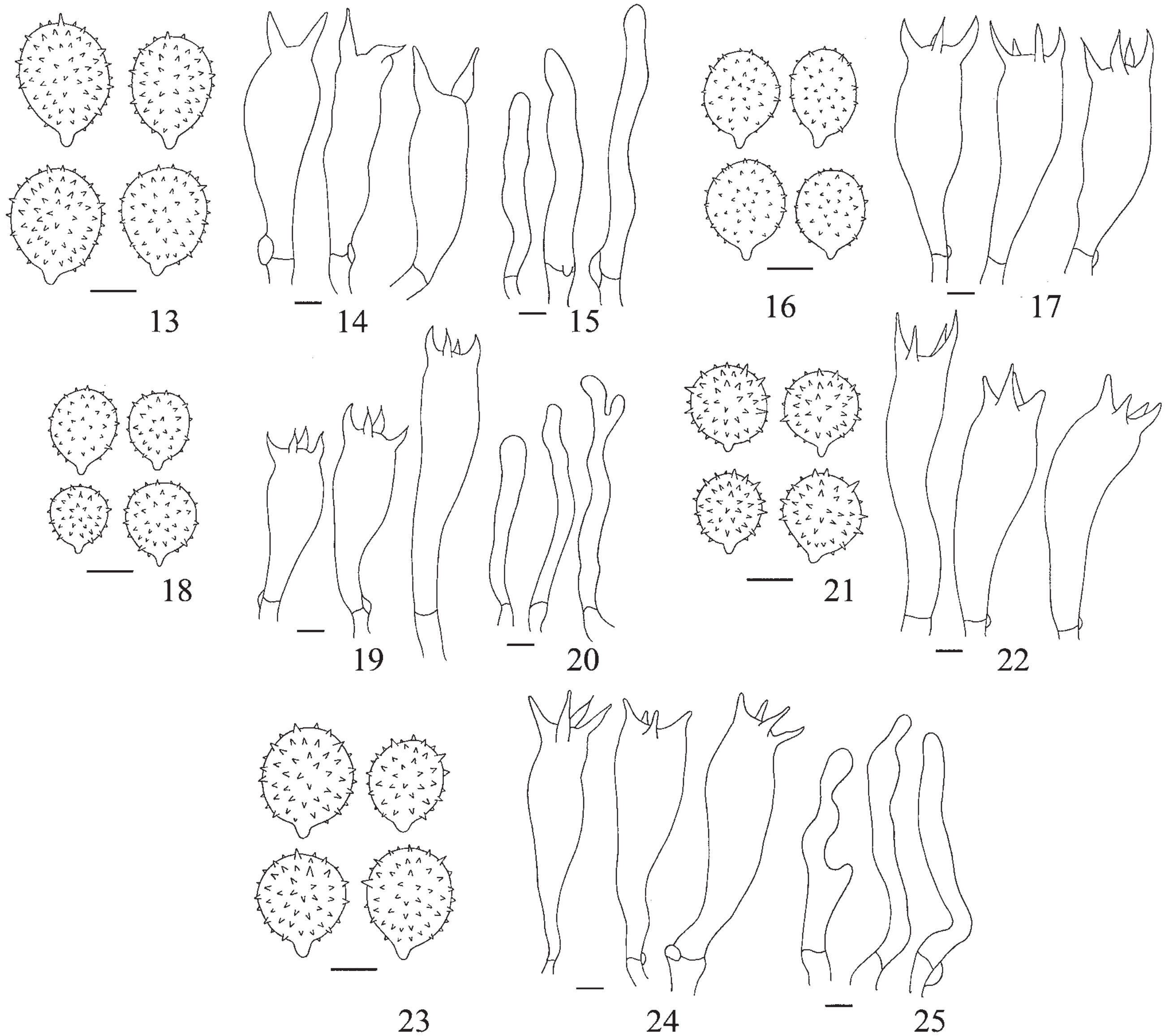
FIGS. 8–12. Scanning electron micrographs of basidiospores of Rocky Mountain alpine *Laccaria* species. 8. *L. pumila* (TWO 501). 9. *L. nobilis* (CLC 1304). 10. *L. laccata* var. *pallidifolia* (CLC 1633). 11. *L. montana* (TWO 613). 12. *L. pseudomontana* (CLC 1625). Bars = 3 μm.

with *Dryas octopetala*, *Betula glandulosa*, *Salix reticulata*, *Salix glauca* and in mixed habitats with *D. octopetala* + unidentified dwarf *Salix* and *Betula glandulosa* + *Salix cf. reticulata*.

Specimens examined. U.S.A. COLORADO. Pitkin/Lake Co.: Sawatch Range, Independence Pass, 14 Aug 1999, *CLC 1370* (MONT); Summit Co.: 10-mile Range, Blue Lake Dam, near Breckenridge, 2 Aug 2001, *CLC 1603* (MONT); 3 Aug 2001, *CLC 1633* (MONT); San Juan Co.: San Juan Mountains, Horseshoe Lake, 6 Aug 2001, *CLC 1655* (MONT); Gunnison/Chaffee Co.: San Juan Mountains, Cottonwood Pass, 12 Aug 2001, *CLC 1724* (MONT).

Comments. *Laccaria laccata* var. *pallidifolia* exhibits a wide range of phenotypic variability (Mueller 1992), and can therefore be difficult to distinguish from several other *Laccaria* species (see comments under other species descriptions). As such, reports of this species in the literature must be viewed with caution. Characters observed in the Rocky Mountain alpine collections were largely concordant with those described by Mueller (1992), with two minor differences. While the range of mean basidiospore length and width observed in the Rocky Mountain alpine *L. laccata* var. *pallidifolia* collections overlaps that noted for the species by Mueller (1992), the range for Rocky Mountain alpine collections has a lower minimum size. Cheilocystidia, reported as absent or scattered to abundant by Mueller (1992), were absent or rare in the Rocky Mountain alpine material. Examination of the reference collection TENN 43090 (TABLE II) showed micromorphological features corresponding to those noted for the Rocky Mountain alpine collections.

Originally described from New York but widely reported from arctic-alpine habitats, *L. laccata* var. *pallidifolia* was collected in the Colorado field sites but not on the Beartooth Plateau during the course of this study. Like alpine *L. nobilis, L. laccata* var. *pallidifolia* is associated with dwarf willows; however, *L. laccata* var. *pallidifolia* occurs with the additional



FIGS. 13–25. Micromorphological features of Rocky Mountain alpine *Laccaria* species. 13–15. *L. pumila*. 13. Basidiospores. 14. Basidia. 15. Cheilocystidia. 16–17. *L. pseudomontana* 16. Basidiospores. 17. Basidia. 18–20. *L. nobilis*. 18. Basidiospores. 19. Basidia. 20. Cheilocystidia. 21–22. *L. laccata* var. *pallidifolia*. 21. Basidiospores. 22. Basidia. 23–25. *L. montana*. 23. Basidiospores. 24. Basidia. 25. Cheilocystidia. Bars = 5 µm.

hosts *Dryas octopetala* and *Betula glandulosa*, and was collected once with shrub *Salix* species. *Laccaria laccata* var. *pallidifolia* is a cosmopolitan, commonly collected species (Mueller 1992). Rocky Mountain subalpine collections are reported from Colorado and Idaho, and host plant families are reported as Pinaceae, Fagaceae and Betulaceae (Mueller 1992).

Laccaria montana Singer, 1973. Sydowia 7:89. FIGS. 5, 11, 23–25

Type: SWITZERLAND: Valais, Borgne de Ferpecle, 1955–1960 m altitude, 11 Jul 1971, *Singer M5464* (F).

For complete descriptions of this species, see Mueller (1992) and Osmundson (2003). Diagnostic features for the Rocky Mountain alpine collections examined are described below.

