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New reports, phylogenetic analysis, and a key to *Lactarius* Pers. in the Greater Yellowstone Ecosystem informed by molecular data

Edward G. Barge[1], Cathy L. Cripps[1]

1 *119 Plant Biosciences Building, Plant Science and Plant Pathology Department, Montana State University, Bozeman, MT, USA 59717*

Corresponding author: *Edward G. Barge* (ebarge9@gmail.com)

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Abstract

The Greater Yellowstone Ecosystem (GYE), located in the Central Rocky Mountains of western North America, is one of the largest nearly intact temperate-zone ecosystems on Earth. Here, *Lactarius* is an important component of ectomycorrhizal communities in many habitat types, from low elevation riparian areas to high elevation conifer forests and alpine tundra. Molecular phylogenetic analyses of ITS and *RPB2* gene sequences along with detailed morphological examination confirm at least 20 *Lactarius* species, as well as three varieties, and one unresolved species group in the GYE. Eight taxa are reported from the GYE for the first time, and nearly every major ectomycorrhizal host plant in the GYE appears to have at least one *Lactarius* species associated with it. Broad intercontinental distributions are suggested for alpine *Salix* and *Betula* associates, and for certain subalpine *Picea* and aspen (*Populus* spp.) associates. Some species appear to be restricted to western North America with *Pinus, Pseudotsuga* or *Abies*. The distribution and/or host affinities of others is not clear due in part to ambiguous host assignment, taxonomic problems or the relative rarity with which they have been reported.

Key words

ITS, *RPB2*, Russulaceae, Rocky Mountains, fungal biodiversity, ectomycorrhizal, systematics

Introduction

The Greater Yellowstone Ecosystem (GYE), located in the Central Rocky Mountains of North America, is one of the largest nearly intact temperate-zone ecosystems on Earth. While a definitive boundary does not exist, the GYE roughly includes Yellowstone National Park at its center, Grand Teton National Park, and portions of surrounding national forests and other lands in Montana, Wyoming, and Idaho (Keiter and Boyce 1991) (Figure 1). The Rocky Mountains, which stretch from Northern Alaska to Northern New Mexico make up the defining landform upon which the ecosystem rests. The mosaic of geology and microclimates created by the Rocky Mountains form a variety of distinct habitats for plants and fungi in the GYE from low elevation grasslands and sagebrush steppe to high elevation alpine tundra (Marston and Anderson 1991, Knight 1994).

The genus *Lactarius* Pers. (Russulales, Russulaceae) is an important component of ectomycorrhizal fungal communities throughout the Rocky Mountains, where it associates with most major ectomycorrhizal plant families. *Lactarius* as originally defined, includes species with sporocarps that exude a milky latex when damaged, in addition to the amyloid ornamented basidiospores characteristic of the family. The original genus is now recognized as nonmonophyletic and has been split into three genera within Russulaceae: *Lactarius*, *Lactifluus* (Pers.) Roussel, and *Multifurca* Buyck & Hoffstetter (Buyck et al. 2008, 2010); although approximately 80% of the traditional species are still retained in *Lactarius* sensu stricto (Verbeken and Nuytinck 2013).

Lactarius is well-documented from the Rocky Mountains and western North America (Hesler and Smith 1979, Laursen and Ammirati 1982, Methven 1997, Bessette et al. 2009, Geml et al. 2009). For alpine areas of the Rocky Mountains, including material from the GYE, Cripps and Barge (2013) and Barge et al. (2016) delineated six to seven species, most with broad, intercontinental distributions using molecular and morphological techniques. Other previous reports of *Lactarius* from the GYE specifically include McKnight (1982), Moser and McKnight (1987), Cripps and Miller (1993), Cripps (2001, 2003, 2011), Mohatt et al. (2008), Cripps and Horak (2008), Cripps and Antibus (2011), Cripps and Eddington (2005, 2012), and Cripps et al. (2016). While the above-cited works provide crucial information on *Lactarius* occurring in western North America and the Rockies, we felt it would be beneficial to provide an updated summary of the genus in the Greater Yellowstone Ecosystem as a whole, report new records, add phylogenetic information, and bring to light groups which may require further taxonomic clarification.

For this study, collections of *Lactarius* from the GYE are evaluated through detailed morphological study and phylogenetic analyses of sequences from two genetic loci: nuclear rDNA ITS1–5.8S–ITS2 (ITS region) and the region between conserved domains six and seven of the second largest subunit of the RNA polymerase II (*RPB2*) gene. Data were compared to type specimens and specimens from type localities where available, and to related taxa represented by sequences in databases (GenBank, UNITE). Information previously generated in Barge et al. (2016) was also included and forms the backbone of this study. A key to species, morphological descriptions,

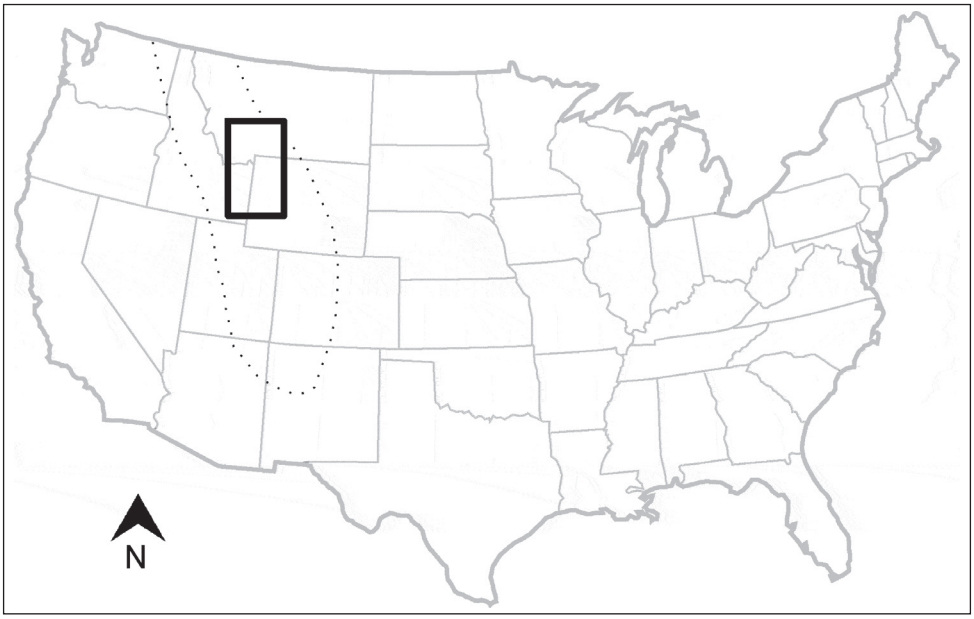

Figure 1. Map showing the location of the Greater Yellowstone Ecosystem (GYE). The GYE is located in the Central Rocky Mountains of North America and includes over 20 mountain ranges, with Yellowstone National Park at its center, Grand Teton National Park, and portions of surrounding national forests and other lands in Montana, Wyoming, and Idaho. The GYE is outlined by the black box, and the Rocky Mountains by the dotted line.

insight into ecology and distribution, as well as species photographs are provided. The key should also be relevant elsewhere in the Rocky Mountains, however, less so where host plants not present in the GYE occur, such as Northwestern Montana, and Northern Idaho. Genus-specific guides covering western North American species include Hesler and Smith (1979), Methven (1997), Bessette et al. (2009), and the Pacific Northwest Key Council's Key to *Lactarius* species in the Pacific Northwest (http://www.svims.ca/council/Lactar.htm).

Methods

Study sites

This study was performed in the GYE (Figure 1), with a focus on northern portions of the ecosystem. Major ectomycorrhizal host plants targeted include *Populus* spp. (cottonwoods) and *Alnus incana* (L.) Moench (gray alder) in riparian areas; *Pinus flexilis* James (limber pine), *Pseudotsuga menziesii* (Mirb.) Franco (Douglas fir), *Cercocarpus ledifolius* Nutt. (curl-leaf mountain mahogany) and *Populus tremuloides* Michx. (quaking aspen) in low to mid-elevation montane areas; *Pinus contorta* Dougl. ex Loud.

(lodgepole pine), *Pinus albicaulis* Engelm. (whitebark pine), *Picea engelmannii* Parry ex Engelm. (Engelmann spruce), *Abies lasiocarpa* (Hook.) Nutt. (subalpine fir), *Betula glandulosa* Michx. (dwarf birch), and *Arctostaphylos uva-ursi* (L.) Spreng. (kinnikinnick) in mid to high-elevation montane areas; and dwarf willows (*Salix arctica* Pall., *S. reticulata* L.), shrubby willows (*S. glauca* L., *S. planifolia* Pursh), *Dryas octopetala* L. (mountain avens), *Betula glandulosa*, and *Arctostaphylos uva-ursi* at or above treeline. *Pinus ponderosa* Dougl. ex Laws., which occurs sporadically along the northeastern edge of the ecosystem, was not surveyed. The locations of specimens are included in the Taxonomy section under Specimens examined and locations of specimens used in the phylogenetic analysis are shown in Table 1.

Taxon sampling and processing

Sporocarps were collected from late May to late September 1992–2015. All collections were described in detail when fresh, and select collections were photographed. Ectomycorrhizal host plants near sporocarps were noted for each collection. Sporocarps were dried on an electric, warm-air dryer and deposited in the Montana State University herbarium (MONT). For comparison, additional specimens were obtained from numerous herbaria. For Rocky Mountain material, most herbarium specimens studied originated from the Montana State University Herbarium (MONT), the Denver Botanic Gardens' Sam Mitchel Herbarium of Fungi, Denver, Colorado (DBG), and the University of Michigan fungal herbarium, Ann Arbor, Michigan (MICH). See Barge et al. (2016), for a complete list of herbaria.

Morphological descriptions

Macromorphological measurements and descriptions were made from fresh material. Micromorphological descriptions and measurements were made from dry material reconstituted in ethanol and 2.5% KOH. In Melzer's reagent, length and width were measured at 1000× magnification for a random sample of 25 basidiospores per collection, excluding ornamentation and the hilar appendix. The length to width ratio (Q) was calculated for each basidiospore. Length and width were measured at 400× magnification for a random sample of 10 pleuromacrocystidia and 10 cheilomacrocystidia per collection. Morphological descriptions for alpine specimens were previously reported in Barge et al. (2016).

Phylogenetic analysis

DNA extraction, PCR amplification, and sequencing of the ITS region and partial *RPB2* gene were performed as in Barge et al. (2016) or at ALVALAB, Santander, Spain

Table 1. Voucher, locality information and GenBank or UNITE (UDB) accession numbers for DNA sequences used in the phylogenetic analysis. Herbarium acronyms follow Thiers http://sweetgum.nybg.org/ih/ (continuously updated). Specimens from the Greater Yellowstone Ecosystem (GYE) are in bold type. Newly generated accessions are in bold type.

