

Notes on the genus *Lactarius* from the Rocky Mountain alpine zone in regard to Finnish arctic-alpine species

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Lactarius is an important ectomycorrhizal genus (Basidiomycota, Russulales) and a subset of species occur in arctic and alpine habitats. These species are well known in Europe, Greenland, Svalbard and Scandinavia; however there is scant information from the Rocky Mountain alpine zone in North America. Here we report five *Lactarius* species from above 3000 m at latitude 45° N in the northern Rockies and above 3700 m at latitude 36° – 38° N in the southern Rockies. *Lactarius lanceolatus*, *L. nanus*, *L. salicis-reticulatae* and *L. repraesentaneus* are reported with *Salix* species and *L. glyciosmus* with *Betula glandulosa*. All have been recorded from Finland at 68° – 70° N at much lower elevations (300–1000 m) in the alpine, subarctic and subtemperate zones.

Key words: ectomycorrhizal, North America, Rocky Mountains, Russulales, *Salix*, arctic-alpine mycology

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Introduction

Lactarius is a diverse genus with over 400 species described worldwide (Verbeken 2001). In the northern hemisphere, *Lactarius* is ectomycorrhizal and particular species may be restricted to certain host plants (Heilmann-Clausen et al. 1998). A limited number of *Lactarius* species occur in arctic and alpine habitats in the Northern Hemisphere where they are primarily associated with *Salix*, *Betula* and *Dryas*. Research has shown that shrubs (primarily willows) are expanding their range in arctic and alpine tundra (Sturm et al. 2001). DeSlippe et al. (2011) suggest that increased mycorrhizal diversity and larger mycorrhizal networks may further increase shrub expansion in the arctic, highlighting the importance of ectomycorrhizal fungi in this

system. Thus the limited number of ectomycorrhizal fungi (including *Lactarius*) able to associate with shrubs in cold, harsh environments may become increasingly important as climate change shifts microbial communities (Cripps & Eddington 2005).

Thirty to forty species of *Lactarius* have been reported from arctic-alpine habitats in Alaska (Miller et al. 1973, Laursen & Ammirati 1982, Geml et al. 2009), the Canadian Arctic (Ohenoja 1972, Ohenoja & Ohenoja 1993, 2010), Greenland (Lange 1955, Knudsen & Borgen 1982, Borgen et al. 2006), Svalbard (Ohenoja 1971, Gulden & Torkelsen 1996, Geml et al. 2012), Iceland (Hallgrímsson 1993), Norway (Gulden et al. 1985, Gulden & Jenssen 1988, Gulden 2005), Sweden (Knudsen & Vesterholt 2012) Finland (Kallio & Kankainen 1964, Kallio

1982, Korhonen 1984, Gulden et al. 1985, Ohe-
noja 1996, Knudsen & Vesterholt 2012), the Alps
(Favre 1955, Kühner 1975, Bon 1985, Senn-Irlet
1988, Bon 1998, Graf 1994, Jamoni 1995, Krän-
zlin 2005), the Pyrenees (Corriol 2008), the Car-
pathians (Ronikier 2008), and the Urals (Knud-
sen & Mukhin 1998).

A few papers have addressed other genera
from the Rocky Mountain alpine zone south of
the Canadian border, including *Amanita* (Cripps
& Horak 2010), *Laccaria* (Osmundson et al.
2005), *Inocybe* (Cripps et al. 2010), *Arrhenia*
(Cripps & Horak 2006) and *Hebeloma* (Miller
& Evenson 2001) but none have addressed the
genus *Lactarius* in the North American alpine
tundra outside of Alaska, Greenland, and Arctic
Canada. In North America, over 200 species of
Lactarius have been reported by Hesler & Smith
(1979) but arctic-alpine species were not covered.

Previously, a few *Lactarius* species were in-
cluded in checklists from the Rocky Mountain
alpine zone (Cripps & Horak 2008, Cripps &
Ammirati 2010a,b) and here we report actual
collection data with ecological notes. Most are
the first official reports of these species from
the Rocky Mountain alpine zone south of the
Canadian border. All of the species reported are
known from Finland at lower elevations and
comparisons will be made as to ecology. Results
from phylogenetic analysis of the internal tran-
scribed spacer (ITS) region of ribosomal DNA
and the region between conserved domains 6 and
7 of the nuclear gene encoding the second large-
est subunit of RNA polymerase II (*rpb2*) are cur-
rently being compiled for North American and
Eurasian (including some Finnish) collections
of the taxa presented in this paper. This article
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Material and methods