Pileus 0.5–2.5 (–3.5) cm in diam, convex becoming plane or occasionally uplifted, with shallow central depression or rarely a low broad umbo, glabrous or minutely scaly, especially when dry; translucent-striate to plicate-sulcate; orange brown (6D7 to 6B5-6C6), red brown or brick red (7D6-7E8), mildly to strongly hygrophanous, drying to pale orange buff (5C6); margin involute to decurved, often uplifted-undulating in age, entire or occasionally crenate, occasionally splitting in age. *Lamellae* adnate or rarely short

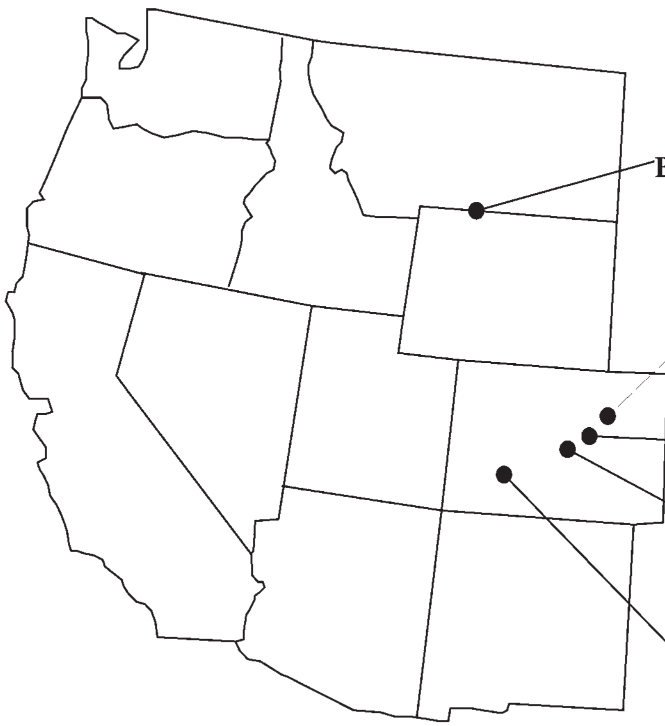


FIG. 26. Map of the western United States showing locations of collecting sites and the Central/Southern Rocky Mountain alpine distributions of *Laccaria* spp.

decurrent, moderately thick, broad (occasionally narrow or ventricose), subdistant, greyish orange (5B5–7B5) or pinkish orange-brown (6C5–6C7). *Stipe* 10–28 (–47) × (1–) 2–4 mm, equal, solid becoming hollow in age, glabrous or minutely fibrillose; concolorous with pileus, brownish-orange or red-brown (5C5–7D6). Basal tomentum white, scant to moderately dense. *Context* thin, white to pale orange-brown.

Basidia four-spored. *Basidiospores* 8–11 (–12) × (7–) 8–9.5 (–10.5) µm (mean = 9–10 × 8.6–9 µm), Q = 1–1.29 (Q^m = 1.04–1.16), subglobose to broadly ellipsoidal or occasionally globose, hyaline, echinulate; echinulae =1.8 (–2.5) µm in length, 0.4–1 (–1.4) µm wide at base.

Culture morphology. Culture not obtained.

Rocky Mountain alpine habitat and distribution. Scattered to gregarious, rarely solitary; usually among mosses; occurring in alpine habitats on the Beartooth Plateau. Only one collection observed from alpine field sites in Colorado, collected in the San Juan Mountains. Associated primarily with the shrub willows *Salix planifolia* and *S. glauca*; also found in association with the dwarf willow *Salix arctica* in Wyoming.

Specimens examined. USA. COLORADO. Jackson Co.: Colorado State Forest, Cameron Pass, 15 Sep 1981, *TENN 42880* (TENN); Larimer Co.: Roosevelt National Forest, Blue Lake Trail, 13 Sep 1981, *TENN 42877* (TENN); San Juan Co.: San Juan Mountains, Mineral Basin, 30 Jul 2002, *CLC 1853* (MONT); Summit Co.: Front Range, Loveland Pass Lake, 20 Aug 1999, *DBGH 20424* (DBGH). MONTANA. Carbon Co.: Beartooth Plateau, near source of Quad Creek, 10 Aug 1999, *TWO 264* (MONT); 28 Jul 2001, *TWO 441* (MONT); Carbon Co. at Wyoming State Line, Beartooth Plateau, Highline Trailhead, 1 Aug 2000, *TWO 319* (MONT); 14 Jul 2001, *TWO 369* (MONT); 3 Aug 2001, *TWO 504* (MONT); 3 Aug 2001, *TWO 505* (MONT); 16 Aug 2001, *TWO 540* (MONT); 19 Aug 2001, *TWO 559* (MONT); 19 Aug 2001, *TWO 561* (MONT); 18 Jul 2002, *TWO 613* (MONT); 15 Aug 2002, *TWO 710* (MONT). WYOMING. Park Co.: Beartooth Plateau, north of Frozen Lake, 31 Jul 2001, *TWO 477* (MONT); 4 Aug 2001, *TWO 512* (MONT); 17 Aug 2001, *TWO 553* (MONT); 1 Sep 2001, *TWO 591* (MONT).

Comments. Characters observed in Rocky Mountain *L. montana* collections were largely concordant with those described by Mueller (1992), with two minor differences. While the range of mean basidiospore length and width observed in the Rocky Mountain collections overlaps that noted for the species by Mueller (1992), the range for the Rocky Mountain collections has a lower maximum size. Cheilocystidia, reported as absent except in one collection by Mueller (1992), were absent in some of the Rocky Mountain alpine collections while scattered to abundant in others. Examination of the reference collection TENN 42880 (TABLE II) showed micromorphological features corresponding to those of the Rocky Mountain alpine collections.

Laccaria montana appears similar in the field to *L. pumila*, *L. tortilis* and small, striate forms of *L. laccata* var. *pallidifolia* (Mueller 1992), as well as to the newly described taxon *L. pseudomontana* (see comments under that species). *Laccaria laccata* var. *pallidifolia* differs by having smaller, globose to subglobose basidiospores. *Laccaria tortilis* and *L. pumila* differ by having two-spored basidia (see additional comments under *L. pumila*). Mueller (1992) states that at least some previous arctic reports of *L. tetraspora* (e.g. Kobayasi et al 1967, Miller et al 1982) are *L. montana*. Lahaie (1981) reports *L. montana* to have been collected near *Betula nana* and *Arctostaphylos alpina* from an arctic site on the Tuktoyaktuk Peninsula, Northwest Territories, Canada. *Laccaria montana* is reported in Rocky Mountain subalpine habitats in Colorado, Idaho, Montana and Wyoming, in association with *Betula* spp., *Salix* spp. and species in the Pinaceae.

Laccaria nobilis Smith apud G.M. Mueller. Mycotaxon 20: 105–108, 1984. FIGS. 3, 9, 18–20

Type: USA: Colorado, Larimer Co., Roosevelt National Forest, Rayah Wilderness, Blue Lake Trail, 13 September 1981 *G.M. Mueller 1198* (TENN 42527) (TENN).

For a complete description of this species, see Mueller (1992). Diagnostic features for the Rocky Mountain alpine collections examined are described below.

Pileus (10–) 20–50 (–70) mm in diam, convex, occasionally nearly plane with shallow central depression in age; nearly glabrous when young, becoming minutely scaly with concentrically-arranged fine scales in age, not striate; pale pinkish orange or dark orange, occasionally darker at margin, hygrophanous, drying to pale orange; margin involute becoming decurved to uplifted, entire or undulating slightly, occasionally rimulose in age. *Lamellae* adnate to adnexed, broad, moderately thick, subdistant, pink. *Stipe* 20–50 × 3–8 mm, equal or more frequently gradually basally enlarged to clavate, robust, tough, solid becoming hollow at least in some collections; surface longitudinally striate, rough-fibrous; concolorous with or paler than pileus, pale whitish orange or pale orange-brown, apex pink in some young specimens. Basal tomentum generally white under field conditions, but noted as violet in one collection. *Context* white, pale orange, pinkish-white or pale violet.

Basidia four-spored. *Basidiospores* 5.4–9.5 × (4–) 5–7.8 (–8.6) μm (mean = 6.2–8 × 5.5–7 μm), Q = 1–1.32 (Q^m = 1.06–1.15), subglobose or broadly ellipsoidal, hyaline, echinulate; echinulae =1.5 (–2.5) μm in length, (0.2–) 0.4–1.2 μm wide at base. *Cheilocystidia* filiform, cylindrical to irregular, hyaline, 29–44 × 1–4 μm; absent to abundant.