Taxon	Voucher	Location	ITS	*RPB2*
L. akahatsu	JN2004-141 (GENT)	Thailand	KF133269	KF133333
L. albocarneus	AV98-080 (GENT)	France	KF241545	NA
L. alnicola	EB0064-14 (MONT)	Gallatin Range, MT, U.S.A.	**KX394276**	NA
L. alpinus v. *alpinus*	FNL GNP-125 (DAOM)	Newfoundland, Canada	KX094937	NA
L. alpinus* v. *mitis	EB161-15 (MONT)	Red Lodge, MT, U.S.A.	**KX394277**	NA
L. alpinus v. *mitis*	DBG-F-021979 (DBG)	Pike National Forest, CO, U.S.A.	**KX394278**	**KX394303**
L. aspideoides	RL Shaffer 6957 (MICH)	Emmet Co., MI, U.S.A.	KR090893	NA
L. aspideus	JV24534 (TURA)	Varsinais-Suomi, Finland	KR090894	KR090972
L. atroviridis	AV05-306 (GENT)	U.S.A.	KF133270	KF133334
L. aurantiacus	JV94-422 (C)	Uppland, Sweden	KR090896	KR090974
L. cf. *aurantiacus*	JV15112F (TURA)	Nordland, Norway	KR090895	KR090973
L. auriolla	RW1601 (GENT)	Sweden	KF133257	KF133321
L. barrowsii	EB015-15 (MONT)	Story Hill, Bozeman, MT, U.S.A.	**KX394279**	NA
L. barrowsii	N Gray 91878 (RMS)	Washington, U.S.A.	EF685047	NA
L. barrowsii	States J AEF 1271 (MICH)	Arizona, U.S.A.	EF685046	NA
L. badiosanguineus	EB200-13 (MONT)	Gallatin Range, MT, U.S.A.	**KX394280**	NA
L. badiosanguineus	EB0069-14 (MONT)	Tobacco Root Mtns., MT, U.S.A.	**KX394281**	NA
L. badiosanguineus	DBG-F-017093 (DBG)	Front Range, CO, U.S.A.	**KX394282**	**KX394304**
L. badiosanguineus	AV04-235 (GENT)	France	KF432983	NA
L. badiosanguineus	AV10-044 (GENT)	Norway	KR025578	KR025655
L. brunneohepaticus	PAM08090315 (LIP)	Corse-du-Sud, France	HQ714726	HQ714858
L. brunneoviolaceus	Verbeken 04-220 (GENT)	France	KJ742392	NA
L.* aff. *brunneoviolaceus	CLC3098 (MONT)	Beartooth Plateau, MT, U.S.A.	**KX394283**	NA
L. aff. *brunneoviolaceus*	CLC2133 (MONT)	Finse, Norway	KR090899	KR090977
L. caespitosus	EB102-13 (MONT)	Gallatin Range, MT, U.S.A.	**KX394284**	**KX394305**
L. caespitosus	EB121-13 (MONT)	Madison Range, MT, U.S.A.	**KX394285**	**KX394306**
L. camphoratus	UE04.09.2004-5 (UPS)	Sweden	DQ422009	DQ421933
L. chrysorrheus	UE04.10.2002-8 (UPS)	Italy	KF133261	KF133325
L. citriolens	UE20.09.2004-03 (UPS)	Sweden	DQ422003	DQ421931
L. controversus	EB110-15 (MONT)	Beartooth Mtns, MT, U.S.A.	**KX394286**	NA
L. controversus	UP508	Sweden	DQ658881	NA
L. controversus	AV00-117 (GENT)	Italy	KF241544	NA
L. cuspidoaurantiacus	LM4823 (XAL)	Mexico	KF891367	KF891374
L. cuspidoaurantiacus	LM4908 (XAL)	Mexico	KF891366	KF891373
L. cyathuliformis	PAM08100409 (LIP)	Orne, France	HQ714738	HQ714869
L. dryadophilus	EL57-10 (GB)	Latnjavagge, Sweden	KR090902	KR090980
L. deliciosus	JN2001-046 (GENT)	Slovakia	KF133272	KF133337

Taxon	Voucher	Location	ITS	*RPB2*
"*L. deliciosus* v. *deterrimus*"	JR Herr 650 (RMS)	Wyoming, U.S.A.	EF685056	NA
L. deliciosus v. *olivaceosordidus*	J Ammirati 10762 (RMS)	Washington, U.S.A.	EF685059	NA
"*L. deliciosus*" group	EB0063-14 (MONT)	Gallatin Range, MT, U.S.A.	**KX394287**	NA
"*L. deliciosus*" group	EB089-15 (MONT)	Madison Range, MT, U.S.A.	**KX394288**	NA
"*L. deliciosus*" group	EB107-15 (MONT)	Hellroaring Plateau, MT, U.S.A.	**KX394289**	NA
"*L. deliciosus*" group	EB0047 (MONT)	Sawatch Range, CO, U.S.A.	**KX394290**	NA
L. deterrimus	UE05.09.2004-04 (UPS)	Sweden	UDB000866	NA
L. evosmus	UP536	Sweden	DQ58882	NA
L. evosmus	UE27.09.2002-1 (UPS)	France	UDB000860	NA
L. flavopalustris	JV23334 (TURA)	Koillismaa, Finland	KR090904	KR090982
L. flexuosus	UE06.09.2002-1 (UPS)	Sweden	DQ421992	DQ421925
L. fulvissimus	JN2012-025 (GENT)	Germany	KR025576	KR025660
L. glyciosmus	TWO269 (MONT)	Beartooth Plateau, MT, U.S.A.	KR090905	KR090983
L. glyciosmus	EB133 (MONT)	San Juan Range, CO, U.S.A.	KR090909	KR090986
L. glyciosmus	M Moser 19810148 (IB)	Femsjö, Sweden	KR090910	NA
L. helvus	UE08.09.2004-1 (UPS)	Sweden	KF133263	KF133327
L. hepaticus	JN02-049 (GENT)	Belgium	KF432980	KR025674
L. hysginoides	JV28432 (TURA)	Koillismaa, Finland	KR090914	KR090988
L. intermedius	f324 (AQUI)	Italy	UDB000368	NA
L. kauffmanii	F28471 (UBC)	British Columbia, Canada	KP406573	NA
L. lacunarum	JKLAC11092901 (GENT)	Germany	KF432982	KR025638
L. lanceolatus	CLC2358 (MONT)	Beartooth Plateau, MT, U.S.A.	KR090918	KR090992
L. lanceolatus	EB105-13 (MONT)	Beartooth Plateau, WY, U.S.A.	KR090919	KR090993
L. lanceolatus (Holotype)	F4239 (VPI)	Beaufort Lagoon, AK, U.S.A.	KR090915	KR090989
L. lapponicus	JV28335 (TURA)	Koillismaa, Finland	**KX394291**	NA
L. leonis	TU106315 (TU)	Estonia	UDB011465	NA
L. lepidotus	PAM08090304 (LIP)	Corse-du-Sud, France	HQ714722	HQ714854
L. lignyotus	UE06.09.2003-5 (UPS)	Sweden	DQ421993	DQ421926
L. lilacinus	EDB08101401 (LIP)	France	HQ714748	HQ714879
L. lilacinus	RW3774 (GENT)	Belgium	KF133275	KF133340
L. luculentus v. *luculentus*	AH Smith 79943 (MICH)	OR, U.S.A.	KR090920	NA
L. luculentus* v. *laetus	EB097-15 (MONT)	Crazy Mtns., MT, U.S.A.	**KX394292**	NA
L. luculentus v. *laetus*	DBG-F-024643 (DBG)	CO, U.S.A.	KR090922	KR090994
L. luridus	OB11-011 (GENT)	Belgium	KF241547	NA
L. mammosus	UE09.09.2004-5 (UPS)	Sweden	KF133265	NA
L. montanus	EB120-13 (MONT)	Madison Range, MT, U.S.A.	KR090925	KR090996
L. montanus	CLC3001 (MONT)	Tobacco Root Mtns., MT, U.S.A.	KR090926	KR090997
L. montanus (Paratype)	AH Smith 81954 (MICH)	Bonner County, ID, U.S.A.	KR090924	NA
L. nanus	EB106-13 (MONT)	Beartooth Plateau, MT, U.S.A.	KR090928	KR091000
L. nanus	CLC1716 (MONT)	San Juan Range, CO, U.S.A.	KR090929	KR091001
L. nanus	Bon 89093 (LIP)	Savoie, France	KR090935	NA
L. necator	AV04-231 (GENT)	France	KF133276	KF133341

Taxon	Voucher	Location	ITS	*RPB2*
L. olivinus	TU101411 (TU)	Estonia	UDB019698	NA
L. olivinus	TU106674 (TU)	Estonia	UDB015721	NA
L.* aff. *olivinus	EB0051-14 (MONT)	Silver Gate, MT, U.S.A.	**KX394293**	NA
L. olympianus	EB0070-14 (MONT)	Tobacco Root Mtns., MT, U.S.A.	**KX394294**	NA
L. olympianus	J Nuytinck 2003-032 (GENT)	U.S.A.	EF685079	NA
L. pallescens (Holotype)	AH Smith 81936 (MICH)	Boundary County, ID, U.S.A.	KR090938	NA
L. pallidomarginatus (Holotype)	EB0041 (MONT)	San Juan Range, CO, U.S.A.	KR090940	KR091010
L. pseudodelicatus	CLC512 (MONT)	Teton Range, ID, U.S.A.	**KX394295**	NA
L. pseudomucidus	F16301 (UBC)	British Columbia, Canada	EU486439	NA
L. aff. *pseudouvidus*	U Peintner 20040156 (IB)	Trentino, Italy	KR090942	KR091014
L. pubescens	EB300-15 (MONT)	Silver Bow Co., MT, U.S.A.	**KX394296**	NA
L. pubescens	CLC539 (MONT)	Cinnabar Basin, MT, U.S.A.	**KX394297**	NA
L. pubescens	CLC1611 (MONT)	Front Range, CO, U.S.A.	**KX394298**	NA
L. pubescens	UE15.09.2002-2 (UPS)	Sweden	DQ421996	DQ421929
L. pubescens	UP516	Sweden	DQ658884	NA
L. quieticolor	UE10.09.2004-1 (UPS)	Sweden	DQ422002	DQ421930
L. quietus	UE16.09.2004 (UPS)	Sweden	KF133264	KF133328
L. repraesentaneus	EB107-13 (MONT)	Beartooth Plateau, MT, U.S.A.	KR090949	KR091021
L. repraesentaneus	CLC1747 (MONT)	Sawatch Range, CO, U.S.A.	KR090951	KR091023
L. repraesentaneus	EL92-07 (GB)	Latnjavagge, Sweden	KR090953	KR091025
L. romagnesii	UE29.09.2006-6 (UPS)	France	DQ421989	DQ421923
L. rubrilacteus	EB13-040 (MONT)	Bridger Range, MT, U.S.A.	**KX394299**	NA
L. rubrilacteus	SL Miller 19-04 (RMS)	California, U.S.A.	EF685085	NA
L. rufus	EB125-13 (MONT)	Gallatin Range, MT, U.S.A.	**KX394300**	**KX394307**
L. rufus	JN2002-008 (GENT)	Norway	KF241543	NA
L. rufus	DG15 (AMG)	United Kingdom	UDB001601	NA
L. salicis-herbaceae	CLC1536 (MONT)	Sismiut, Greenland	KR090955	KR091027
L. salicis-reticulatae	EB0057-14 (MONT)	Beartooth Plateau WY, U.S.A.	KR090958	KR091029
L. salicis-reticulatae	JV15133 (TURA)	Sweden	KR090961	KR091032
L. aff. *salicis-reticulatae*	CLC1710 (MONT)	San Juan Range, CO, U.S.A.	KR090962	KR091033
L. sanguifluus	Hue470 (UPS)	Germany	UDB000876	NA
L. scrobiculatus	JN01-058 (GENT)	Slovakia	KF432968	NA
L. scrobiculatus	TU117089 (TU)	Latvia	UDB022822	NA
L. sphagneti	PL2805 (herb. P. Leonard)	United Kingdom	KF133268	KF133332
L. spinosulus	AT2003068 (UPS)	Sweden	KF133262	KF133326
L. subdulcis	JV2006-024 (GENT)	Belgium	KF133279	KF133344
L. subflammeus (Holotype)	AH Smith 83602 (MICH)	Tillamook County, OR, U.S.A.	KR090967	NA
L. substriatus	AH Smith 83693 (MICH)	Tillamook Co., OR, U.S.A.	KR090968	NA
L. subviscidus (Paratype)	AH Smith 83066 (MICH)	Lewis Co., WA, U.S.A.	KR090970	NA
L. tabidus	ED2008-026 (GENT)	Belgium	KT165309	KR025667
L. thyinos	A Voitk23-08-2004 (GENT)	Canada	KF133271	KF133336