In North America the Rocky Mountains extend from New
Mexico to Alaska and consists of widely dispersed frag-
mented islands of alpine tundra on mountain tops. In this
study, all sites are south of the U.S.A. – Canadian border
(Fig. 1). The study sites in the north-central Rocky
Mountains are on the Beartooth Plateau above treeline
at 3000 m a.s.l. and extend along the Montana/Wyoming

border at latitude 45° N (Fig. 2). The plateau is comprised
of a mosaic of meadows, wetlands and talus fields with
predominantly granite-derived soils (Johnson & Bill-
ings 1962). The southern Rocky Mountain sites sit above
the treeline at 3700 m a.s.l. in the Front Range, Sawatch
Range, and San Juan Range of Colorado at latitudes
between 36° N and 38° N. These sites extend along the
Continental Divide encompassing a wide range of alpine
habitats, including meadows, wetlands, dwarf *Salix* and
Dryas patches, and talus fields (Eddleman & Ward 1984).
The soils throughout the range of study sites in Colorado
vary considerably, from granitic to limestone-derived.
Climatic data for the southern tundra is scarce but can be
found in Bowman & Seastedt (2001).

The primary ectomycorrhizal plants of Rocky Mountain
alpine areas include dwarf willows *Salix reticulata* L.,
S. arctica Pall. and rarely *S. rotundifolia* Trautv. and
S. cascadiensis Cockerell. Of shrub willows *S. glauca* L. is
more common in the south and *S. planifolia* Pursch is
more common in the north; the bog-birch *Betula glandu-
losa* Michx. occurs only sporadically in each area (Scott
1995). The mat forming *Dryas octopetala* L. is host to
some ectomycorrhizal fungi in this alpine environment,
however no *Lactarius* species were found in association
with this plant.

Specimens were collected from late July to late August
and from 1997 through 2011. Selected collections were
photographed and described in detail. All were dried
and stored either at Montana State University, Bozeman
(MONT) or the Institute of Integrative Biology, ETH,
Zurich, Switzerland (ZT). Dried material was reconsti-
tuted with ethanol and microscopic features examined in
Melzer's solution (spores) or 2.5% potassium hydroxide
(cystidia and basidia). For a random sample of 25 ba-
sidiospores, length and width was measured, excluding
ornamentation and hilar appendix. Maximum height of
the ornamentation was also measured, and the pattern of
ornamentation described. Length and width of ten pleu-
rocystidia, ten cheilocystidia and five basidia were mea-
sured (data not shown). Comparisons were made to known
species of *Lactarius* for identification. Comparisons to
species from Finland are included for each species as to
occurrence and ecological notes.

Results and discussion

Lactarius glyciosmus (Fr.) Fr.

Short diagnosis for Rocky Mountain specimens:
this species is recognized by the glaucous, more
or less papillate, pale gray-brown to mauve
(purple-brown), azonate to slightly zoned pi-
leus, cream to pale orange lamellae, pale yellow
to drab orange-brown stipe, watery, clear latex,
mild taste and odor of coconut. The spores are
6–9 × 5–7 μm, on average 7.6 × 6 μm, broadly
ellipsoid to ellipsoid, with ornamentation up to