Culture morphology. Dikaryotic mycelia on PDA and MMN moderately fast-growing; pale violet becoming bright violet then fading to red-brown, pale violet or nearly white.

Rocky Mountain alpine habitat and distribution. Solitary to scattered, occurring in alpine habitats in the Front Range, Sawatch Range and San Juan Mountains in Colorado. Associated with dwarf willows including *Salix arctica* and *S. reticulata* and shrub willows including *Salix planifolia* and *S. glauca*.

Specimens examined. USA. COLORADO: Summit/Clear Creek Co.: Front Range, Loveland Pass, 7 Aug 1999, *CLC 1304* (MONT); San Juan Co.: San Juan Mountains, Black Bear Basin, 3 Aug 2000, *CLC 1445* (MONT); 3 Aug 2000, *ZT 9048* (ZT); Mineral Basin, 7 Aug 2001, *CLC 1672* (MONT); Stony Pass, 28 Jul 2002, *CLC 1825* (MONT); Horseshoe Lake, 6 Aug 2001, *CLC 1656* (MONT); Cinnamon Pass, 10 Aug 2001, *CLC 1709* (MONT); Pitkin/Chaffee Co.: Sawatch Range, Independence Pass, 10 Aug 1999, *ZT 7478* (ZT); 11 Aug 1999, *CLC 1347* (MONT); 13 Aug 1999, *CLC 1365* (MONT); 14 Aug 1999, *ZT 7472* (ZT); 6 Aug 2000, *CLC 1469* (MONT); 13 Aug 2001, *CLC 1742* (MONT); Pitkin Co.: Sawatch Range, Linkins Lake Valley, 8 Aug 2000, *CLC 1482* (MONT).

Comments. *Laccaria nobilis* is distinguished by having medium to large-sized, robust, minutely scaly basidiomata, relatively small, subglobose or broadly ellipsoidal basidiospores produced on four-spored basidia, and violet mycelial growth on PDA and MMN media. The ranges of mean basidiospore length and width observed in the Rocky Mountain alpine *L. nobilis* collections overlap those noted for the species by Mueller (1992), but with lower minima and maxima. Cheilocystidia, noted as absent for the species (Mueller 1992), ranged from absent (in most collections) to abundant in the alpine collections. The presence of a violet basal tomentum was noted in only one collection (CLC 1482); however, molecular analyses indicated that this collection was closely related to otherwise morphologically similar collections that lacked violet coloration, including the collection CLC 1469 that exhibited no ITS sequence divergence from CLC 1482. These findings indicate that violet pigmentation in the basal tomentum, while useful for identification, may be rare under field conditions in the Rocky Mountain alpine zone and that the lack of this character in collections of the *L. bicolor* species complex has likely led to their inclusion in some cases under *L. laccata* var. *pallidifolia* (e.g., Lahaie 1981). *Laccaria nobilis* can be distinguished by production of violet mycelial mats on PDA and MMN media, underscoring the value of attempting to obtain tissue cultures from field specimens to facilitate identification. Storing fresh basidiomes of subalpine *L. bicolor* that originally lacked violet basal mycelia in a covered plastic container under refrigeration has resulted in new growth of violet mycelia at the base of the stipe (Osmundson unpubl); this method may represent a simpler alternative to obtaining tissue cultures of members of this species complex for observing mycelial coloration.

Laccaria nobilis and *L. laccata* var. *pallidifolia* are the two taxa with medium-sized to large-sized basidiomes collected at alpine field sites during the course of this study. Both have four-spored basidia and globose to subglobose basidiospores; *L. laccata* var. *pallidifolia* generally, though not always, has larger basidiospores. Because of these overlaps in basidiospore size and shape, *L. nobilis* can be difficult to distinguish from *L. laccata* var. *pallidifolia* in the absence of a violet basal tomentum and/or mycelial culture. However, in the present study, basidiome stature and surface texture were found to be useful characters for distinguishing the two species: *L. nobilis* basidiomes were consistently more robust than *L. laccata* var. *pallidifolia*, with minutely scaly pilei and basally enlarged to nearly clavate, rough fibrous-striate stipes. Distinctions based on these characters were supported by molecular data. *Laccaria nobilis* was collected at alpine field sites in Colorado, but was not found on the Beartooth Plateau.

Described previously only from the western and Great Lakes regions of North America, *L. nobilis* is here reported for the first time from arctic-alpine habitats and for the first time in occurrence with non-Pinaceae hosts.

This phylogenetic analysis of rDNA ITS sequence data provides additional support for distinguishing three species within the *L. bicolor* complex (*L. bicolor*, *L. nobilis* and *L. trichodermophora*), previously supported by mating studies, morphological differences, and RFLP patterns (Mueller 1992, Mueller and Gardes 1991). In this analysis, the Rocky Mountain alpine collections formed a well-supported clade with the type specimen of *L. nobilis*, which was collected from a subalpine locality in Colorado. An additional Rocky Mountain subalpine collection (*TWO 752*) included in this analysis formed a well-supported clade with the designated Representative Specimen of *L. bicolor*.

Laccaria pseudomontana Osmundson, C. Cripps, et G.M. Muell., sp. nov. FIGS. 4, 12, 16–17

Species insignis basidiomeis parvis et atroaurantio-brunneis vel rubro-brunneis, basidiis tetrasporibus, basidiosporis late ellipsoideis et subtiliter echinulatis. Habitu *Laccaria montana* Singer similis, differt basidiosporis leviter plus ellipsoideis, spinis brevibus et angustis, basidiomeis saepe minoribus.

HOLOTYPUS: USA. COLORADO. Summit Co.: 10-mile Range, Blue Lake Dam, near Breckenridge, 23 Aug 2001, *C.L. Cripps 1625* (MONT).

Pileus 4–10 (–18) mm in diam, convex to plane, glabrous, slightly striate; dark orange or red-brown, hygrophanous; margin decurved, entire or crenate. *Lamellae* adnate or subdecurrent, thick, subdistant, pink; edges entire; lamellulae present. *Stipe* 10–15 × 1–2 mm, equal, glabrous or fibrous-striate, dark orange-brown or red-brown. Context thin, white.

Pileipellis of interwoven, inamyloid, cylindrical, mostly repent hyphae with widely scattered fascicles of hyphae oriented nearly perpendicular to pileal surface. Hyphae hyaline or having intracellular pigment appearing pale orange-brown in 3% KOH. *Stipitipellis* of parallel, cylindrical, repent, inamyloid, hyaline hyphae. *Caulocystidia* absent. *Lamellar trama* of subparallel to interwoven, hyaline, inamyloid hyphae. Subhymenium undifferentiated. *Clamp connections* present in all tissues. *Pleurocystidia* absent. *Cheilocystidia* absent. *Basidia* clavate, hyaline, 32.5–37.5 × 10–12.5 μm, four-spored; sterigmata =8 μm in length. *Basidiospores* (6.5–) 7.5–10.8 × 6.5–9.5 μm (mean = 8–9.8 × 6.8–8.4 μm), Q = 1.04–1.39 (Q^m = 1.16–1.18), subglobose or broadly ellipsoidal, hyaline, echinulate; echinulae =1 (–1.8) μm in length, 0.4–0.6 μm wide at base.

Culture morphology. Culture not obtained.

Rocky Mountain alpine habitat and distribution. Scattered, usually among mosses; collected in alpine habitats in the 10-mile Range and San Juan Mountains in Colorado. Associated with *Salix glauca*, an unidentified shrub *Salix* sp., and in a mixed stand of *Salix planifolia* and *Betula glandulosa*. Not reported from the Beartooth Plateau.

Material examined. USA. COLORADO. Summit Co.: 10-mile Range, Blue Lake Dam, near Breckenridge, 23 Aug 2001, *CLC 1625* (HOLOTYPE;

MONT); Pitkin/Lake Co.: San Juan Mountains, Independence Pass, 15 Aug 2001, *CLC 1771* (MONT); San Juan Co.: San Juan Mountains, U.S. Basin, 8 Aug 2001, *CLC 1682* (MONT).