Taxon	Voucher	Location	ITS	*RPB2*
L. torminosus	RW3183 (GENT)	Czech Republic	KF133281	KF133346
L. trivialis	UE27.08.2002-17a (UPS)	Sweden	DQ421991	DQ421924
L. tuomikoskii	TU101882 (TU)	Finland	UDB016033	NA
L.* aff. *tuomikoskii	EB052-14 (MONT)	Silvergate, MT, U.S.A.	**KX394301**	NA
L. uvidus	mh0963 (TUB)	Germany	AY606957	NA
L. vietus	UE11.19.2004-1 (UPS)	Sweden	KF133267	KF133331
L. aff. *wenquanensis*	LTH143 (GENT)	Thailand	EF141537	NA
L. zonarioides	E Bizio 2516 (MCVE)	Italy	JF908300	NA
L. zonarius	UE27.09.2002-4 (UPS)	France	EU278678	EU278679
L. zonarius* v. *riparius	CLC2933 (MONT)	Bozeman, MT, U.S.A.	**KX394302**	NA

(http://www.alvalab.es/index.html). Raw sequences were edited and contigs constructed with SeqTrace 0.8.1 (Stucky 2012).

In addition to the sequences generated in this study, select close BLAST matches to the ITS region of GYE specimens and select additional ITS and *RPB2* sequences mainly from Buyck et al. (2008), Verbeken et al. (2014), and Wisitrassameewong et al. (2016) were downloaded from GenBank (http://www.ncbi.nlm.nih.gov/) and UNITE (https://unite.ut.ee/). Many sequences generated in Barge et al. (2016) were also included.

Alignments were performed with MUSCLE (http://www.ebi.ac.uk/Tools/msa/muscle/) under default parameters and manually edited using PhyDE v.0.9971 (http://www.phyde.de/index.html). Ambiguously aligned regions of the ITS alignment were highlighted and removed with the online version of GBlocks 0.91b (Castresana 2000) under the least stringent settings. Also removed was a 268–269 base pair insertion present in the ITS1 region of several taxa (Barge et al. 2016, Rosenblad et al. 2016).

Maximum likelihood (ML) analyses were carried out using RAxML v.8 (Stamatakis 2014) on the CIPRES Science Gateway (Miller et al. 2010). Previous phylogenetic analyses by Barge et al. (2016) suggested that *Lactarius romagnesii* Bon and *L. lignyotus* Fr. of subg. *Plinthogalus* (Burl.) Hesler & A.H. Sm. form a monophyletic group distinct from subg. *Piperites* (Fr.) Kauffman and *Russularia* (Fr.) Kauffman which contain all of the ingroup species of interest in this study. Thus, *L. lignyotus* and *L. romagnesii* were selected as outgroup taxa. An ML search combined with rapid bootstrapping was run until bootstrap convergence was reached using the autoMRE option. The GTRGAMMA model was estimated separately for ITS1, 5.8S, ITS2, *RPB2* exon first, second and third codon positions, and *RPB2* intron. Single-gene and combined ML analyses were performed. Slight conflicts were detected between ITS and *RPB2* phylogenies, however, the conflicts received low support (bootstrap support <70%), thus the combined phylogeny was used. The program TreeGraph2 (Stöver and Müller 2010) was used to draw and edit the final tree.

Results

A total of 27 ITS and 5 *RPB2* sequences were generated in this study (Table 1). Based on morphological and molecular examination we report 20 *Lactarius* species, three varieties, and one putatively unresolved species group from the GYE. *Lactarius alpinus* v. *mitis* Hesler & A.H. Sm., *L. badiosanguineus* Kühner & Romagn., *L. barrowsii* Hesler & A.H. Sm., *L.* aff. *brunneoviolaceus* M.P. Christ., *L. luculentus* v. *laetus* Hesler & A.H. Sm., *L.* aff. *olivinus* Kytöv., *L. pseudodelicatus* A.H. Sm., and *L.* aff. *tuomikoskii* Kytöv. are reported from the GYE for the first time. In addition, the first publicly available vouchered sequences are provided for *L. alpinus* v. *mitis*, *L. lapponicus* (syn.: *L. duplicatus*), *L. pseudodelicatus*, and *L. zonarius* v. *riparius*; the first publicly available vouchered sequences from North America are provided for *L. badiosanguineus*, *L.* aff. *brunneoviolaceus*, *L.* aff. *olivinus*, and *L.* aff. *tuomikoskii*.

Subgenera *Piperites* and *Russularia* are well-represented in the GYE, however, species of subg. *Plinthogalus* appear to be absent, as are species of the recently segregated genus *Lactifluus*. Most major ectomycorrhizal host plants in the Greater Yellowstone Ecosystem appear to have at least one *Lactarius* species associated with them (Table 2).

The phylogenetic position of species for which molecular data was obtained is shown (Figure 2). The backbone of the phylogeny is poorly resolved, thus we refrain from

Table 2. Major ectomycorrhizal host plants in the Greater Yellowstone Ecosystem (GYE) with putatively associated *Lactarius* species. (?) denotes host plant uncertainty.

Host Plant	*Lactarius* species
Abies lasiocarpa	*L. caespitosus*, *L. luculentus* v. *laetus* (?)
Alnus incana	*L. alpinus* v. *mitis*
Arctostaphylos uva-ursi	"*L. deliciosus*" group
Betula glandulosa/*Betula* spp.	*L. glyciosmus*, *L. pubescens*
Cercocarpus ledifolius	None detected
Dryas octopetala	None detected
Picea engelmannii	*L. alnicola*, *L. badiosanguineus*, "*L. deliciosus*" group, *L. luculentus* v. *laetus* (?), *L. montanus*, *L. olympianus*, *L. rufus* (?), *L. repraesentaneus*, *L.* aff. *olivinus* and *L.* aff. *tuomikoskii*
Pinus albicaulis	"*L. deliciosus*" group, *L. rufus* (?)
Pinus contorta	"*L. deliciosus*" group (?), *L. rufus*
Pinus flexilis	*L. barrowsii*, "*L. deliciosus*" group
Pinus ponderosa	None detected
Pseudotsuga menziesii	*L. rubrilacteus*
Populus tremuloides	*L. controversus*, *L. pseudodelicatus*, *L. pubescens*
Populus spp. (cottonwoods)	*L. zonarius* v. *riparius*
Salix spp. (alpine)	*L.* aff. *brunneoviolaceus*, *L. nanus*, *L. lanceolatus*, *L. pallidomarginatus*, *L. repraesentaneus* (?), *L. salicis-reticulatae*
Salix spp. (subalpine)	None detected

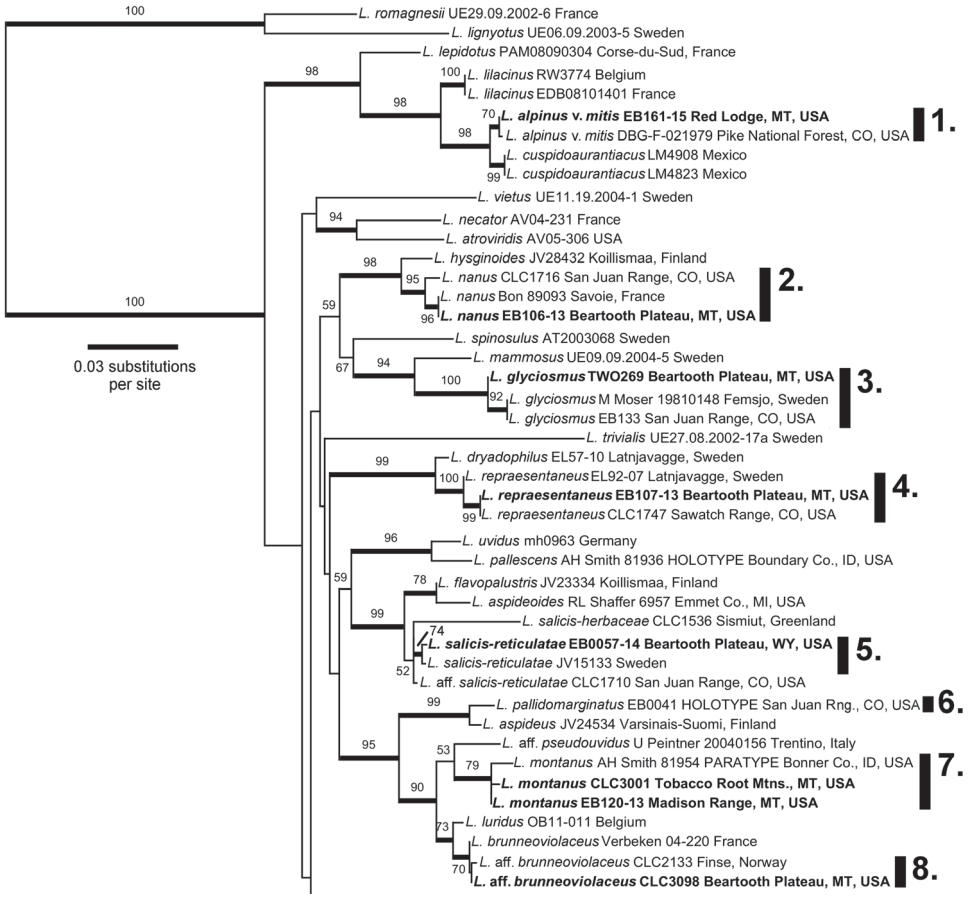

Figure 2A. Upper part of maximum likelihood phylogeny of ITS and *RPB2* molecular data. Bootstrap support values ≥ 50% are shown above or below branches leading to clades. Thickened branches lead to clades receiving ≥ 70% bootstrap support. Boldface type labels represent specimens from the Greater Yellowstone Ecosystem (GYE). Boldface numbers refer to the taxa treated in the Key and Taxonomy sections.

making any novel inferences regarding broad-scale infrageneric relationships. Species are organized in the Taxonomy section based on the phylogenetic results. See comments under individual species in the Taxonomy section for discussion of relationships.