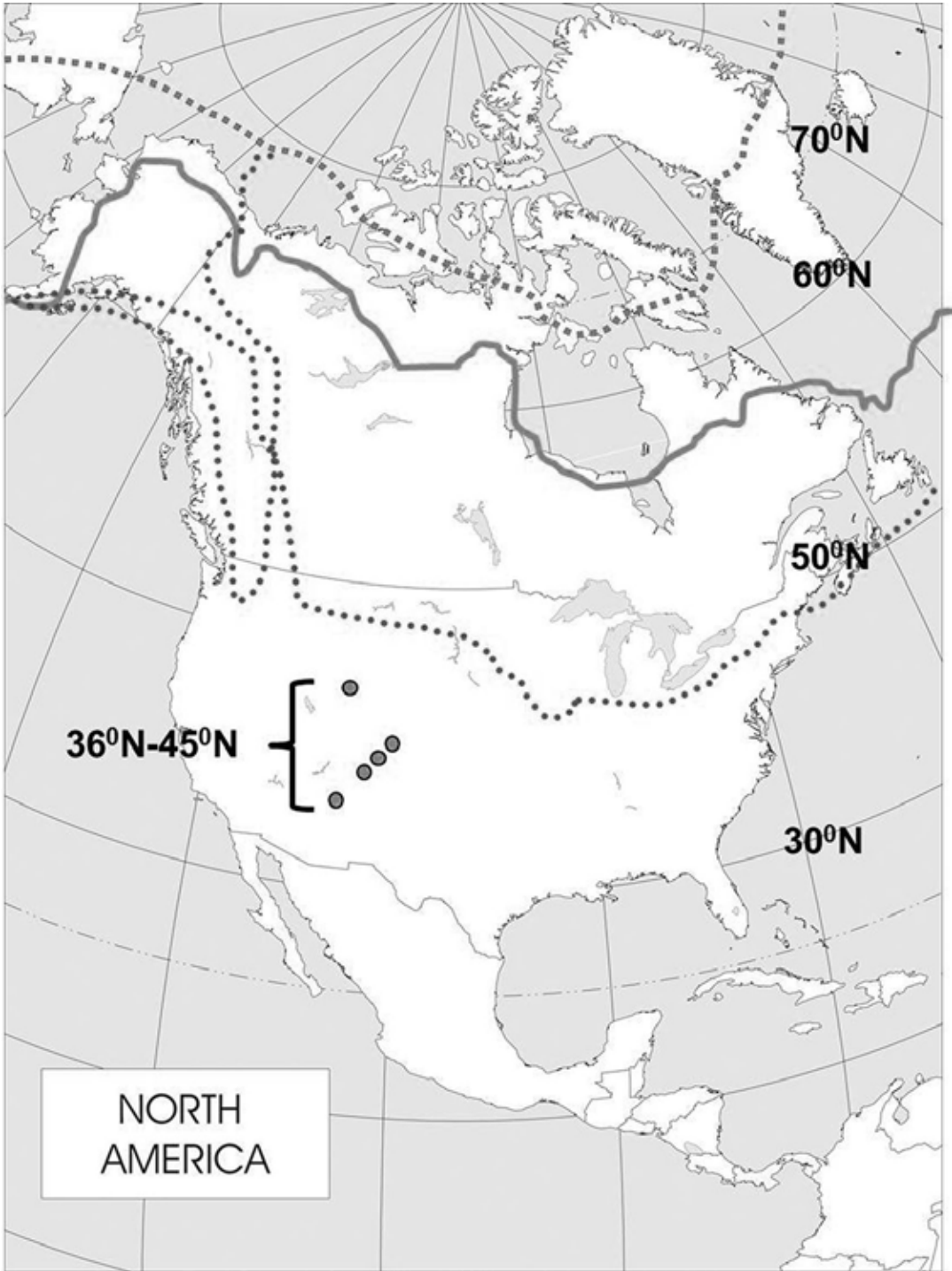


Fig.1. Map of collecting sites in the Rocky Mountain alpine zone. The highest dotted line indicates the boundary of the high Arctic; solid line is the northern limit of trees; lower dotted line is the extent of sheet glaciers; and the dots locate the collecting sites.



Fig. 2. Beartooth Plateau, Rocky Mountains, USA: latitude 45°N and elevation 3300 m. Photo: C. Cripps.



Fig. 3. Example of *Lactarius nanus* (EB 125) in the Rocky Mountain alpine zone. Photo: C. Cripps.

0.5 μm high, consisting of elongated warts and ridges forming an incomplete reticulum. It is the only *Lactarius* species we have found with alpine *Betula glandulosa* in the Rocky Mountains in this region.

Rocky Mountain ecology: This species occurs in the low alpine zone (3000 m) on the Beartooth Plateau and also in the alpine–subalpine zone in Colorado with *Betula glandulosa*. This species is not often encountered as *Betula* is rare in the alpine zone of the Rocky Mountains south of the Canadian border. It also occurs with bog birch below timberline.

Specimens studied: U.S.A. Colorado. Gunnison County, Cumberland Pass/Quartz Creek, 4.VIII.2001 *Cripps 1652* (MONT). Montana. Carbon County, Beartooth Pass, 28.VII.1997 *Cripps 1134* (MONT), 10.VIII.1999 *Osmundson 269* (MONT), 19.VIII.1999 *Cripps 1380* (MONT), 13.VIII.2007 *Horak 1273* (ZT). Wyoming. Park County, Beartooth Plateau, 8.VIII.1998 *Cripps 1217* (MONT).

Smith & Hesler (1979) reported this species from subalpine habitats with *Betula* and *Alnus* from eastern, central, and western U.S.A. and Canada. For arctic-alpine areas of North America, it has also been reported from Alaska (Laursen & Ammirati 1982, Geml et al. 2009), the Northwest Territories of arctic Canada (Ohenoja & Ohenoja 1993, 2010) and Québec (Hutchison et al. 1988) near mixed *Betula* and *Salix* spp. It is also known from Greenland (Knudsen & Borgen 1982, Elborne & Knudsen 1990, Borgen et al. 2006) and many arctic-alpine areas across the northern hemisphere where it associates primarily with *Betula* species. This includes Iceland (Halgrímsson 1993), the Alps (Bon 1985, 1998, Graf 1994) and Svalbard (Gulden & Torkelsen 1996). It is recorded from Finland and other Scandinavian countries with *Betula* in alpine as well as subtemperate and subarctic areas at low elevations (Kallio & Kankainen 1964, Korhonen 1984, Ohenoja 1996, Knudsen & Vesterholt 2012). Subalpine fruiting bodies can be much larger than our alpine specimens and there appears to be large variation in size and coloration for this species (Heilmann-Clausen et al. 1998).