Comments. *Laccaria pseudomontana* is distinguished by having small, dark orange or red-brown basidiomes, four-spored basidia and moderately sized, broadly ellipsoidal, finely echinulate basidiospores. *Laccaria pseudomontana* closely resembles *L. montana* in both macro- and micromorphology; however, *Laccaria pseudomontana* often has smaller basidiomes than *L. montana* and has basidiospores with shorter and narrower echinulae and a slightly more ellipsoidal shape than does *L. montana*. Although two of the *L. pseudomontana* collections examined had smaller (0.5–1.5 cm), red-brown basidiomes, the third collection had a basidiome morphology indistinguishable from that of typical *L. montana* collections and was distinguishable from *L. montana* only by basidiospore characters. Though difficult to distinguish from *L. montana*, collections of *L. pseudomontana* formed a distinct, well-supported clade in phylogenetic analyses of rDNA-ITS sequence data.

The present study included one alpine and two subalpine herbarium collections previously identified as *L. montana* and collected in Colorado. The two subalpine collections were included in Mueller's (1992) monographic study and were used as nomenclatural reference specimens to represent *L. montana* for the present study. One of these subalpine collections (TENN 42877) corresponds to Beartooth Plateau *L. montana* collections in terms of basidiospore shape and echinulae dimensions. Basidiospores of the other subalpine reference collection (TENN 42880) and the alpine reference collection (DBG 20424) appear more similar to *L. pseudomontana* than to the Beartooth Plateau *L. montana* collections. Examination of the holotype of *L. montana* (Singer M5464, F) by Mueller (1992) showed basidiospores having a globose to broadly ellipsoidal shape (Q = 1–1.11 [–1.26]) and uncrowded, 1.5–1.8 mm long echinulae, characters that correspond to those of the Beartooth Plateau *L. montana* collections. Further morphological and molecular analyses including collections of *L. montana* sensu lato will be necessary to determine the distribution and abundance of *L. pseudomontana*.

Laccaria pseudomontana can be distinguished from small *L. laccata* var. *pallidifolia* basidiomes by having more ellipsoidal (higher average length to width ratio) basidiospores with shorter, narrower echinulae and often by having a darker basidiome coloration, and from *L. pumila* by having four-spored basidia and smaller basidiospores with shorter, narrower echinulae.

Laccaria pseudomontana is associated with shrub willows (*Salix* spp.) in Colorado and is not reported from the Beartooth Plateau.

Laccaria pumila Fayod, Annali Accad. Agric. Torino 35:91, 1893. FIGS. 7, 8, 13–15

Type: FRANCE: dept. Alpes maritimes, Col de la Cayolle, 2500 m altitude, 18 Jul 1976, *J. Trimbach 1463* (L, neotype *fide* Mueller and Vellinga, 1986).

For complete descriptions of this species, see Mueller (1992) and Osmundson (2003). Diagnostic features for the Rocky Mountain alpine collections examined are described below.

Pileus 5–15 (–35) mm in diam, convex to plane or nearly omphaloid, often with slight central depression, usually translucent-striate, glabrous or minutely fibrillose, occasionally lubricous; pale orange-brown (6D8) or nearly red-brown, strongly hygrophanous; margin decurved, often becoming uplifted in age, entire, irregular or slightly eroded. *Lamellae* adnate to short decurrent, narrow or moderately broad, moderately thick or thick, subdistant, greyish-orange or pinkish orange (6B5–6B6), occasionally forked. *Stipe* (6–) 15–35 (–50) × 1–4 mm, equal, solid, often tough; glabrous or minutely fibrillose, pale pinkish brown, pinkish orange or dark orange-red (6D7); base of stipe often opaque, whitish. Basal tomentum white, moderately dense to lacking entirely. *Context* thin, white to pale orange.

Basidia two-spored. *Basidiospores* (8–) 9–13.5 (–15) × (6.8–) 7.5–10.5 (–14.5) μm (mean = 9.5–11.4 × 8–9.5 (–10.5) μm), Q = 1–1.3 (Q^m = 1.08–1.18), subglobose to broadly ellipsoidal or occasionally globose, hyaline, echinulate; echinulae =1.5 (–2) μm in length, 0.4–1 (–1.2) μm wide at base.

Culture morphology. Dikaryotic mycelia on PDA and MMN slow-growing; white.

Rocky Mountain alpine habitat and distribution. Solitary to scattered or gregarious, usually among mosses; occurring in alpine habitats in the Sawatch Range and San Juan Mountains in Colorado and the Beartooth Plateau in Montana/Wyoming. Primarily associated with dwarf willows in Colorado, and with the shrub willows *Salix planifolia* and *S. glauca* in Montana and Wyoming.

Specimens examined. USA. COLORADO. Summit/Clear Creek Co.: Front Range, Loveland Pass, 7 Aug 1999, *ZT 8068* (ZT); San Juan County: San Juan Mountains, Black Bear Basin, 3 Aug 2000, *CLC 1446* (MONT); 3 Aug 2000, *ZT 9049* (ZT); Cinnamon Pass, 1 Aug 2000, *CLC 1435* (MONT); 10 Aug 2001, *CLC 1699* (MONT); Mineral Basin, 30 Jul 2002, *CLC 1850* (MONT); *CLC 1851* (MONT); Stony Pass, 28 Jul 2002, *CLC 1819* (MONT); Emma Lake, 31 Jul 2002, *CLC 1872* (MONT); Ouray Co.:

San Juan Mountains, Imogene Pass, 29 Jul 2002, *CLC 1835* (MONT); 29 Jul 2002, *CLC 1837* (MONT); Lake Co.: Sawatch Range, Haggeman's Pass, 14 Aug 1998, *CLC 1252* (MONT); Pitkin/ Lake Co.: San Juan Mountains, Independence Pass, 8 Aug 2000, *ZT 9083* (ZT). MONTANA. Carbon Co.: Beartooth Plateau, near source of Quad Creek, 10 Aug 1999, *TWO 265* (MONT); 10 Aug 1999, *TWO 268* (MONT); 31 Jul 2000, *TWO 314* (MONT); 21 Aug 2000, *TWO 335* (MONT); 21 Aug 2000, *TWO 337* (MONT); 21 Aug 2000, *TWO 348* (MONT); 28 Jul 2001, *TWO 442* (MONT); 30 Jul 2001, *TWO 465* (MONT); 5 Aug, 2001, *TWO 520* (MONT); 27 Aug 2002, *TWO 716* (MONT); 27 Aug 2002, *TWO 717* (MONT); 27 Aug 2002, *TWO 718* (MONT); At Wyoming state line, Beartooth Plateau, Highline Trailhead, 30 Jul 1997, *ZT 6232* (ZT); 7 Aug 1998, *CLC 1201* (MONT); 19 Aug 2001, *TWO 560* (MONT); 19 Aug 2001, *TWO 562* (MONT); 15 Aug 2002, *TWO 709* (MONT); 28 Aug 2002, *TWO 726* (MONT); 28 Aug 2002, *TWO 730* (MONT); Clark Fork Picnic Area (subalpine, with *Salix* shrubs and possibly conifers), 12 Jul 2001, *TWO 362* (MONT); 19 Jul 2001, *TWO 374* (MONT); McLaren mine tailings (subalpine, with conifers and *Salix* shrubs), 21 Jul 2001, *TWO 411* (MONT). WYOMING. Park Co.: Beartooth Plateau, north of Frozen Lake, 29 Jul 1997, *CLC 1104* (MONT); 21 Aug 1999, *CLC 1404* (MONT); 3 Aug 2001, *TWO 501* (MONT); 21 Aug 2001, *CLC 1777* (MONT); 1 Sep 2001, *TWO 589* (MONT); North of Gardner Headwall, 31 Jul 2002, *TWO 663* (MONT); Beartooth Highway, near Top of the World Store (subalpine, with *Salix* shrubs), 21 Jul 2001, *TWO 409* (MONT).