Key to *Lactarius* species of the Greater Yellowstone Ecosystem

Due to dry conditions common throughout the Rocky Mountains, *Lactarius* sporocarps collected here often do not exude any noticeable latex. However, for species which have changing latex, the cut flesh often displays characteristic color changes similar to the latex or reacts with the latex to display a characteristic color, and it typi-

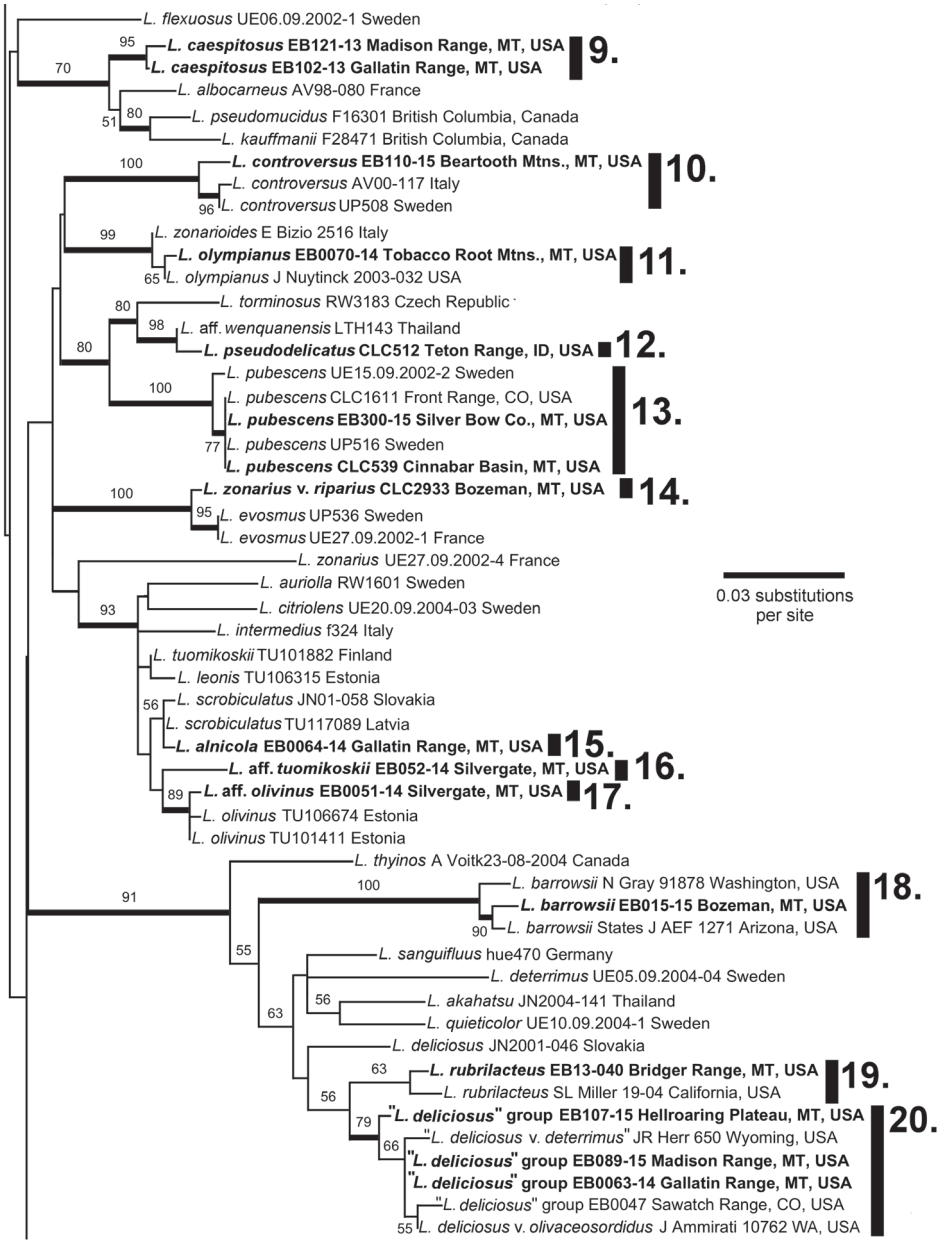

Figure 2B. Middle part of maximum likelihood phylogeny of ITS and *RPB2* molecular data. Bootstrap support values ≥ 50% are shown above or below branches leading to clades. Thickened branches lead to clades receiving ≥ 70% bootstrap support. Boldface type labels represent specimens from the Greater Yellowstone Ecosystem (GYE). Boldface numbers refer to the taxa treated in the Key and Taxonomy sections.

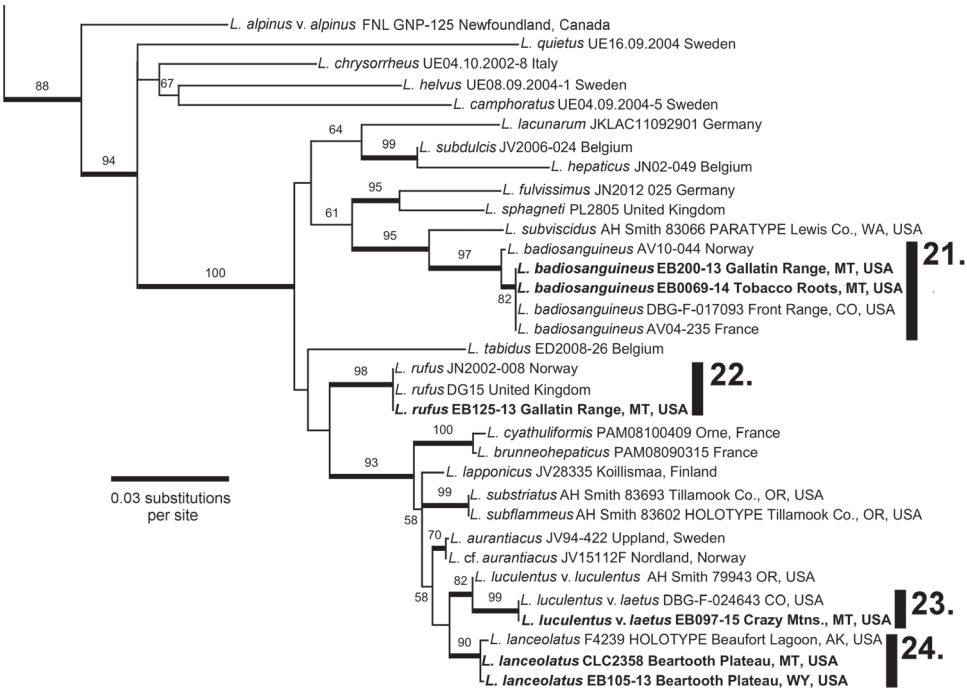

Figure 2C. Lower part of maximum likelihood phylogeny of ITS and *RPB2* molecular data. Bootstrap support values ≥ 50% are shown above or below branches leading to clades. Thickened branches lead to clades receiving ≥ 70% bootstrap support. Boldface type labels represent specimens from the Greater Yellowstone Ecosystem (GYE). Boldface numbers refer to the taxa treated in the Key and Taxonomy sections.

cally does so under dry conditions even when no latex is detected. Thus, if no latex is detected, examining cut surfaces of sporocarps for color change can be very useful for identifying *Lactarius* species.

1 Latex orange to red; cut flesh staining orange to red and eventually green ... **2**
– Latex watery or whitish, unchanging or becoming violet or yellow; cut flesh unchanging or staining lilac, yellow or brownish ... **4**
2 Latex orange, often undetectable; cut flesh staining orange to ± red and eventually green; with conifers ... **20. "*L. deliciosus*" group**
– Latex red, often undetectable; cut flesh quickly staining red and eventually green ... **3**
3 Pileus cream to pale straw yellow, lamellae dingy pinkish orange to creamy yellow-orange; with *Pinus flexilis* and possibly other *Pinus* spp. ... **18. *L. barrowsii***
– Pileus light brown to yellow-orange to dingy orange; lamellae pinkish cinnamon to dull pink; with *Pseudotsuga menziesii*, and possibly *Pinus* spp. ... **19. *L. rubrilacteus***

4 Latex unchanging or turning violet; cut flesh staining violet **5**
– Latex unchanging or turning yellow; cut flesh unchanging or staining yellow or brownish **9**
5 Pileus cream to yellowish **6**
– Pileus violaceous to brownish or greyish **7**
6 Pileus margin bearded; stipe scrobiculate; with *Picea engelmannii* and possibly *Salix glauca* in subalpine to low alpine krummholz habitats ..... **4. *L. repraesentaneus***
– Pileus margin glabrous; stipe non-scrobiculate; with *Salix* spp. in alpine areas ..... **5. *L. salicis-reticulatae***
7 Subalpine with conifers in the spruce-fir zone; pileus cuticle staining green in KOH ..... **7. *L. montanus***
– Alpine with *Salix*; pileus cuticle staining green in KOH or not **8**
8 Pileus light tan to light brown; pileus cuticle unchanging in KOH ..... **6. *L. pallidomarginatus***
– Pileus brownish with lavender hues; pileus cuticle staining green in KOH .... **8. *L.* aff. *brunneoviolaceus***
9 Pileus margin conspicuously bearded or tomentose at least when young ... **10**
– Pileus margin glabrous or only very finely pubescent **14**
10 Latex unchanging or turning yellow; cut flesh staining yellow; with conifers... **11**
– Latex unchanging; cut flesh unchanging or staining brownish; with hardwoods **12**
11 Pileus with matted fibrils especially near the margin, pale yellow-cream to yellow-tan; margin densely bearded; under *Picea engelmannii* ..... **16. *L.* aff. *tuomikoskii***
– Pileus with appressed scales of confluent hairs especially near the margin, cream to olive-buff to orange-tan; margin merely tomentose to cottony; under *Picea engelmannii*. ..... **17. *L.* aff. *olivinus***
12 Pileus azonate to faintly zonate and predominately cream to pinkish; with aspen or *Betula* ..... **13. *L. pubescens***
– Pileus zonate and predominately yellow-buff to orange-brown; with aspen or cottonwood **13**
13 Pileus yellow-buff to pale orange-brown, lighter toward the margin; odor orange-citrusy; with aspen ..... **12. *L. pseudodelicatus***
– Pileus yellow-brown to orange brown, ± lighter toward the margin; odor sweet, fruity; with cottonwood ..... **14. *L. zonarius* v. *riparius***
14 Pileus reddish, red-brown or orange **15**
– Pileus whitish, yellowish or brownish **20**
15 Taste acrid **16**
– Taste mild to slightly bitter **17**
16 Pileus red-brown to orange-brown, azonate; with conifers ..... **22. *L. rufus***
– Pileus rich to dull orange, zonate; with conifers ..... **11. *L. olympianus***

17 Pileus finely rimulose to minutely squamulose; with *Alnus*..... .....**1. *L. alpinus* v. *mitis***
– Pileus smooth; with conifers or *Salix*..... 18
18 Alpine with *Salix* ..... **24. *L. lanceolatus***
– Subalpine with conifers.....**19**
19 Pileus red-brown to orange-brown, often lighter toward the margin..... ..... **21. *L. badiosanguineus***
– Pileus bright orange to yellow-orange to orange-brown, evenly colored ....**23. *L. luculentus* v. *laetus***
20 Pileus brownish or pinkish buff; taste mild to only slightly acrid.....**21**
– Pileus whitish, yellowish, brownish or gray-brown; taste acrid **22**
21 Odor mild; taste mild to slightly acrid; arctic-alpine with *Salix*...**2. *L. nanus***
– Odor of coconut; taste mild to slightly acrid; alpine to subalpine with *Betula* .....**3. *L. glyciosmus***
22 Pileus yellowish; flesh staining yellow; with *Picea engelmannii* ....**15. *L. alnicola***
– Pileus whitish, brownish or vinaceous.....**23**
23 Pileus whitish overall; lamellae pinkish; with aspen..... **10. *L. controversus***
– Pileus more brown to gray-brown overall; lamellae white to cream; with *Abies*.....**9. *L. caespitosus***

Taxonomy

1. *Lactarius alpinus* v. *mitis* Hesler & A.H. Sm.
Figure 3

Description. Pileus 8–20 mm in diameter (to 80 mm in Hesler and Smith 1979), plano-convex to infundibuliform, ± papillate, dry, finely rimulose to minutely squamulose, red-brown to orange-brown to pinkish cinnamon; margin finely crenulate, incurved when young, becoming straight to wavy in age. Lamellae adnate to subdecurrent, subdistant to crowded, cream to creamy tan, discoloring slightly darker where damaged. Stipe 8–23 × 5–8 mm (30–50 × 10–15 mm in Hesler and Smith 1979), equal to slightly clavate, smooth, dry, pale creamy yellow to creamy tan, solid, becoming hollow. Context concolorous with pileus. Latex scarce, watery, white, unchanging. Odor mild. Taste mild.