Lactarius lanceolatus O.K. Mill. & Laursen

Short diagnosis for Rocky Mountain specimens: this is the only species found to date from our alpine sites with an overall orange brown or red brown fruiting body and pale orange lamellae and stipe. The latex is colorless, the taste mild, and odor faint. Spores are 7–9 \times 6.5–8 μm , on average 8.6 \times 7.2 μm , subglobose to ellipsoid; ornamentation is to 0.5 μm high, of fine ridges and isolated warts forming an incomplete reticulum. Cystidia are large and lanceolate, but this may not be completely diagnostic as other species also have long cystidia.

Rocky Mountain ecology: This species is recorded in the alpine zone with willow (primarily *S. reticulata*) from several areas of the Beartooth Plateau at elevations of 3100–3300 m.

Specimens examined: U.S.A. Montana. Carbon County, Beartooth Plateau, Highline Trail, 20.VIII.1999 *Cripps 1389* (MONT), 5.VIII.2008 *Cripps 2358* (MONT), 1.VIII.1997 *Horak 6214* (ZT), 7.VIII.1998 *Horak 6412* (ZT); Solifluction Terraces, 13.VIII.2007 *Cripps 2319* (MONT).

Lactarius lanceolatus was first described from the Alaskan tundra (Miller et al. 1973) and is also reported from Arctic Canada (Ohenoja & Ohenoja 1993, 2010) for North America. A taxon with an affinity to this species has been described by Laursen & Ammirati (1982) from Alaska with *Salix* and *Betula*. *Lactarius lanceolatus* is reported from Greenland (Borgen et al. 2006), Siberia (Knudsen & Muhkin 1998), Svalbard (Gulden & Jenssen 1988, Gulden & Torkelsen 1996) and the Alps (Bon 1998) mostly with *Salix* species. It may have been reported from other Arctic-alpine areas as *L. aurantiacus* (Pers. : Fr.) Gray. It is reported from the Enontekiön Lappi area of Finland, Swedish Lapland (Kühner 1975), Northern Norway (Gulden et al. 1985) and other Scandinavian countries (Knudsen & Vesterholt 2012) at much lower elevations.

Lactarius nanus J. Favre

– Fig. 3

Short diagnosis for Rocky Mountain specimens: this species is recognized by the tiny fruiting bodies (typically 1–2 cm in diam.), moist, mauve

or brownish cap, well-separated pale orange lamellae, pale orange stipe, clear latex, sharp taste and indistinct odor. Spores are $7\text{--}10 \times 6\text{--}8 \mu\text{m}$, on average $8.4 \times 6.9 \mu\text{m}$, subglobose to ellipsoid; the ornamentation is to around $0.7 \mu\text{m}$ high, of ridges and warts, connected to form an incomplete reticulum.

Rocky Mountain ecology: this species occurs in wet areas of the alpine zone with dwarf *Salix* species, primarily *S. arctica* on our sites in both the northern and southern Rocky Mountains from 3100–3840 m.

Specimens examined: U.S.A. Colorado. San Juan County, San Juan Mountains, Black Bear Pass, 11.VIII.2001 *Cripps 1716* (MONT), Cinnamon Pass, 27.VIII.2002 *Cripps 1801* (MONT), 11.VIII.2001 *Horak 9529* (ZT). Montana. Carbon County, Beartooth Plateau, Highline Trailhead, 8.VIII.1998 *Cripps 1221* (MONT), 8.VIII.1998 *Horak 6422* (ZT), 21.VIII.1999 *Cripps 1403* (MONT), 11.VIII.2012 *EB 125* (MONT).

The tiny *L. nanus* occurs with dwarf willows and is easily overlooked because of its small size and drab color. The first report of this species in North America was from the Beartooth Plateau at 3200 m. with *Salix reticulata* and *Salix* spp. (Moser & McKnight 1987). Here we extend its range with the first reports from the southern Rockies still with dwarf willow. It is also reported from arctic Canada with *Salix* (Ohenoja & Ohenoja 1993, 2010) and from Greenland (Knudsen & Borgen 1982, Borgen et al. 2006). It occurs in many other arctic-alpine habitats (Favre 1955, Kühner 1975, Graf 1994, Jamoni 1995, Gulden & Torkelsen 1996, Gulden et al. 1985, Bon 1998, Corriol 2008, Ronikier 2008). Ronikier (2008) suggests it may be more common in the alpine than the arctic and she presents a complete list of references. It is also reported with *S. herbacea* L. (Gulden et al. 1985, Graf 1994) and *S. retusa* L. (Kränzlin 2005). This species is known from several Nordic countries and from Finnmark (Ohenoja 1996), and is reported as possibly occurring in Finland (Gulden et al. 1985).

Lactarius repraesentaneus Britzelm.

Short diagnosis for Rocky Mountain specimens: this robust species has a thick golden brown cap with bearded margin, ochre lamellae and stipe, lilac-staining milk, a mild taste and fruity odor. Spores are $8\text{--}11 \times 6\text{--}9 \mu\text{m}$ in diameter, on average $9.2 \times 7.4 \mu\text{m}$, subglobose to ellipsoid; ornamentation is up to $0.7 \mu\text{m}$ high comprised of somewhat broad ridges, forming an incomplete to almost complete reticulum.