Comments. Characters observed in Rocky Mountain *L. pumila* collections were largely concordant with those described by Mueller (1992). The ranges of mean basidiospore length and width observed in the Rocky Mountain alpine collections overlap those noted for the species by Mueller (1992), but with lower minimum and maximum sizes. Examination of the reference collection TENN 42553 (TABLE II) showed micromorphological features corresponding to those of the Rocky Mountain alpine collections examined. *Laccaria pumila* appears to be indistinguishable from *L. montana* on the basis of macromorphological characteristics alone in Rocky Mountain alpine habitats; however, the two taxa are easily distinguished micromorphologically, with *L. pumila* having two-spored basidia and slightly larger basidiospores. Biological differences between two-spored and four-spored species may be ecologically relevant: Tommerup et al (1991) suggest that secondary homothallism (i.e. production of single basidiospores containing both mating type nuclei required for formation of a dikaryotic mycelium), as demonstrated in the two-spored species *Laccaria fraterna*, may represent an advantage in primary successional or disturbed sites. *L. pumila* and *L. montana* are distributed sympatrically on the Beartooth Plateau.

Laccaria pumila is reported by Mueller (1992) as appearing similar to *L. tortilis* and to small, striate forms of *L. laccata* var. *pallidifolia*. *Laccaria pumila* can be distinguished from *L. laccata* var. *pallidifolia* by having larger, more broadly ellipsoidal basidiospores and two-spored basidia, and from *L. tortilis* (Bolton) Cooke by having fewer globose basidiospores with shorter, narrower echinulae. *Laccaria tortilis* has been reported from subalpine habitats in Colorado, Montana, Oregon and Washington (O.K. Miller Jr. unpubl, Mueller 1992), but was not observed in alpine habitats during the present study. Mueller (1992) states that previous arctic records of *L. tortilis* (Kobayasi et al. 1967, Lange 1955) are most likely *L. pumila* and that *L. altaica*, commonly reported from arctic-alpine habitats, is a synonym of *L. pumila*; Sivertsen (1993), however, considers *L. pumila* and *L. altaica* to be distinct species differing in basidiospore shape and echinulae density. Examination of Kobayashi et al.'s (1967) basidiospore illustrations confirms Mueller's identification of this taxon as *L. pumila*. In addition to occurring in alpine habitats, *L. pumila* was found in subalpine habitats in Montana in association with *Salix* spp. and *Populus tremuloides* (Cripps and Osmundson unpublished). Mueller (1992) reports collections from Rocky Mountain subalpine habitats in Wyoming and Colorado, and reports *L. pumila* to be associated with *Salix* spp, *Betula* spp., and species in the Pinaceae.

DISCUSSION

The present study represents the first report on North American alpine *Laccaria* species. Five species, one previously undescribed and another reported for the first time from arctic-alpine habitats, are reported from the Rocky Mountain alpine zone: *L. laccata* var. *pallidifolia, L. montana, L. nobilis, L. pumila* and *L. pseudomontana*. Phylogenetic analyses of rDNA ITS sequences revealed clades corresponding to circumscribed morphological species and aided in distinguishing morphological traits useful for reliably identifying *Laccaria* species in the Rocky Mountain alpine zone.

The five taxa described here can be distinguished on the basis of macromorphological and/or micromorphological characters. *Laccaria pumila, L. montana* and *L. pseudomontana* are distinguished by having small basidiomes, often with translucent-striate pilei, and having relatively large, subglobose to broadly ellipsoidal basidiospores. In the phylogenetic analysis of rDNA ITS sequence data, *L. montana* and *L. pumila* form a single, unresolved clade in the strict consensus tree, with only moderate bootstrap support. Due to this lack of phylogenetic resolution as well as the observed consistency in the number of spores per basidia (the primary character used to delimit the two species) within collections (Mueller 1992), *L. montana* and *L. pumila* are maintained as distinct taxa in this study; additional collections and wider geographic sampling are necessary for more clearly establishing the relationship between these two taxa. An additional taxon, described here as *Laccaria pseudomontana* and having small, dark orange to red-brown basidiomata, was collected in Colorado alpine habitats. Originally thought to represent a small form of *L. laccata* var. *pallidifolia* or *L. montana*, these specimens formed a distinct, well-supported clade in the phylogenetic analyses.

Laccaria nobilis and *L. laccata* var. *pallidifolia* in the Rocky Mountain alpine zone are characterized by producing larger basidiomes (longer stipes and generally broader pilei) than the other species described in the present study. Though an important diagnostic character-violaceous lamellae and violet tomentum at the base of the stipe when young and fresh (Mueller 1992)-was generally lacking in the Rocky Mountain collections, the present study describes other macromorphological and basidiospore characters that distinguish the two species in the North American alpine zone.

Laccaria laccata var. *pallidifolia* is supported in this analysis as a distinct but morphologically variable taxon including both convex and nearly omphaloid pileal forms and exhibiting a relatively wide range in basidiospore size. This species is highly divergent at the molecular level compared to the other species studied, and is supported by numerous synapomorphic single nucleotide polymorphisms in the ITS region.

In terms of EM associations, *Laccaria nobilis* occurs with *Salix planifolia* and *Salix glauca* (both shrub species) and *S. arctica* and *S. reticulata* (both dwarf species). *Laccaria laccata* var. *pallidifolia* is associated with *Dryas octopetala*, *Betula glandulosa* and *Salix reticulata*, and was collected only once near a shrub *Salix species* (*S. glauca*). *Laccaria pumila* is associated with both dwarf and shrub *Salix* species. *Laccaria montana* is associated predominantly with the shrub willows *S. planifolia* and *S. glauca*. *Laccaria pseudomontana* is associated with *Salix* shrubs, and was encountered in a mixed stand of *Salix* shrubs and *Betula glandulosa*. The three smaller-statured species are nearly always encountered in moss-covered areas in proximity to the EM host plant. The occurrence of sympatric populations of *L. pumila* and *L. montana* on the Beartooth Plateau allows the opportunity to observe differences in small-scale distributional and ecological patterns between the two species. Although *L. pumila* is associated primarily with dwarf *Salix* species and *L. montana* primarily with shrub *Salix* species, the observation that *L. pumila* is occasionally found with *Salix* shrubs suggests that the two species are not spatially isolated on the basis of host specificity alone.

Laccaria nobilis, reported in the present study in association with *Salix* spp., occurs in association with conifer species in subalpine habitats. Host association data therefore suggest that a mycorrhizal host shift has occurred in arctic-alpine populations of this taxon. A similar host shift from gymnosperm (*Pinus*) to angiosperm (*Quercus costaricensis*) hosts has been documented for the closely related species *L. trichodermophora* (Mueller and Strack 1992).

Compared to many arctic-alpine macromycetes, *Laccaria* species generally appear to be widely distributed and not strictly limited to arctic-alpine habitats. The species found in the present study are reported in the literature to occur in other arctic-alpine localities, with the exception of the newly described taxon *L. pseudomontana*, which may be found to be more widely distributed after additional collections previously identified as *Laccaria montana* have been examined, and *L. nobilis*, which has been previously described only from western North America and the Great Lakes region. This result indicates little or no endemicity in Rocky Mountain alpine *Laccaria*, and is concordant with the observation that none of the EM host plants associated with *Laccaria* spp. in this region are endemic to the Rocky Mountain alpine zone. However, smaller-scale differences in distributions were observed between taxa over the geographic area encompassing the central and southern Rocky Mountain alpine zone: The two taxa characterized by more robust basidiomes (*L. laccata* var. *pallidifolia* and *L. nobilis*) and the smaller *L. pseudomontana* are reported only from the Colorado field sites, *Laccaria pumila* occurs commonly in both Colorado and Montana/Wyoming, and *Laccaria montana* is regularly collected on the Beartooth Plateau, but was only collected once in Colorado during the course of this study (FIG. 26). A number of factors, including EM host specificity, climate and soil conditions, ecological community setting and geologic, evolutionary or dispersal events, might contribute to the observed distributions; however, more extensive sampling might reveal fewer differences between regions than were observed in this study.

The ability of many *Laccaria* species to be grown and manipulated in the laboratory has made this an important genus for applied and experimental work with EM fungi. In addition, the role of some *Laccaria* species as early post-disturbance mycorrhizal associates in arctic-alpine habitats (e.g. Graf 1994, Jumpponen et al 2002) suggests a possible use in reclamation of high altitude habitats; a better understanding of species limits, geographic distributions, host associations and ecological roles of alpine species can provide a foundation for the development of plant-fungal systems for such use. The wide distribution of the genus in arctic-alpine habitats highlights the potential use of *Laccaria* as a model genus for evolutionary studies in arctic-alpine mycorrhizal macromycetes; a robust taxonomic classification of arctic-alpine taxa is a necessary foundation for such studies. In general, host specificity, successional patterns and species-specific ecological interactions are poorly understood for EM fungi in arctic-alpine habitats, and these subjects offer important avenues for both observational and experimental studies.