Basidiospores 7–9.5 × 5–7.5 µm, Q = 1.3–1.5, ellipsoid; ornamentation forming a broken to partial reticulum. Pleuromacrocystidia 60–100 × 6–10 µm, numerous, strongly projecting, mucronate to fusoid; apex acute to moniliform. Cheilomacrocystidia 50–80 × 6–10 µm, numerous, strongly projecting, mucronate to fusoid; apex acute to moniliform.

Ecology and distribution. In western and into eastern North America with *Alnus*. In the GYE only one collection has been made thus far and it was from a riparian area near *Alnus incana* and *Populus trichocarpa*, late summer. Further sampling under *Alnus* in the Rocky Mountains is necessary.

Figure 3. *Lactarius alpinus* v. *mitis*. Top collection EB161-15 under *Alnus incana* and *Populus trichocarpa*, Red Lodge, Montana, USA. Bottom collection EB516-15 under *Alnus rubra*, western Oregon, USA. Scale bars: 2 cm. Photos by E. Barge.

Specimens examined. U.S.A. MONTANA: Carbon County, Red Lodge, along Rock Creek, under *Alnus incana* and *Populus trichocarpa*, 6 Sept 2015, EB161-15 (MONT).

Discussion. This is the first report of *L. alpinus* v. *mitis* from the GYE. According to Hesler and Smith (1979), *L. alpinus* v. *mitis* has duller pileus and lamellae colors than *L. alpinus* v. *alpinus* Peck, which typically develops bright yellow to apricot colors; variety *mitis* also has longer and more conspicuous macrocystidia and a mild rather than slowly acrid taste. The collection described here likely did not reach full maturity, and the basidiomes are smaller than reported in Hesler and Smith (1979). Phylogenetic analyses including material of *L. alpinus* v. *alpinus* from near the type locality suggest that *L. alpinus* v. *mitis* and *L. alpinus* v. *alpinus* are distinct species (Figure 2A, 2C), however a more in depth analysis incorporating type material of at least *L. alpinus* v. *mitis* should be carried out before making this determination final. For an interesting discussion on *L. alpinus* see Nuytinck and Voitk (2016) and Rochet et al. (2011).

While *L. alpinus* v. *mitis* appears to be quite distantly related to *L. alpinus* v. *alpinus*, it is very closely related to the European *L. lilacinus* (Lasch) Fr., the recently described Mexican *L. cuspidoaurantiacus* Montoya, Bandala & Garay-Serr., and to a lesser extent *L. lepidotus* Hesler & A.H. Sm., all of which are also associated with *Alnus* (Figure 2A). *Lactarius lilacinus* is typically more pink to violet in color and has a fruity smell. *Lactarius cuspidoaurantiacus* appears to have more yellow-orange basidiomes, more orange colored, distant lamellae, and a *Pelargonium*-like odor (Montoya et al. 2014). *Lactarius lepidotus* has a more gray-brown to beige pileus. Neither *L. lilacinus*, *L. cuspidoaurantiacus* or *L. lepidotus* have been reported from the Rocky Mountains.

2. *Lactarius nanus* J. Favre

Figure 4

The following morphological description includes data from Colorado specimens listed in Barge et al. (2016).

Description. Pileus 10–50 mm in diameter, shallowly convex to plano-convex becoming plane to infundibuliform, ± papillate, smooth, slightly viscid to dry, with whitish glaucous coating when immature, easily rubbing away or fading in age, deep brown to gray-brown to liver brown with lighter and darker areas present, often lighter toward margin, becoming lighter overall upon desiccation; margin straight when young becoming upturned and wavy to convoluted in age. Lamellae adnate to subdecurrent, subdistant, cream when immature becoming dingy cream to light tan in age, sometimes with a faint pinkish tinge, discoloring to dingy tan where damaged. Stipe 5–30 × 3–15 mm, equal to clavate, central, smooth, dry, at first covered with whitish glaucous coating as in pileus, pale apricot to dingy cream-tan, hollow. Context dingy cream to brownish. Latex scarce to undetectable, watery, white, unchanging. Odor mild. Taste mild to slightly acrid.

Basidiospores 7–10.5(–12) × 5–8 µm, Q = 1.1–1.6, subglobose to ellipsoid; ornamentation forming an incomplete reticulum. Pleuromacrocystidia 53–96.5(–114) × 6.5–11.5 µm, scattered to abundant, lanceolate; apex acute to moniliform. Cheilo-

Figure 4. *Lactarius nanus*. Collection EB106-13 near *Salix arctica* (pictured), *S. reticulata*, and *S. planifolia*, Beartooth Plateau, Montana, USA. Scale bar: 2 cm. Photo by E. Barge.

macrocystidia 26–91.5 × 7.5–10 µm, scattered to abundant, subulate to linear; apex acute to rounded.

Ecology and distribution. Widespread in arctic-alpine areas in the Northern Hemisphere with *Salix*. In the GYE and elsewhere in the Rocky Mountains it occurs above tree line in alpine areas with *Salix arctica*, *S. reticulata*, and *S. planifolia*, late summer.

Specimens examined. U.S.A. MONTANA: Carbon County, Beartooth Plateau, Highline Trail, among shrubby and dwarf *Salix*, 7 Aug 1998, CLC1221 (MONT); among *Salix reticulata* and other *Salix* spp., 8 Aug 1998, ZT6422 (MONT); among *Salix arctica*, *S. planifolia* and *S. reticulata*, 18 Aug 2013, EB106-13 (MONT). WYOMING: Park County, Beartooth Plateau, Frozen Lakes, among *Salix arctica*, 21 Aug 1999, CLC1403 (MONT); Park County, Beartooth Plateau, Solifluction Terraces, among *Salix arctica*, *S. planifolia* and *S. reticulata*, 11 Aug 2012, EB125 (MONT).

Discussion. *L. nanus* is morphologically and phylogenetically close to *L. hysginoides* Korhonen & T. Ulvinen (Figure 2A), however, the latter has a more cinnamon-toned pileus, smaller basidiospores (6.5–8.5 × 4.9–7.1 µm), and occurs in boreal areas with *Betula*, *Picea* and *Salix*; it has not been reported from the Rocky Mountains. *Lactarius pallidomarginatus* Barge and C.L. Cripps is also similar, however, it is a violet staining species. Differences between *L. nanus* and *L. glyciosmus* (Fr.) Fr. are discussed in the comments section under the latter.

3. *Lactarius glyciosmus* (Fr.) Fr.

Figure 5

The following morphological description includes data from Colorado specimens listed in Barge et al. (2016).

Description. Pileus 15–50 mm in diameter, broadly convex, later becoming plane with or without a depressed center and small papilla, smooth, dry, azonate to lightly zoned especially near the margin, pale gray-brown to violet-brown with a whitish glaucous coating when immature, fading in age; margin incurved when young and remaining so or becoming straight in age. Lamellae adnate to subdecurrent, subdistant to crowded, cream to pale pinkish to pale yellow-orange. Stipe 10–40 × 3–12 mm, equal to slightly clavate, central to eccentric, smooth, dry, buff or pale salmon with a faint glaucous coating at first as in pileus, stuffed, becoming hollow, often white-mycelioid toward the base. Context pale cream. Latex scarce to undetectable, watery, white, unchanging. Odor of coconut. Taste mild to slightly acrid.

Basidiospores 7–9 × 5–7 µm, Q = 1.2–1.4, broadly ellipsoid to ellipsoid, ornamentation forming an incomplete to nearly complete reticulum. Pleuromacrocystidia 45.5–63.5 × 6.5–7.5 µm, scarce to scattered, subclavate to lanceolate; apex rounded to mucronate. Cheilomacrocystidia 33–66 × 5–9 µm, scattered to abundant, cylindrical to subclavate; apex rounded.

Ecology and distribution. Widespread in the Northern Hemisphere in temperate, boreal, and arctic-alpine areas with *Betula*. In the GYE and elsewhere in the Rocky Mountains, it occurs in subalpine and alpine areas with *Betula glandulosa* and possibly other *Betula* spp., late summer.

Specimens examined. U.S.A. MONTANA: Carbon County, Beartooth Plateau, Birch Site, near *Betula glandulosa*, 29 July 1997, CLC1134 = ZT6096 (MONT); 8 Aug 1998, CLC1217 (MONT); 10 Aug 1999, TWO269 (MONT); 19 Aug 1999, CLC1380 (MONT); 13 Aug 2007, ZT12723 (MONT); Carbon County, Hellroaring Plateau, Hellroaring Creek, near *Betula glandulosa*, 9 Aug 2015, EB111-15 (MONT). WYOMING: Park County, Beartooth Plateau, Island Lake, near *Betula glandulosa*, 6 Sept 2015, EB160-15 (MONT).

Discussion. *Lactarius glyciosmus* is very closely related to *L. mammosus* Fr. (Figure 2A), however, the latter has a browner pileus, stouter stature, and ecology with Pinaceae (although it has been reported with *Betula*) (Heilmann-Clausen et al. 1998). *Lactarius vietus* (Fr.) Fr. has a distinct pale zone near the stipe apex, latex that dries greenish gray, longer pleuromacrocystidia (50–90 × 7–12 µm), a mild to slightly fruity odor, and a strongly acrid taste (Heilmann-Clausen et al. 1998). The presence of *L. mammosus* and *L. vietus* in the Rocky Mountains is unclear. *Lactarius trivialis* (Fr.) Fr., which has been reported from the GYE (McKnight 1982), but could not be confirmed, is typically larger with slightly larger basidiospores (7.3–10 × 5.9–7.8 µm), more numerous pleuromacrocystidia, and a mild to acidic-fruity odor (Heilmann-Clausen et al. 1998).