Rocky Mountain ecology: This species occurs on our northern and southern Rocky Mountain sites in the alpine zone. The fleshy *L. repraesentaneus* appears to occur with *Salix glauca* in alpine areas of Colorado on the more calcareous soils of Cottonwood and Independence Pass (elevations of 3600–3700 m). It is also reported from the Beartooth Plateau where *S. glauca* is present (elevation 3000 m). Most areas are near krummholz where conifers are possible. These are the first reports of this species in Rocky Mountain alpine habitats.

Specimens examined: U.S.A. Colorado. Gunnison/Chaffee County, Sawatch Range, Cottonwood Pass, 4.VIII.2001 *Cripps 1643* (MONT); Pitkin/Lake County, Sawatch Range, Independence Pass, 14.VIII.2001 *Cripps 1747* (MONT), 14.VIII.2001 *Horak 9837* (ZT), 15.VIII.2001 *Horak 9537* (ZT). Wyoming. Park County, Beartooth Plateau, Frozen Lakes, 21.VIII.1999 *Cripps 1394* (MONT). Montana. Carbon County, Beartooth Plateau, East side, Site 1, 21.VIII.2002 *Cripps 1971* (MONT), 13.VIII.2007 *Cripps 2318* (MONT).

This species is also known to occur in subalpine habitats with conifers, particularly in spruce–fir forests of the northern USA and southern Canada (Hesler & Smith 1979). This includes Alaska, California, Colorado, Maine, Michigan, New Mexico, New Jersey, Vermont and Ontario. It is also reported from arctic areas of Alaska (Laursen & Ammirati 1982, Geml et al. 2009) and Greenland (Elborne & Knudsen 1990, Knudsen & Borgen 1982, Borgen et al. 2006) in North America. It has been found in subalpine areas of Europe with *Betula nana* (Heilmann-Clausen et al. 1998). It is known from arctic and alpine habitats in the Alps (Bon 1998) and Iceland (Hal-

grímsson 1993). In Finland and Scandinavia it occurs in the hemiboreal to subarctic/subalpine and alpine zones (Kallio & Kankainen 1964, Korhonen 1984, Ohenoja 1996, Knudsen & Vesterholt 2012) and is reported with *Picea* and *Betula*.

Lactarius salicis-reticulatae Kühner

Short diagnosis for Rocky Mountain specimens: this species is recognized by the viscid pale yellow pileus, pale orange or yellow pink lamellae, pale yellow cream stipe, white latex staining lilac, mild taste and fruity odor. Spores are 9–12 × 7.5–10 µm, on average 10.3 × 8.3 µm, subglobose to broadly ellipsoid; ornamentation is up to 0.3 µm high, of ridges and irregular warts, not forming a complete reticulum.

Rocky Mountain ecology: it occurs in the alpine zone with *Salix* species and particularly the dwarf willow *S. reticulata* and the shrubby willow *S. planifolia*. On the Beartooth Plateau it is at elevations of 3000 to 3200 m and in the southern Rocky Mountains at elevations of 3600 to 3800 m.

Specimens examined: **U.S.A. Colorado.** Pitkin/Lake County, Sawatch Range, Independence Pass, 13.VIII.2001 *Cripps 1741* (MONT), 13.VIII.2001 *Horak 9536* (ZT); San Juan County, San Juan Mountains, Stony Pass, 9.VIII.2001 *Cripps 1689* (MONT), 9.VIII.2001 *Horak 9792* (ZT), 13.VIII.2011 *Barge 0039* (MONT), Cinnamon Pass, 10.VIII.2001 *Cripps 1710* (MONT), Black Bear Pass, 11.VIII.2001 *Horak 9538* (ZT), Maggie Gulch, 11.VIII.2011 *Barge 0036* (MONT); Summit County, Front Range, 14.VIII.1997 *Cripps 1155* (MONT), 8.VII.1999 *Horak 8094* (ZT). **Montana.** Carbon County, Beartooth Plateau, Highline Trailhead, 8.VIII.1998 *Cripps 1211* (MONT), 8.VIII.2008 *Cripps 2378* (MONT); East side, Site 1, 29.VII.1997 *Cripps 1136* (MONT), 30.VII.1997 *Horak 6099* (ZT), 17.VIII.2011 *Cripps 2776* (MONT).