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LITERATURE CITED

Bills S, Podila GK, Hiremath S. 1999. Genetic engineering of an ectomycorrhizal fungus *Laccaria bicolor* for use as a biological control agent. Mycologia 91(2):237–242.

Bon M. 1985. Stage mycologie alpine Lanslebourg (Savoie) de 1–3 septembre 1984. Bull Féd Myc Dauphiné Savoie 96:19–25.

———. 1987. Quelques recoltes mycologiques de la zone alpine au 7ème convegno di micologia—Fiera di Primiero (Italie). Mic Ital 17(3):267–270.

———, Cheype J-L. 1987. Mycologie alpine au Col du Joly. Bull Féd Myc Dauphiné-Savoie 106:22–27.

Borgen T. 1993. Svampe i Grønland. Atuakkiorfik, Nuuk. 112 p.

———, Elborne SA, Knudsen H. 2000. A preliminary checklist of the basidiomycota of Greenland. Draft presented at 6th International Symposium on Arctic-Alpine Mycology, Kangerlussuaq & Sismiut, Greenland, Aug 11–21, 2000.

Boudier E, Fischer E. 1895. Rapport sur les espèces de champignons trouvées pendant l'assemblée à Genève et les excursions faites en Valais par les Sociétés de Botanique de France et de Suisse du 5 au 15 août 1894. Bull Soc Bot France 41:237–249.

Bresinsky A. 1966. Beitragx zur Kenntnis der Pilzflora im subarktischen Bereich der Torne-Lappmark. Zeitschr Pilzk 32:1–26.

Christiansen MP. 1941. Studies in the larger fungi of Iceland. The Botany of Iceland 3(2):191–227.

Costantin J. 1921. Sur la biologie alpestre. Comptes Rendus des Séances de L'académie des Sciences 173:537–540.

Cripps CL. 2002. Alpine macrofungi of North America (Rocky Mountains) [abstract]. 7th International Mycological Congress, Oslo, Norway, Aug 11–17, 2002.

———, Eddington LE. 2005. Distribution of mycorrhizal types among alpine vascular plant families on the Beartooth Plateau, Rocky Mountains, USA, in reference to large-scale patterns in Arctic-alpine habitats. Arctic, Antarctic and Alpine Research 37(2):177–188.

———, Horak E. 1999. Arctic and alpine mycota, Rocky Mountains, USA: a preliminary report [abstract]. 16th International Botanical Congress, St. Louis, Missouri, Aug 1–7, 1999.

———, ———, Osmundson T. 2001. Rocky Mountain alpine project: documenting agarics above treeline [abstract]. Mycological Society of America annual meeting, Salt Lake City, Utah, Aug 25–29. 2001.

———, ———, ———. 2002. Arctic alpine mycota (Agaricales), Rocky Mountain tundra, USA: cold climate mushrooms above treeline [abstract]. Mycological Society of America annual meeting, Corvallis, Oregon, June 23–26, 2002.

Dobbs CG. 1942. Note on the larger fungi of Spitsbergen. J Bot 80:94–102.

Edwards K, Johnstone C, Thompson C. 1991. A simple and rapid method for the preparation of plant genomic DNA for PCR analysis. Nucleic Acids Research 19(6):1349.

Eisfelder I. 1962. Höhere Pilze aus dem Pitztal (Tirol). Ber Bayer Bot Ges 35:28–38.

Esteve-Raventós F, González V, Arenal F. 1997. El génereo *Entoloma* (Fr.: Fr.) P. Kummer (Agaricales) en el piso alpino y subalpino del Parque Nacional de Ordesa y zonas limítrofes. Lucas Mallada 8:41–71.

Eynard M. 1977. Contribution a l'étude écologique des Agaricales des groupements à *Salix herbacea*. [Thèse]. Univ. Lyon 183 p. As cited in Graf, 1994.

Favre J. 1955. Les champignons supérieurs de la zone alpine du Parc National Suisse. Ergebn Wissensch Unters Schweiz Nat 5 (N.F.) 33:1–212.

Fellner R, Landa J. 1989. Notes to collections of fungi from

Svalbard. In: Abstracts, 10th Congress Europ Mycol, Tallinn, p. 32.

Ferdinandsen C, Winge Ø. 1907. Plantes récoltées à la côte nord-est du Grönland. C. Champignons In: Duc d'Orleans: Croisière oceanographique accomplie à bord de la Belgica dans la mer du Grönland, 1905. Bruxelles, 13 p.

Friedrich K. 1940. Untersuchungen zur Oekologie der höheren Pilze. Pflanzenforschung 22:1–52.

———. 1942. Pilzökologische Untersuchungen in den Oetztaler Alpen. Ber Deutsch Bot Ges 60:218–232.

———, Bruns T. 1993. ITS primers with enhanced specificity for basidiomycetes—application to the identification of mycorrhizae and rusts. Mol Ecol 2:113–118.

Gardes M, White TJ, Fortin JA, Bruns TD, Taylor JW. 1991. Identification of indigenous and introduced symbiotic fungi in ectomycorrhizae by amplification of nuclear and mitochondrial ribosomal DNA. Can J Bot 69:180–190.

Grabherr G, Gottfried M, Gruber A, Pauli H. 1995. Patterns and current changes in alpine plant diversity. In: Chapin FS, Korner C., eds. Arctic and Alpine Biodiversity. Ecol Stud. Vol. 113. Berlin: Springer-Verlag. p 167–182.

Graf F. 1994. Ecology and sociology of macromycetes in snow-beds with *Salix herbacea* L. in the alpine Valley of Radont (Grisons, Switzerland). Diss Bot 235. Berlin-Stuttgart: J. Cramer. 242 p.

———. 1997. Ectomycorrhiza in alpine soil bioengineering. Actes du Deuxieme Colloque Ecologie et Biogeographie Alpines, La Thuile, Italy, p 335–342.

Gulden G, Lange M. 1971. Studies in the macromycete flora of Jotunheimen, the central mountain massif of South Norway. Nor J Bot 18:1–48.

———, Torkelsen AE. 1996. Part 3: Fungi I. Basidiomycota: Agaricales, Gasteromycetales, Aphyllophorales, Exobasidiales, Dacrymycetales and Tremellales. In: Elvebakk A, Prestrud P., eds. A catalogue of Svalbard plants, fungi, algae and cyanobacteria. Norsk Polarinstitutt Skrifter 198. p 173–206.

Hagen A. 1950. Notes on Arctic fungi. 1. Fungi from Jan Mayen. Norsk Polarinst. Skr. Oslo 93:1–11.

Hallgrímsson H. 1981. Islenzkir hattsveppir. 5. Preliminary account of the Icelandic species of Tricholomataceae. Acta Bot Isl 6:29–41.

———. 1998. Checklist of Icelandic fungi V: Agarics. Náttúrufræðistofnun Íslands.

———, Kristinsson H. 1965. Ueber die Höhengrenzen der Pflanzen im Eyafjardarsvaedinu, Nord-Island. Flora 3:67–68.

Heim R. 1924. Une exposition mycologique automnale à Gap. Bull Soc Mycol France 40:193–206.

Henning E. 1885. Bidrag till svampfloran i Norges sydligare fjelltrakter. Oefvers Kongl Vet Akad Förhandl 5:49–74.

Hinkova Zw. 1958. Ueber die Verbreitung der Höheren Pilze im östlichen Rila-Gebirge (Bulgarien). Bulg Akad Nauk 6:131–160.

Horak E. 1960. Die Pilzvegetation im Gletschervorfeld (2290–2350 m) des Rotmoosferners in den Oetztaler Alpen. Nova Hedwigia 4:487–507.

Jacobsson S. 1984. Notes on the agarics in subalpine and alpine areas of western Märjedalen, Central Sweden. Windahlia 14:43–64.