Figure 5. *Lactarius glyciosmus*. Collection EB111-15 under *Betula glandulosa*, Hellroaring Plateau, Montana, USA. Scale bar: 2 cm. Photo by E. Barge.

Lactarius nanus has larger basidiospores (7–10.5(–12) × 5–8 µm), larger and differently shaped pleuromacrocystidia (53–96.5(–114) × 6.5–11.5 µm), a mild odor, and associates with *Salix*.

4. *Lactarius repraesentaneus* Britzelm.

Figure 6

The following morphological description includes data from Colorado specimens listed in Barge et al. (2016).

Description. Pileus 60–100 mm in diameter, convex to plano-convex usually with a depressed center and sometimes with a papilla, smooth at center, becoming increasingly hairy to bearded toward margin, viscid to dry, azonate, surface orange-brown at center, becoming pale yellow-brown to cream toward margin; hairs pale yellow-brown to red-brown; margin strongly incurved, remaining so or becoming nearly straight in age. Lamellae adnate to decurrent, crowded, cream to pale-yellow, staining violet where damaged. Stipe 30–70 × 15–35 mm, stout, equal to clavate, viscid to dry, cream to pale-yellow, often with numerous dingy yellow, golden yellow, yellow-brown, or light orange-brown scrobicules, hollow. Context white, staining violet where damaged. Latex scarce to abundant, white, becoming violet. Odor spicy-floral, resinous. Taste resinous to slightly acrid.

Figure 6. *Lactarius repraesentaneus*. Collection EB107-13 near krummholz *Picea engelmannii* and *Salix glauca*, Beartooth Plateau, Montana, USA. Scale bar: 2 cm. Photo by E. Barge.

Basidiospores 8–10.5 × 6–8.5 µm, Q = 1.1–1.4, broadly ellipsoid to ellipsoid; ornamentation forming an incomplete to dense reticulum. Pleuromacrocystidia 78.5–145 × 9–13 µm, scattered to abundant, strongly projecting, subfusiform to lanceolate; apex acute to moniliform. Cheilomacrocystidia 56–140 × 7.5–13 µm, scattered to abundant, strongly projecting, subfusiform to lanceolate; apex acute moniliform.

Ecology and distribution. Widespread in the Northern Hemisphere in temperate, boreal, and arctic-alpine areas with *Picea, Betula*, and possibly *Salix*. In the GYE, it occurs in the spruce-fir and krummholz zone, typically near *Salix glauca* and *Picea engelmannii*, sometimes also intermixed with *Arctostaphylos uva-ursi* and *Betula glandulosa*, late summer.

Specimens examined. U.S.A. MONTANA: Carbon County, Beartooth Plateau, Birch Site, among *Salix glauca* and krummholz *Picea engelmannii*, 12 Aug 2002, CLC1971 (MONT); 13 Aug 2007, CLC2318 (MONT); 18 Aug 2013, EB107-13 (MONT); Carbon County, Hellroaring Plateau, Hellroaring Creek, among *Arctostaphylos uva-ursi*, *Salix glauca* and krummholz *Picea engelmannii*, 9 Aug 2015, EB116-15 (MONT). WYOMING: Park County, Beartooth Plateau, Frozen Lakes, among *Salix glauca* and krummholz *Picea engelmannii*, 21 Aug 1999, CLC1394 (MONT).

Discussion. Due to its conspicuously bearded margin, and violet staining tissue, *L. repraesentaneus* is difficult to confuse with anything else in the Rocky Mountains. It is very closely related to the arctic-alpine *Dryas* and *Salix* associate *L. dryadophilus* Kühner (Figure 2A), however, the latter features a cream to yellow, smoother pileus with hairs restricted to near the margin, and a basidiospore ornamentation consisting of sparse, thinner ridges (Heilmann-Clausen et al. 1998). *Lactarius dryadophilus* has

not been reported from the Rocky Mountains. *Lactarius repraesentaneus* and other violet-staining species such as *L. uvidus* (Fr.) Fr., *L. aspideus* (Fr.) Fr., *L. salicis-reticulatae* Kühner, *L. montanus* (Hesler & A.H. Sm.) Montoya & Bandala, *L. pallidomarginatus*, and *L. brunneoviolaceus* M.P. Christ., etc. occur together in a weakly supported clade, that corresponds with section *Uvidi* (Konr.) Bon (Figure 2A).

5. *Lactarius salicis-reticulatae* Kühner

Figure 7

The following morphological description is based on Barge et al. (2016).

Description. Pileus 20–40 mm in diameter, convex to broadly convex, usually with a depressed center, smooth, viscid to dry, azonate, cream, pale yellow, or pale ocher, sometimes darker toward the center, staining violet where damaged; margin incurved, remaining so or becoming merely downturned in age. Lamellae adnate to subdecurrent, subdistant to distant, cream, pale yellow, or pale orange-ocher often with a pinkish-buff tint, staining violet where damaged. Stipe 15–20 × 10–15 mm, equal to clavate, viscid to dry, cream to pale-yellow, staining violet where damaged, hollow. Context white, staining violet where damaged. Latex scarce to undetectable, watery, white, becoming violet. Odor mild to slightly sweet. Taste mild.

Basidiospores (7–)8.5–11.5 × (7–)8–10 µm, Q = (1–)1.1–1.4, subglobose to ellipsoid; ornamentation forming an incomplete reticulum. Pleuromacrocystidia 76–101.5 × 7.5–11.5 µm, scarce, strongly projecting, subfusiform to fusiform; apex rounded to acute to moniliform. Cheilomacrocystidia 68.5–91.5 × 7.5–10.5 µm, scattered to abundant, strongly projecting, subfusiform to fusiform; apex acute to rounded to moniliform.

Ecology and distribution. Widespread in arctic-alpine areas in the Northern Hemisphere with *Salix*. In the GYE, it occurs in alpine areas with *S. arctica*, *S. reticulata*, as well as shrubby *Salix* spp., sometimes also intermixed with *Dryas octopetala*, late summer.

Specimens examined. U.S.A. MONTANA: Carbon County, Beartooth Plateau, Birch Site, among *Salix reticulata*, 17 Aug 2011, CLC2776 (MONT); Carbon County, Beartooth Plateau, Highline Trail, among dwarf *Salix* spp., 8 Aug 1998, CLC1211 (MONT); Carbon County, Hellroaring Plateau, Hellroaring Creek, under shrubby *Salix* sp., 8 Aug 2015, EB112-15 (MONT); among shrubby *Salix* sp. and *S. reticulata*, 8 Aug 2015, EB113-15 (MONT); among *Dryas octopetala*, shrubby *Salix* sp. and *S. reticulata*, 8 Aug 2015, EB117-15 (MONT), EB118-15 (MONT), EB119-15 (MONT); Sweet Grass County, Crazy Mountains, above Blue and Granite Lakes, among *Salix arctica*, 1 Aug 2015, EB101-15 (MONT). WYOMING: Park County, Beartooth Plateau, Gardner Lake, under shrubby *Salix* sp., 16 Aug 2014, EB0057-14 (MONT).

Discussion. *Lactarius aspideoides* Burl., described from eastern North America is closely related (Figure 2A), however, it is generally larger, with a somewhat zonate pileus. It also has more crowded lamellae that lack salmon-colored hues, slightly smaller

Figure 7. *Lactarius salicis-reticulatae*. Collection EB0057-14 under shrubby *Salix* sp., Beartooth Plateau, Wyoming, USA. Scale bar: 2 cm. Photo by E. Barge.

basidiospores (7–10 × 7–8–µm) with broader ridges, a bitter to slightly acrid taste, and a subalpine ecology (Hesler and Smith 1979). The status of *L. aspideoides* in western North America is unclear. *Lactarius aspideus*, another similar species which was described from northern Europe with *Salix*, has smaller basidiospores (6.7–9.5 × 5.6–7.8 µm) with denser reticulation, more crowded, creamier colored lamellae, and a habitat mainly in subalpine areas (Heilmann-Clausen et al. 1998). The presence of *L. aspideus* in North America is unclear. *Lactarius salicis-herbaceae* Kühner, a closely related (Figure 2A) arctic-alpine *Salix* associate, which has not been reported from the Rocky Mountains, has darker yellow to yellow-brown sporocarps, pale cream to grayish buff lamellae, and more densely reticulate basidiospores (Heilmann-Clausen et al. 1998).

6. *Lactarius pallidomarginatus* Barge & C.L. Cripps

Figure 8

The following morphological description is from Colorado material which includes the holotype and all are listed in Barge et al. (2016)

Description. Pileus 20–50 mm in diameter, convex to broadly convex to plane with or without a depressed center, smooth, subviscid to dry, azonate, blotchy light tan to light brown, developing violet stains, lighter (to cream) toward margin; margin in-

Figure 8. *Lactarius pallidomarginatus*. Collection EB0041 under *Salix planifolia*, San Juan Mountains, Colorado, USA. Scale bar: 2 cm. Photo by E. Barge.

curved when young, remaining so or becoming nearly straight in age. Lamellae adnate to subdecurrent, subdistant to slightly crowded, white to pale yellow-cream, staining violet where damaged. Stipe 10–40 × 5–10 mm, equal to slightly clavate, smooth, dry, white to cream, staining violet where damaged, hollow. Context white to cream, staining violet where damaged. Latex scarce to undetectable, watery, white, staining tissue violet. Odor mild. Taste mild.

Basidiospores 8–10 × 6.5–8 µm, Q = 1.1–1.4, broadly ellipsoid to ellipsoid; ornamentation forming an incomplete to dense reticulum. Pleuromacrocystidia 81.5–112 × 9–10 µm, scarce to scattered, cylindrical to lanceolate; apex acute to moniliform. Cheilomacrocystidia 48–101.5 × 7.5–13 µm, scattered, cylindrical to lanceolate; apex acute to moniliform.

Ecology and distribution. Known from only a few alpine localities in the central and southern Rocky Mountains with *Salix planifolia* and possibly also *S. glauca*, late summer.

Specimens examined. U.S.A. WYOMING: Sublette County, Wind River Range, Union Peak, near *Salix glauca*, 22 Aug 1994, ZT5229 (MONT).

Discussion. This species was recently described (Barge et al. 2016) from the alpine zone in Southern Colorado with *Salix*. It is tentatively included here because a collection morphologically matching the type was made by Dr Egon Horak from the Wind

River Range of Wyoming (technically in the southern GYE) with *Salix glauca*. Interestingly, out of all of the species examined thus far, *L. pallidomarginatus* appears most closely related to the bright yellow, violet-staining *Salix* associate *L. aspideus* (Figure 2A), to which it bares little resemblance.

In the Rocky Mountains, *L. pallidomarginatus* is most easily confused with *L. nanus*, *L. glyciosmus*, *L. montanus,* and *L.* aff. *brunneoviolaceus*. The basidiomes of *L. nanus* do not stain violet where damaged and it produces basidiospores with thicker, more jagged ridges, and macrocystidia with more rounded apices (see Barge et al. 2016). *Lactarius glyciosmus* also does not stain violet where damaged, it has an odor of coconut, slightly smaller basidiospores (7–9 × 5–7 µm), and smaller cheilomacrocystidia (33–66 × 5–9 µm). The closely related violet-staining *L. montanus* produces basidiomes which are typically much more robust and stain green on the stipe and pileus surface with KOH. *Lactarius montanus* also has a strongly resinous odor and taste, and is mainly subalpine with conifers. See comments under *L.* aff. *brunneoviolaceus* for features differentiating *L. pallidomarginatus* from that taxon. See Barge et al. (2016) for features differentiating *L. pallidomarginatus* from the European taxon *L. pseudouvidus* Kühner.