The only report we could find from North America is from Greenland (Borgen et al. 2006); it does not yet appear to be reported from Alaska at least under this name. It may be the same as collections called *L. aspideoides* Burlingham by

Laursen & Ammirati (1982) from Alaska and by Hutchison et al. (1988) from Québec. This is the first record for *L. salicis-reticulatae* in the Rocky Mountains other than a previous brief listing (Cripps & Horak 2008). It is widespread in arctic-alpine habitats and appears restricted to this zone and is not reported from subalpine forests. It is known from the Alps (Jamoni 1995, Bon 1998) and is typically recorded with dwarf willows, particularly *S. reticulata* and less commonly *S. herbacea* and *Dryas* (Jamoni 2008). It occurs in Finland, Norway and Sweden with dwarf and shrubby *Salix* and *Betula* (Kühner 1975, Korhonen 1984, Gulden 2005, Knudsen & Vesterholt 2012).

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References

- Bon, M. 1985: Quelques nouveaux taxons de la flore mycologique alpine. – Bulletin Trimestriel de la Fédération Mycologique Dauphiné-Savoie 25: 23–30.
- Bon, M. 1998: Clé monographique des lactaires alpins. – Bulletin Trimestriel de la Fédération Mycologique Dauphiné-Savoie, Juillet 150: 15–22.
- Borgen, T.A., Elborne, S.A. & Knudsen, H. 2006: A checklist of the Greenland basidiomycetes. In: Boertmann, D. & Knudsen, H. (eds). Arctic and Alpine Mycology 6. Proceedings of the Sixth International Symposium on Arcto-Alpine Mycology (ISAM 6), Greenland, 11–21 August 2000. – Meddelelser om Grønland, Bioscience 56: 37–59.
- Bowman, W.D. & Seastedt, T.R. (eds) 2001: Structure and Function of an Alpine Ecosystem: Niwot Ridge, Colorado. – 337 pp. Oxford Press. New York.
- Corriol, G. 2008: Checklist of Pyrenean alpine-stage macrofungi. In: Høiland, K. & Økland, R.H. (eds). Arctic and Alpine Mycology 7. – Sommerfeltia 31: 29–99.
- Cripps, C.L. & Ammirati, J. (eds) 2010a: Arctic and Alpine Mycology 8. – North American Fungi 5: 1–232.
- Cripps, C.L. & Ammirati, J. 2010b: Eighth International Symposium on Arctic-alpine Mycology (ISAM), Beartooth Plateau, Rocky Mountains, USA 2008. In: Cripps, C.L. & Ammirati, J.A. (eds). Arctic and Alpine Mycology 8. Proceedings of the Eighth International Symposium on Arctic-Alpine Mycology (ISAM 8), Beartooth Plateau, Rocky Mountains, U.S.A. August 6–11, 2008. – North American Fungi 5: 1–8.
- Cripps, C.L. & Eddington, L.E. 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 & Alpine Research* 37: 177–188.
- Cripps, C.L. & Horak, E. 2006: Ecology and worldwide distribution of *Arrhenia auriscalpium*: a true arctic-alpine fungus. In: Boertmann, D. & Knudsen, H. (eds). *Arctic and Alpine Mycology 6. Proceedings of the Sixth International Symposium on Arcto-Alpine Mycology (ISAM 6)*, Greenland, 11–21 August 2000. – *Meddelelser om Grønland, Bioscience* 56: 17–24.
- Cripps, C.L. & Horak, E. 2008: Checklist and Ecology of the Agaricales, Russulales and Boletales in the alpine zone of the Rocky Mountains (Colorado, Montana, Wyoming) at 3000–4000 m a.s.l. In: Høiland, K. & Økland, R.H. (eds). *Arctic and Alpine Mycology 7. – Sommerfeltia* 31: 101–121.
- Cripps, C.L. & Horak, E. 2010: *Amanita* in the Rocky Mountain alpine zone, USA: New records for *A. nivalis* and *A. groenlandica*. In: Cripps, C.L. & Ammirati, J.A. (eds). *Arctic and Alpine Mycology 8. Proceedings of the Eighth International Symposium on Arctic-Alpine Mycology (ISAM 8)*, Beartooth Plateau, Rocky Mountains, U.S.A. August 6–11, 2008. – *North American Fungi* 5: 9–22.
- Cripps, C.L., Larsson, E. & Horak, E. 2010: Subgenus *Mallochybe* (*Inocybe*) in the Rocky Mountain alpine zone with molecular reference to European arctic-alpine material. In: Cripps, C.L. & Ammirati, J.A. (eds). *Arctic and Alpine Mycology 8. Proceedings of the Eighth International Symposium on Arctic-Alpine Mycology (ISAM 8)*, Beartooth Plateau, Rocky Mountains, U.S.A. August 6–11, 2008. – *North American Fungi* 5: 97–126.
- DeSlipe, J.R., Hartmann, M., Mohn, W. & Simard, S. 2011: Long-term experimental manipulation of climate alters the ectomycorrhizal community of *Betula nana* in Arctic tundra. – *Global Change Biology* 17: 1625–1636.