Jumpponen A, Trappe JM, Cázares E. 2002. Occurrence of ectomycorrhizal fungi on the forefront of retreating Lyman Glacier (Washington, USA) in relation to time since deglaciation. Mycorrhiza 12:43–49.

Kalamees K, Vaasma M. 1993. Mycobiota of alpine and subalpine sites of Kamchatka. In: Petrini O, Laursen GA., eds. Arctic and Alpine Mycology. Vols. 3–4. Berlin-Stuttgart: J Cramer. p 121–131.

Kallio P, Kankainen E. 1964. Notes on the macromycetes of Finnish Lapland and adjacent Finnmark. Ann Univ Turku A, II:32. (Rep Kevo Subarctic Sta 1):178–235.

Karsten PA. 1872. Fungi ex insulis Spetsbergen et Beeren Eiland collecti. Oefvers. K. Vet Akad Förhandl 2:91–108.

Kernaghan G, Currah RS. 1998. Ectomycorrhizal fungi at tree line in the Canadian Rockies. Mycotaxon 69:39–80.

Klironomos JN, Hart MM. 2001. Animal nitrogen swap for plant carbon. Nature 410:651–652.

Kobayasi Y, Hiratsuka N, Korf RP, Tubaki K, Aoshima K, Soneda M, Sugiyama J. 1967. Mycological studies of the Alaskan arctic. Annual Report of the Institute for Fermentation, Osaka 3:1–138.

———, Tubaki K, Soneda M. 1968. Enumeration of the higher fungi, moulds and yeasts of Spitsbergen. Bulletin of the Natural Science Museum Tokyo, 11(1), 33–80.

———, Hiratsuka N, Otani Y, Tubaki K, Udagawa S, Sugiyama J, Konno K. 1971. Mycological studies of the Angmagssalik region of Greenland. Bull Nat Sci Mus Tokyo 14:1–96.

Körner C. 1999. Alpine plant life: functional plant ecology of high mountain ecosystems. Berlin: Springer-Verlag. 338 p.

Kornerup A, Wanscher JH. 1967. Methuen Handbook of Colour. 2nd ed. London: Methuen Co. 243 p., 30 pl.

Kropp BR, Mueller GM. 1999. *Laccaria*. In: Cairney JWG, Chambers SM., eds. Ectomycorrhizal Fungi: Key Genera in Profile. Berlin: Springer Press. p 65–88.

Kühner R, Lamoure D. 1986. Catalogue des Agaricales (Basidiomycetes) de la zone alpine du Parc Nationale de la Vanoise et des régions limitrophes. Trav Sci Parc Nat Vanoise 15:103–187.

Lahaie DG. 1981. The genus *Laccaria* in the boreal forest of eastern Canada [Master's thesis]. Toronto: University of Toronto. 211 p.

Lamoure D. 1982. Agaricales de la zone alpine du Parc National des Ecrins. Trav. Scient. Parc Nat. Ecrins 2:119–123.

———, Lange M, Petersen PM. 1982. Agaricales found in the Godhavn area, W. Greenland. Nord J Bot 2:85–90.

Lange M. 1946. Mykologiske indtryk fra Lapland. Friesia 3:161–170.

———. 1948. Macromycetes I: The Gasteromycetes of Greenland. Meddelelser om Grønland 147(4):1–32.

———. 1955. Macromycetes II: Greenland Agaricales (Pleurotaceae, Hygrophoraceae, Tricholomataceae,

Amanitaceae, Agaricaceae, Coprinaceae, and Strophariaceae). Meddelelser om Grønland 147(11):1–69.
———. 1957. Macromycetes III: I. Greenland Agaricales, Macromycetes caeteri. II. Ecological and plant geographical studies. Meddelelser om Grønland 148(2): 1–125.
———, Skifte O. 1967. Notes on the macromycetes of northern Norway. Acta Borealia 23. 51 p.
Largent DL, Johnson D, Watling R. 1977. How to identify mushrooms to genus III: microscopic features. Eureka, California: Mad River Press. 148 p.
Larsen P. 1923. Fungi. In: Gandrup J., ed., A botanical trip to Jan Mayen Danks Bot Ark 4:23–24.
———. 1932. Fungi of Iceland. Bot Ice 9:449–607.
Laursen GA, Ammirati JF. 1982. The FISAM [First International Symposium on Arcto-Alpine Mycology] in retrospect. In: Laursen GA, Ammirati JF., eds. Arctic and alpine mycology. Seattle: University of Washington Press. p 532–544.
———, Chmielewski MA. 1982. The ecological significance of soil fungi in arctic tundra. In: Laursen GA, Ammirati JF., eds. Arctic and alpine mycology. Seattle: University of Washington Press. p 432–488.
Lebedeva L. 1927. Champignons de la côte arctique de la Sibérie. Trav. Comm. Etude Rep Aut Sov Soc Iakoute 12:1–23.
Lei JY, Wong KKY, Piché Y. 1991. Extracellular concanavalin A-binding sites during early interactions between *Pinus banksiana* and two closely related genotypes of the ectomycorrhizal basidiomycete *Laccaria bicolor*. Mycol Res 95(3):357–363.
Lindblom AE. 1841. Förtekning öfver de på Spetsbergen och Beeren Eiland anmärkta växter. Bot Not 1839–1840:153–158.
Linder DH. 1947. Fungi. In: Polunin N., ed., Botany of the Canadian eastern Arctic. Bull Nat Mus Can 97: 234–283.
Linkins A, Antibus R. 1982. Mycorrhizae of *Salix rotundifolia* in coastal arctic tundra. In: Laursen GA, Ammirati JF., eds. Arctic and alpine mycology. Seattle: University of Washington Press. p 509–525.
Lo Bue G, Montacchini F, Ceruti A. 1994. Macromycetes of the alpine belt: mycocoenological investigations in the western Italian Alps by multivariate methods. Coenoses 9(3):103–153.
Lutzoni F, Wagner P, Reeb V, Zoller S. 2000. Integrating ambiguously aligned regions of DNA sequences in phylogenetic analyses without violating positional homology. Syst Biol 49:628–651.
Marx DH. 1969. The influence of ectotrophic mycorrhizal fungi on the resistance of pine roots to pathogenic infections. I. Antagonism of mycorrhizal fungi to root pathogenic fungi and soil bacteria. Phytopathology 59:153–163.
Miadlikowska J, McCune B, Lutzoni F. 2002. *Pseudocyphellaria perpetua*, a new lichen from Western North America. The Bryologist 105:1–10.
Miller OK Jr. 1982a. Mycorrhizae, mycorrhizal fungi and fungal biomass in subalpine tundra at Eagle Summit, Alaska. Holarc Ecol 5:125–134.
———. 1982b. Higher fungi in Alaskan subarctic tundra and taiga plant communities. In: Laursen GA, Ammirati JF., eds. Arctic and alpine mycology. Seattle: University of Washington Press. p 123–149.
———, Laursen GA, Calhoun WF. 1974. Higher fungi in Arctic plant communities. U.S. IBP, Tundra Biome Data Rep 74–76.
———, ———, Farr DF. 1982. Notes on Agaricales from arctic tundra in Alaska. Mycologia 74(4):576–591.
Møller FH. 1945. Fungi of the Faeröes. 1. Basidiomycetes. Copenhagen. 295 p.
Moncalvo JM, Lutzoni FM, Rehner SA, Johnson J, Vilgalys R. 2000. Phylogenetic relationships of agaric fungi based on nuclear large subunit ribosomal DNA sequences. Syst Biol 49(2):278–305.
Mueller GM. 1991. The Swedish taxa of *Laccaria* (Tricholomataceae) with notes on their distribution. Nord Jour Bot 10:665–680.
———. 1992. Systematics of *Laccaria* (Agaricales) in the continental United States and Canada, with discussions on extralimital taxa and descriptions of extant types. Fieldiana, Botany, New Series 30:1–158.
———, Strack BA. 1992. Evidence for a mycorrhizal host shift during migration of *Laccaria trichodermophora* and other agarics into neotropical oak forests. Mycotaxon 65:249–256.
———, Vellinga EC. 1986. Taxonomic and nomenclatural notes on *Laccaria* B. & Br.: *Laccaria amethystea, L. fraterna, L. laccata, L. pumila*, and their synonyms. Persoonia 13(1):27–43.
Müller E, Magnuson JA. 1987. On the origin and ecology of alpine plant parasitic fungi. In: Laursen GA, Ammirati JF, Redhead SA., eds. Arctic and Alpine Mycology II. New York: Plenum Press. p 3–16.
Murr J. 1920. Die Pilze unserer Alpen. Feldk. Anzeiger, 62–70(4.VIII.–1.IX.1920):1–5.
Nespiak A. 1953. Mycotrophy of the alpine vegetation of the Tatra Mts. Acta Soc Bot Pol 22:97–125.
———. 1961. Research on mycotrophism of the alpine vegetation in the granite parts of the Tatra Mts. over the limit of *Pinus mugho*. Acta Soc Bot Pol 22:97–125.
Ohenoja E. 1971. The larger fungi of Svalbard and their ecology. Rep. Kevo Subarctic Res Stat 8:122–147.
Onipchenko FVG, Kaverina EN. 1989. Makromyceten der Hochgebirgsregionen des Naturschutzparkes von Teberda (NW-Kaukasus). Wasserpflanzen, Flechten, Pilze und Moose in Naturschutzparken der RSFSR, ZNIL 28–34.
Osmundson TW. 2003. Systematics of Rocky Mountain alpine *Laccaria* (Basidiomycota, Agaricales, Tricholomataceae) and ecology of Beartooth Plateau alpine macromycetes [Master's thesis]. Bozeman: Montana State Univ. 246 p.
Parmalee JA. 1969. Fungi of central Baffin Island. The Canadian Field Naturalist 83:48–53.
Petersen PM. 1977. Investigations on the ecology and phenology of the macromycetes in the Arctic. Meddelelser om Grønland 199:1–72.
Podila GK, Zheng J, Balasubramanian S, Sundaram S, Hiremath S, Brand JH, Hymes MJ. 2002. Fungal gene