7. *Lactarius montanus* (Hesler & A.H. Sm.) Montoya & Bandala

Figure 9

Description. Pileus 30–100 mm in diameter, convex to ± depressed–convex to infundibuliform, viscid, smooth, azonate to zonate, zones consisting of darker spots arranged concentrically, gray–brown to vinaceous–gray to violet–brown; margin straight to slightly incurved when young, becoming straight and ± wavy. KOH on pileus cuticle and stipe green. Lamellae adnate to subdecurrent, crowded to subdistant, cream, discoloring violet where damaged with rust brown stains also often present on older material. Stipe 30–70 × 10–30 mm, equal to clavate, smooth with light tomentum often present especially toward base, dry, white to light brown, discoloring violet and eventually rust brown where damaged, solid, becoming hollow. Context white, discoloring violet and eventually rust brown where damaged. Latex scarce to copious, white, staining tissue violet. Odor strongly resinous. Taste strongly resinous.

Basidiospores 7–10.5 × 6–8 µm, Q = 1.2–1.5, broadly ellipsoid to ellipsoid; ornamentation forming a broken to partial reticulum. Pleuromacrocystidia 50–90 × 5–10 µm scarce to scattered, fusoid–acuminate; apex acute to moniliform. Cheilomacrocystidia 30–55 × 4–9 µm, scarce, fusoid–acuminate; apex acute to moniliform.

Ecology and distribution. Under conifers in western North America. In the GYE, it occurs in wet areas, often along streams in the montane spruce-fir and krummholz zones, possibly always in the presence of *Picea engelmannii*, summer and fall.

Specimens examined. U.S.A. MONTANA: Madison County, Madison Range, Mirror Lake, swampy area under *Abies lasiocarpa* and *Picea engelmannii*. 3 Sept 2013, EB120-13 (MONT); Madison County, Tobacco Root Mountains, Branham Lakes, under *Picea engelmannii* and *Salix planifolia*, 31 Aug 2013, CLC3001 (MONT), under

Figure 9. *Lactarius montanus*. Top collection EB0072-14 and bottom collection EB0073-14 under *Picea engelmannii*, Tobacco Root Mountains, Montana, USA. Scale bars: 2 cm. Photos by E. Barge.

Picea engelmannii, 1 Sept 2014, EB0071-14 (MONT), EB0072-14 (MONT), EB0073-14 (MONT).

Discussion. In western North America, similar species with violet-staining flesh include *L. pallescens* Hesler & A.H. Sm., *L. californiensis* Hesler & A.H. Sm., and *L.*

cordovaensis Hesler & A.H. Sm. *Lactarius pallescens* and *L. californiensis* are generally more white overall in color, have a slightly acrid to acrid taste (not strongly resinous), and do not stain green in KOH. *Lactarius cordovaensis* has orange–tan lamellae when young, and possibly slightly smaller basidiospores (7.5–9.5 × 6.5–8 µm). *Lactarius uvidus*, a European species whose presence has not been confirmed molecularly for North America, typically has a lighter pileus, a bitter taste (not strongly resinous), and does not stain green in KOH. Previous reports of *L. uvidus* from the GYE (McKnight 1982) and the Central and Southern Rocky Mountains in general likely refer to *L. montanus*. See comments under *L.* aff. *brunneoviolaceus* and *L. pallidomarginatus* for features differentiating *L. montanus* from those taxa.

8. *Lactarius* aff. *brunneoviolaceus* M.P. Christ.

Figure 10

Description. Pileus 30–60 mm in diameter, convex to slightly depressed–convex, smooth, viscid, faintly zonate, brownish with lavender hues, marbled, whitish near margin; margin incurved and faintly tomentose when young. KOH on pileus cuticle green. Lamellae adnate, crowded, cream, staining violet where damaged. Stipe 25–30 × 20–25 mm, clavate, smooth, white with hoary coating, staining violet where damaged, hollow. Context not observed. Latex white, unchanging, staining tissue violet. Odor sweet. Taste mild, becoming slightly bitter.

Basidiospores 8–12 × 6.5–8 µm, Q = 1.2–1.5, broadly ellipsoid to ellipsoid; ornamentation forming an incomplete reticulum. Pleuromacrocystidia 40–90 × 8–12 µm, scattered to numerous, subfusiform to fusiform; apex mucronate. Cheilomacrocystidia 40–88 × 7–12 µm, numerous, fusiform; apex mucronate.

Ecology and distribution. *Lactarius brunneoviolaceus* occurs in arctic-alpine areas with *Salix*. The species described here was found growing near tree line (krummholz spruce present) on the Beartooth Plateau amongst *Salix reticulata* and *S. planifolia*, late summer.

Specimens examined. U.S.A. MONTANA: Custer County, Beartooth Plateau, Birch Site, among krummholz *Picea engelmannii*, *Salix reticulata* and *Salix planifolia*, 15 Aug 2014, CLC3098 (MONT).

Discussion. More collections and molecular data from this species are needed, however, this is the first report of a species from the GYE, and to the best of our knowledge, North America, bearing affinities to the arctic-alpine *Salix* associate *L. brunneoviolaceus*. Unfortunately, high quality sequence data was not obtained for this collection, and only a small portion of ITS1 could be used for phylogenetic analyses, which placed it with *L. brunneoviolaceus*. Morphologically, it is also a close match, except that the pileus of the species described here stains green with KOH, which is not historically mentioned for *L. brunneoviolaceus*. It is possible that the pileus of *L. brunneoviolaceus* stains green in KOH as well but that it has not been thoroughly tested. In CLC2133 from Norway, another specimen closely matching *L. brunneoviolaceus* which was examined, the pileus (of dried material) also stained green in KOH.

Figure 10. *Lactarius* aff. *brunneoviolaceus*. Collection CLC3098 near *Salix reticulata* (pictured), *S. planifolia*, and krummholz *Picea engelmannii*, Beartooth Plateau, Montana, USA. Scale bar: 2 cm. Photo by C. Cripps.

This species is very closely related to *L. montanus* (Figure 2A), however, the latter features slightly smaller basidiospores (7–10.5 × 6–8 µm, although sometimes to 12 µm long), and is typically below tree line with conifers. *Lactarius pallidomarginatus*, which is also closely related, has lighter colored, less violaceous pilei that do not stain green in KOH, and smaller basidiospores (8–10 × 6.5–8 µm).

9. *Lactarius caespitosus* Hesler & A.H. Sm.

Figure 11

Description. Pileus 35–100 µm in diameter, convex to broadly convex to nearly plane, ± centrally depressed, viscid to dry, smooth, more or less azonate, cream to pale gray–brown to pale vinaceous–brown, ± discoloring ochraceous in places; margin incurved when young, becoming straight in age. Lamellae adnate to subdecurrent, crowded to subdistant, white at first, becoming pale creamy buff, ± discoloring ochraceous to brown where damaged. Stipe 30–80 × 10–35 mm, equal to clavate, viscid to dry, smooth, white, developing ochraceous to faintly violet areas where damaged, solid, becoming hollow. Context white. Latex scarce to undetectable, white, unchanging. Odor mild. Taste acrid.

Figure 11. *Lactarius caespitosus*. Top collection EB0074-14 under *Abies lasiocarpa*, Tobacco Root Mountains, Montana, USA. Bottom collection EB095-15 under *Abies lasiocarpa* and *Picea engelmannii*, Crazy Mountains, Montana, USA. Scale bars: 2 cm. Photos by E. Barge.

Basidiospores 8–12 × 7–9 µm, Q = 1.2–1.4, broadly ellipsoid to ellipsoid; ornamentation forming a broken to partial reticulum. Pleuromacrocystidia 50–110 × 8–12 µm, scattered to numerous, subcylindric to fusoid; apex rounded to acute.

Cheilomacrocystidia 40–60 × 8–12 µm, scattered to abundant, clavate to mucronate; apex rounded to acute.

Ecology and distribution. In mountainous areas in western North America with conifers. Hesler and Smith (1979) report it as the common montane *Lactarius* of wet places in the spruce-fir zone of the Rocky Mountains during the summer and early fall. In the GYE, it occurs in wet depressions and near seeps as well as in drier upland sites in the montane spruce-fir zone, possibly always in the presence of *Abies lasiocarpa*, summer to fall.

Specimens examined. U.S.A. MONTANA: Gallatin County, Gallatin Range, East Fork Hyalite Creek, under *Abies lasiocarpa* and *Picea engelmannii*, 25 Aug 2015, EB158-15 (MONT); Gallatin County, Gallatin Range, Windy Pass Trail, under *Abies lasiocarpa* and *Pinus contorta*, 10 Aug 2013, EB102-13 (MONT); Madison County, Madison Range, Big Sky, under *Abies lasiocarpa*, *Picea engelmannii* and *Pinus albicaulis*, 4 Sept 2004, CLC2052 (MONT); Madison County, Madison Range, Mirror Lake, under *Abies lasiocarpa*, 3 Sept 2013, EB121-13 (MONT); Madison County, Tobacco Root Mountains, Branham Lakes, under *Abies lasiocarpa*, 1 Sept 2014, EB0074-14 (MONT); Sweet Grass County, Crazy Mountains, Big Timber Creek, under *Abies lasiocarpa* and *Picea engelmannii*, 1 Aug 2015, EB095-15 (MONT). WYOMING: Park County, Beartooth Plateau, Beartooth Lake Campground, under *Abies lasiocarpa* and *Picea engelmannii*, 5 Sept 2015, EB159-15 (MONT).

Discussion. The European *Abies* associate *L. albocarneus* Britzelm. appears to be closely related (Figure 2B), however, it has a lighter cream to dingy whitish pileus, and slowly yellowing latex and flesh (Heilmann-Clausen et al. 1998). The western North American *L. kauffmanii* Hesler & A.H. Sm. and *L. pseudomucidus* Hesler & A.H. Sm. also appear to be related (Figure 2B). *Lactarius kauffmanii* has a dark to blackish brown pileus (although it can be lighter), smaller basidiospores (7–10 × 6.5–8 µm), and a vinaceous to tan stipe. *Lactarius pseudomucidus* typically has a darker and more slimy pileus, a gray to gray–brown stipe, and smaller basidiospores (7–9 × 6–7 µm). Both *L. kauffmanii* and *L. pseudomucidus* may be confined to Douglas fir/western hemlock forests of the Pacific Northwest (Hesler and Smith 1979). The western North American *L. circellatus* v. *borealis* Hesler & A.H. Sm. is also similar, however, its pileus is pruinose at first and generally darker and faintly zonate to zonate, it has a dry stipe (never viscid as in *L. caespitosus*), and its lamellae are unstaining when cut (Hesler and Smith 1979, Methven 1997). *Lactarius trivialis* is also similar, however it appears to be fairly distantly related (Figure 2A); it has purplish gray to vinaceous colors of the pileus at least when young and smaller basidiospores (7.3–10 × 5.9–7.8 µm) (Heilmann-Clausen et al. 1998). *Lactarius argillaceifolius* Hesler & A.H. Sm. and its varieties are also similar, however, all feature a more purplish gray pileus at least when young (similar to *L. trivialis*) and smaller basidiospores. Variety *argillaceifolius* appears to be confined to oak forests in central and eastern North America, v. *megacarpus* Hesler & A.H. Sm. to oak forests in coastal western North America, and v. *dissimilis* Hesler & A.H. Sm. is represented by only one collection from South Carolina (Hesler and Smith 1979).