- Eddleman, L.E. & Ward, R.T. 1984: Phytoedaphic relationships in alpine tundra of north-central Colorado, USA. – *Arctic, Antarctic & Alpine Research* 16: 343–359.
- Elborne, S. & Knudsen, H. 1990: Larger fungi associated with *Betula pubescens* in Greenland. In: Boertmann, D. & Knudsen, H. (eds). *Arctic and Alpine Mycology 6. Proceedings of the Sixth International Symposium on Arcto-Alpine Mycology (ISAM 6)*, Greenland, 11–21 August 2000. – *Meddelelser om Grønland, Bioscience* 33: 77–90.
- Favre, J. 1955: Les champignons supérieurs de la zone alpine du Parc Nationale Suisse. – *Resultats des recherches scientifiques entreprises au Parc Nationale Suisse* 5: 1–212.
- Geml, J., Laursen, G.A., Timling, I., McFarland, J., Booth, G., Lennon, N., Nusbaum, C. & Taylor, D. 2009: Molecular phylogenetic biodiversity assessment of arctic and boreal ectomycorrhizal *Lactarius* Pers. (Russulales; Basidiomycota) in Alaska, based on soil and sporocarp DNA. – *Molecular Ecology* 18: 2213–2227.
- Geml, J., Timling I., Robinson, C., Lennon, N., Nusbaum, C., Brochmann, C., Noordeloos, M.E. & Taylor, D.L. 2012: An arctic community of symbiotic fungi assembled by long-distance dispersers: phylogenetic diversity of ectomycorrhizal basidiomycetes in Svalbard based on soil and sporocarp DNA. – *Journal of Biogeography* 39: 74–88.
- Graf, F. 1994: Ecology and sociology of macromycetes in snow-beds with *Salix herbacea* L. in the alpine Valley of Radont (Grisons, Switzerland). – 242 pp. *Dissertationes Botanicae*. J. Cramer: Berlin.
- Gulden, G. 2005: A preliminary guide to the macromycetes in the Finse area, Hardangervidda, Norway. – Draft presented at ISAM VII, Oslo, Norway.
- Gulden, G., Jenssen, K.M. & Stordal, J. 1985: *Arctic and Alpine Fungi* 1. – 62 pp. Soppkonsulentent. Oslo, Norway.
- Gulden, G. & Jenssen, K.M. 1988: *Arctic and alpine fungi* 2. – 58 pp. Soppkonsulentent. Oslo, Norway.
- Gulden, G. & Torkelsen, A.E. 1996: *Fungi I. Basidiomycota: Agaricales, Aphyllophorales, Exobasidiales, Dacrymycetales and Tremellales*. In: Elvebakk, A. & Prestrud, P. (eds). *A catalogue of Svalbard plants, fungi, algae and cyanobacteria*. – *Norsk Polarinstitutt, Skrifter* 198: 173–206.
- Hallgrímsson, H. 1993: Checklist of Icelandic fungi V: Basidiomycetes. – *Natturfurfa: oistofnun Norourlands: Akureyri Museum of Natural History* (unpublished).
- Heilmann-Clausen, J., Verbeke, A. & Vesterholt, J. 1998: The genus *Lactarius*. – *Fungi of Northern Europe* 2. 287 pp. Danish Mycological Society.
- Hesler, L.R. & Smith, A.H. 1979: *North American species of Lactarius*. – 841 pp. University of Michigan Press. Ann Arbor.
- Hutchison, L., Summerbell, R. & Malloch, D. 1988: Additions to the Mycota of North America and Québec: Arctic and boreal species from Schefferville, Northern Québec. – *Naturaliste canadien* 115: 39–56.
- Jamoni, P.G. 1995: Russulaceae della zona alpina. – *Rivista di Micologia* 38, Supplemento: 75–80.
- Jamoni, P.G. 2008: *Fungi alpine, delle zone alpine superiori e inferiori*. – 544 pp. Associazione Micologica Bresadola, Fondazione centro Studi Micologici. Trento.
- Johnson, P.L. & Billings, W.D. 1962: The alpine vegetation of the Beartooth Plateau in relation to cryopedogenic processes and patterns. – *Ecological Monographs* 32: 105–135.
- Kallio, P. 1982: Aspects of northern Finnish macromycology. – In: Laursen, G.A. & Ammirati, J.F. (eds). *Arctic and Alpine Mycology. The First International Symposium on Arcto-Alpine Mycology*: 410–431. University of Washington Press. Seattle.
- Kallio, P. & Kankainen, E. 1964: Notes on the macromycetes of Finnish Lapland and adjacent Finnmark. – *Reports from the Kevo Subarctic Research Station* 1: 178–235.
- Knudsen, H. & Borgen, T. 1982: Russulaceae in Greenland. – In: Laursen, G.A. & Ammirati, J.F. (eds). *Arctic and Alpine Mycology. The First International Symposium on Arcto-Alpine Mycology*: 216–244. University of Washington Press. Seattle.
- Knudsen, H. & Mukhin, V.A. 1998: The arctic-alpine agaric element in the Polar Urals and Yamal, Western Siberia. – In: Mukhin, V.A. & Knudsen, H. (eds): *Arctic and alpine Mycology* 5. *Proceedings of the Fifth International Symposium on Arcto-Alpine Mycology*