expression in early symbiotic interactions between *Laccaria bicolor* and red pine. Plant and Soil 244:117–128.

Polunin N. 1934. The Flora of Akpatok Island, Hudson Strait. J. Bot. 72:197–204.

Redhead SA. 1989. A biogeographical overview of the Canadian mushroom flora. Can Jour Bot 67:3003–3062.

Reid DA. 1979. Some fungi from Spitsbergen. Reports of the Kevo Subarctic Research Station 15:41–47.

Remy L. 1964. Contribution à l'étude de la flore mycologique briançonnaise. Bull Soc Mycol France 80:459–585.

Rolland L. 1899. Excursions à Chamonix. Bull. Soc Mycol France 25:73–78.

Rostrup E. 1891. Tillaeg til Grønlands svampe (1888). Meddelelser om Grønland 3:591–643.

———. 1894. Øst-Grønlands svampe. Meddelelser om Grønland 18:45–81.

———. 1904. Fungi Groenlandiae orientalis in expeditionibus G. Amdrup 1898–1902. Meddelelser om Grønland 30:113–121.

Saccardo PA, Peck CH, Trelease W. 1910. The fungi of Alaska. Family Agaricaceae. In: Cardot J, et al. eds. Cryptog Bot Harriman Alaska Ser, 5:44–49.

Sambrook J, Fritsch EF, Maniatis T. 1989. Molecular cloning: a laboratory manual. 2nd ed. Cold Spring Harbor, New York: Cold Spring Harbor Laboratory. Vol. 3.

Senn-Irlet B. 1987. Oekologie, Soziologie und Taxonomie alpiner Makromyceten (Agaricales, Basidiomycetes) der Schweizer Zentralalpen [Doctoral dissertation]. Bern: Universitat Bern. 310 p. As cited in Graf 1994.

———. 1988. Macromycetes in alpine snow-bed communities—mycocoenological investigations. Acta Bot Neerl 37(2):251–263.

———. 1992. Botanischer Reichtum am Weg von Davos über die Bergüner Furgga zum Albula: Sommerexcursion 1991 im Anklang an die erste Excursion der Schweizerischen Botanischen Gesellschaft 1890. 6. Makromyzeten (Basidiomycota, Agaricales, Aphyllophorales). Bot Helv 102:49–59.

———. 1993. The mycoflora of alpine mire communities rich in *Salix*. In: Petrini O, Laursen GA., eds. Arctic and alpine mycology 3. Berlin-Stuttgart: J. Cramer. p 235–249.

Singer R. 1930. Pilze aus dem Kaukasus. Ein Beitrag zur Flora des SW Zentralkaukasus. Beih. Bot. Cbl. 46:71–113.

———. 1967. Terrestrial life of Antarctica. In: Bushnell V., ed. Antarctic Map Folio vol Series 5: p. 15–17.

———. 1967. Notes sur le genre *Laccaria*. Bulletin Trimestriel de la Société Mycologique de France 83:104–123.

———. 1977. Die gruppe der *Laccaria laccata* (Agaricales). Plant Sys Evol 126:347–370.

———. 1986. The Agaricales in modern taxonomy. 4th ed. Koenigstein, Germany: Koeltz Scientific Books. 981 p.

Sivertsen S. 1993. *Laccaria pumila* Fayod and *L. altaica* Sing. —are they really synonyms? Polarflokken 17:331–338.

Skifte O. 1979. Storsopp på Svalbard. Ottar 110–112, 29–39. As cited in Gulden & Torkelsen 1996.

Smaglik P. 2000. US climate report underlines local impacts of warming. Nature 405:725.

Swofford DL. 2001. PAUP (Phylogenetic Analysis Using Parsimony) 4.0b command reference. Sunderland, Massachusetts: Sinauer Associates, Inc. 142 p.

Thompson JD, Gibson TJ, Plewniak F, Jeanmougin F, Higgins DG. 1997. The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucl Acids Res 24:4876–4882.

Tomilin BA. 1971. Some data on the geographical distribution and ecology of the fungi in the region of the Taimyr Station. In: Acad. Sci. USSR. Biogeocenoses of Taimyr Tundra and their productivity, p 130–137.

Tommerup IC, Bougher NL, Malajczuk N. 1990. *Laccaria* species ectomycorrhizal with Eucalypts: why does the ecology of bisporic species differ from quadrisporic species? [abstract]. Proceedings of the 8th North American Conference on Mycorrhizae. Jackson, Wyoming, USA, Sep 5–9, 1990.

Trimbach J. 1978. Materiél pour une ''check-list'' des Alpes Maritimes. Doc Mycol VII, 29:39–53.

Väre H, Vestberg M, Eurola S. 1992. Mycorrhiza and root-associated fungi in Spitsbergen. Mycorrhiza 1:93–104.

Vasilkov BP. 1971. Macromycetes in the region of the Taimyr Station. In: Wielgolaski FE, Throsswall T., eds., Proceedings of the 4th. International Meeting on the Biological Productivity of Tundra (Biocenoses of Taimyr Tundra and Their Productivity), Acad Sci USSR, Leningrad. p 145–150.

Watling C, Watling R. 1988. Svalbard fungi. British Schools' Exploration Soc. Rep. 1987–1988. As cited in Gulden & Torkelsen 1996.

Watling R. 1977. Larger fungi from Greenland. Astarte 10:61–71.

———. 1981. Relationships between macromycetes and the development of higher plant communities. In: Wicklow DT, Carroll GC., eds. The Fungal Community: Its Organization and Role in the Ecosystem. New York: Marcel Denker, Inc. p 427–458.

———. 1983. Larger cold-climate fungi. Sydowia, Ann Mycol Ser II 36:308–325.

———. 1987. Larger arctic-alpine fungi in Scotland. In: Laursen GA, Ammirati JF, Redhead SA., eds. Arctic and Alpine Mycology II. New York: Plenum Press. p 17–45.

———. 1992. The fungus flora of Shetland. Edinburgh: Royal Botanical Garden Edinburgh. 98 p.

Weiss M, Yang ZL, Oberwinkler F. 1998. Molecular phylogenetic studies in the genus *Amanita*. Can J Bot 76:1170–1179.

Woldmar AS. 1969. Svalbards storsvampar i litteratur och natur. Friesia 9:283–288.