- (Labytnangi, Russia, August 15-27, 1996): 152–162. Yekaterinburg Publishers. Yekaterinburg, Russia.
- Knudsen, H., & Vesterholt, J., (eds) 2012: *Funga Nordica*. Agaricoid, boletoid, clavarioid, cyphelloid and gasteroid genera. – 1083 pp. Nordsvamp, Copenhagen.
- Korhonen, M. 1984: Suomen rouskut. – 223 pp. Otava. Keuruu, Finland [in Finnish].
- Kränzlin, F. 2005: *Fungi of Switzerland, Volume 6: Russulaceae*. – 317 pp. Verlag Mykologia. Luzern.
- Kühner, R. 1975: Agaricales de la zone alpine: *Lactarius*. – *Bulletin Trimestriel de la Société Mycologique de France* 91: 5–69.
- Lange, M. 1955: *Macromycetes, part II. Greenland Agaricales*. – *Meddelelser om Grønland* 147: 1–69.
- Laursen, G.A. & Ammirati, J.F. 1982: *Lactarii in Alaskan Arctic tundra*. – In: Laursen, G.A. & Ammirati, J.F. (eds): *Arctic and Alpine Mycology. The First International Symposium on Arcto-Alpine Mycology*: 245–281. University of Washington Press. Seattle.
- Miller, O.K., Jr. & Evenson, V. 2001: Observations on the alpine tundra species of *Hebeloma* in Colorado. – *Gilbertson Honorary Volume, Harvard Papers* 6: 155–162.
- Miller, O.K., Jr. Laursen, G. & Murray, B. 1973: Arctic and alpine agarics from Alaska and Canada. – *Canadian Journal of Botany* 51: 43–49.
- Moser, M. & McKnight, K. 1987: *Fungi (Agaricales, Russulales) from the alpine zone of Yellowstone National Park and the Beartooth Mountains with special emphasis on Cortinarius*. – In: Laursen, G.A., Ammirati, J.F. & Redhead, S. (eds). *Arctic and Alpine Mycology* 2: 299–317. Plenum Press. New York.
- Ohenoja, E. 1971: The larger fungi of Svalbard and their ecology. – Report from the Kevo Subarctic Research Station 8: 1221–1247.
- Ohenoja, E. 1972: Preliminary note on the botanical research at Rankin Inlet 1971. – *Muskox* 10: 67.
- Ohenoja, E. 1996: A check-list of the larger fungi in Inari Lapland (NE Finland) and in Finnmark (NE Norway). – *Kevo Notes* 11: 1–44.
- Ohenoja, E. & Ohenoja, M. 1993: *Lactarii of the Franklin and Keewatin Districts of the Northwest Territories, Arctic Canada*. – In: Petrini, O. & Laursen, G.A. (eds). *Arctic and Alpine Mycology* 3–4. Proceedings of the Third and Fourth International Symposium on Arcto-Alpine Mycology. – *Bibliotheca Mycologica* 150: 179–192.
- Ohenoja, E. & Ohenoja, M. 2010: Larger fungi of the Canadian Arctic. – In: Cripps, C.L. & Ammirati, J.A. (eds). *Arctic and Alpine Mycology* 8. Proceedings of the Eighth International Symposium on Arctic-Alpine Mycology (ISAM 8), Beartooth Plateau, Rocky Mountains, U.S.A. August 6-11, 2008. – *North American Fungi* 5: 85–96.
- Osmundson, T.W., Cripps, C.L. & Mueller, G.M. 2005: Morphological and molecular systematics of Rocky Mountain alpine *Laccaria*. – *Mycologia* 97: 949–972.
- Ronikier, A. 2008: Contribution to the biogeography of arctic-alpine fungi: first records in the Southern Carpathians (Romania). In: Høiland, K. & Økland, R.H. (eds). *Arctic and Alpine Mycology* 7. – *Sommerfeltia* 31: 191–211.
- Scott, R.W. 1995: *The alpine flora of the Rocky Mountains*. – 901 pp. University of Utah Press. Salt Lake City.
- Senn-Irlet, B. 1988: *Macromycetes in alpine snow-bed communities – mycocoenological investigations*. – *Acta Botanica Neerlandica* 37: 251–263.
- Sturm, M., Holmgren, J., McFadden, J., Liston, G., Chapin, F.S. & Racine, C.H. 2001: Snow-shrub interactions in Arctic tundra: A hypothesis with climatic implications. – *Journal of Climate* 14: 336–344.
- Verbeke, A. 2001: Worldwide systematics of *Lactarius*: a state of the art. – *Micologia e Vegetazione Mediterranea* 16: 71–88.