10. *Lactarius controversus* Pers.
Figure 12

Description. Pileus 50–120 mm in diameter, depressed–convex to infundibuliform, smooth, viscid to dry, faintly zonate, zones narrow and often more conspicuous near the margin, cream to pale tan–cream, often with tan to rust brown blotches; margin incurved and faintly short–tomentose when young, becoming glabrous and straight to undulating in age. Lamellae adnate to subdecurrent, crowded, creamy pink to pink–tan, discoloring tawny light brown where damaged. Stipe 25–50 × 17–28 mm, short, equal to tapering toward the base, subviscid to dry, smooth, ± scrobiculate, white, discoloring pale yellow to tawny light brown where damaged, solid, becoming hollow. Context white, discoloring tawny light brown. Latex scarce, white, unchanging. Odor faint to slightly spermatic. Taste slowly acrid.

Basidiospores 5.5–8 × 4.5–5.5 µm, Q = 1.2–1.5, broadly ellipsoid to ellipsoid; ornamentation forming a nearly complete reticulum. Pleuromacrocystidia 25–50 × 3–7 µm, scarce, cylindric to fusiform; apex acute to moniliform. Cheilomacrocystidia 25–40 × 3–6 µm, scarce, cylindric to fusiform; apex rounded to acute.

Ecology and distribution. Widely distributed in the northern hemisphere with *Populus* (aspen), *Salix*, and possibly *Betula*. In the GYE it occurs in montane areas near *Populus tremuloides*, summer and fall.

Specimens examined. U.S.A. IDAHO: Teton County, Teton Mountains, under *Populus tremuloides*, CLC290 (MONT). MONTANA: Carbon County, near Red

Figure 12. *Lactarius controversus*. Collection EB110-15 under *Populus tremuloides*, Beartooth Mountains, Montana, USA. Scale bar: 2 cm. Photo by E. Barge.

Lodge, along Rock Creek, under *Populus tremuloides*, 8 Aug 2015, EB110-15 (MONT); Park County, Cinnabar Basin, under *Populus tremuloides*, 18 July 1990, CLC106 (MONT), 2 Aug 1990, CLC116 (MONT), 11 Sept 1991, CLC262 (MONT), 13 July 1992, CLC462 (MONT); Silverbow County, Butte, East Ridge, under *Populus tremuloides*, 15 Aug 1993, CLC699 (MONT). WYOMING: Park County, along Beartooth Highway, under *Populus tremuloides*, 16 Aug 2014, EB0061-14 (MONT).

Discussion. *L. controversus* is fairly easily recognized by its small basidiospores, whitish pileus, pinkish lamellae, acrid taste, and association with aspen. No other species is similar in the Rocky Mountains. While morphological differences between European and GYE material were not detected, there is some molecular divergence, which could indicate separate species, although more material needs to be examined (Figure 2B).

11. *Lactarius olympianus* Hesler & A.H. Sm.

Figure 13

Description. Pileus 20–100 mm in diameter, depressed–convex to infundibuliform, smooth, viscid, zonate, color alternating between rich and dull orange; margin incurved when young becoming straight to wavy in age. Lamellae adnate, crowded to subdistant, cream to dingy yellow, staining orange–brown in age or where damaged.

Figure 13. *Lactarius olympianus*. Collection EB0070-14 under *Picea engelmannii*, Tobacco Root Mountains, Montana, USA. Scale bar: 2 cm. Photo by E. Barge.

Stipe 20–50 × 10–25 mm, equal to tapering toward the base, smooth, white, at first with a white bloom, staining dingy orange–brown where damaged, solid, becoming hollow. Context white. Latex white, unchanging, staining lamellae orange–brown. Odor mild. Taste acrid.

Basidiospores 8–11.5 × 7.5–9.5 µm, Q = 1.1–1.3, broadly ellipsoid; ornamentation forming a broken to nearly complete reticulum. Pleuromacrocystidia 20–50 × 3–6 µm, scattered to numerous, fusiform; apex acute to moniliform. Cheilomacrocystidia 20–35 × 3–6 µm, scattered, fusiform; apex acute to moniliform.

Ecology and distribution. In montane conifer forests in western North America. In the GYE, it occurs in seeps and along streams in the spruce-fir zone possibly always in the presence of *Picea engelmannii*.

Specimens examined. U.S.A. MONTANA: Gallatin County, Gallatin Range, Windy Pass Trail, under *Picea engelmannii*, 4 Aug 2012, EB0114 (MONT); Madison County, Tobacco Root Mountains, Branham Lakes, under *Picea engelmannii*, 1 Sept 2014, EB0070-14 (MONT).

Discussion. This species is very close to and likely conspecific with *L. zonarioides* Kühner & Romagn. (Figure 2B), which occurs in similar habitats and was described from Europe (Hesler and Smith 1979).

12. *Lactarius pseudodelicatus* A.H. Sm.

Figure 14

Description. Pileus 70–140 mm in diameter, broadly depressed–convex to broadly infundibuliform, viscid to dry, smooth to matted–tomentose especially near the margin, zonate to faintly zonate, yellow–buff to buff to pale orange–brown, lighter toward the margin; margin incurved and matted–tomentose to cottony–tomentose when young, remaining so or becoming straight and ± glabrous in age. Lamellae subdecurrent to decurrent, many of them branching, crowded, white to pale cream when young, becoming orange–buff to brown to gray–brown in age. Stipe 20–90 × 15–20 mm, tapering toward the base, smooth, white to pale buff, discoloring brown, often with scattered small scrobicules, hollow. Context firm. Latex copious, white, unchanging. Odor pleasant, fruity, of orange–citrus. Taste acrid.

Basidiospores 6–8 × 5–6.5 µm, Q = 1.2–1.5, broadly ellipsoid to ellipsoid; ornamentation forming a broken to partial reticulum. Pleuromacrocystidia 60–100 × 7–12 µm, numerous, strongly projecting, fusiform; apex acute. Cheilomacrocystidia 40–61 × 7–10 µm, numerous, strongly projecting, fusiform; apex acute.

Ecology and distribution. Originally described from Michigan under aspen. There are very few subsequent reports. In the GYE, it is here reported with *Populus tremuloides* from the Teton Range of Idaho, summer.

Specimens examined. U.S.A. IDAHO: Teton County, Teton, under *Populus tremuloides*, 27 July 1991, CLC233 (MONT), 24 Aug 1991, CLC296 (MONT), 26 July 1992, CLC512 (MONT).

Figure 14. *Lactarius pseudodelicatus*. Collection CLC512 under *Populus tremuloides*, Teton Range, Idaho, USA. Scale bar: 2 cm. Photo by C. Cripps.

Discussion. This represents the first report of this species from the GYE under the name *L. pseudodelicatus*. It was previously reported from the GYE as *L.* cf. *zonarius* Fr. in Cripps and Miller (1993) and Cripps (2001). The European *L. zonarius* has slightly larger basidiospores (6.3–9.2 × 5.1–7.4 µm), shorter pleuromacrocystidia (40–50 × 4–6 µm), and an ecology with *Quercus* (Heilmann-Clausen et al. 1998).

Molecularly, *L. pseudodelicatus* is very close to a specimen identified as *L.* aff. *wenquanensis* Y. Wang & Z.X. Xie, from a humid montane rainforest with *Quercus*, *Castanopsis*, and *Lithocarpus echinops* Hjelmq. in Thailand (Figure 2B) (Le et al. 2007). *Lactarius* aff. *wenquanensis* appears to be less robust with shorter pleuromacrocystidia (54–76 × 9.5–12 µm); it also appears to have a different ecology. *Lactarius wenquanensis* Y. Wang & Z.X. Xie, originally described from China has larger basidiospores (7.5–9.5 × (6–)6.5–7.5 µm) and the type was collected under *Picea* and *Abies*, as opposed to aspen (Wang 2007). *Lactarius torminosus* (Schaeff.) Gray is closely related to *L. pseudodelicatus* (Fig. 2B), however, *L. torminosus* typically has smaller basidiomes, a more pink to brick pileus, slightly larger basidiospores (7.5–9.6 × 5.6–6.9 µm), and associates with *Betula* (Heilmann-Clausen et al. 1998). *Lactarius pubescens* Fr. is also closely related to *L. pseudodelicatus* (Figure 2B), and both associate with aspen in similar habitats. *Lactarius pubescens* is typically less robust and features a more pale pileus, a non-scrobiculate stipe, and smaller pleuromacrocystidia (30–60 × 6.5–10 µm) (Heilmann-Clausen et al. 1998). *Lactarius delicatus* Burl., described from a deciduous forest in Eastern North America produces white latex that turns yellow (Hesler and Smith 1979).

13. *Lactarius pubescens* Fr.
Figure 15

Description. Pileus 20–100 mm in diameter, depressed–convex to infundibuliform, dry, smooth, hairy toward margin, pale cream to cream or pale pinkish buff; margin bearded, incurved when young becoming straight to wavy in age. Lamellae adnate to decurrent, crowded, pale cream to pale pinkish buff. Stipe 25–50 × 10–15 mm, equal, smooth, dry, pale pinkish buff to pale orange, becoming hollow. Context whitish to pale pinkish buff. Latex not abundant, white, unchanging. Odor fragrant. Taste acrid.

Basidiospores 6–8.5 × 4–6 µm, Q = 1.2–1.5, broadly ellipsoid to ellipsoid; ornamentation forming an incomplete reticulum. Pleuromacrocystidia 25–55 × 7–10 µm, scattered, clavate to fusiform; apex acute to moniliform. Cheilomacrocystidia 25–48 × 5–9 µm, numerous, clavate to fusiform; apex acute to moniliform.

Ecology and distribution. Originally described from Europe and apparently widespread with *Betula* and aspen. It also appears to associate with certain herbaceous plants in alpine areas (China) based on publicly available sequences on GenBank isolated from ectomycorrhizal root tips. In the GYE, it occurs with *Populus tremuloides* and *Betula*.

Specimens examined. U.S.A. MONTANA: Deerlodge County, Anaconda Superfund site, under *Betula* sp., 24 Sept 1996, CLC1045 (MONT); Park County, Gallatin Range, Cinnabar Basin, under *Populus tremuloides*, 1992, CLC539 (MONT); Silver Bow County, 23 Sept 2015, EB300-15 (MONT).

Figure 15. *Lactarius pubescens*. Collection EB303-15 under *Betula* sp., Boise, Idaho, USA. Scale bar: 2 cm. Photo by E. Barge.

Discussion. Morphologically and molecularly (at least at the ITS region), material from the GYE is identical to European material (Figure 2B). In North America, Hesler and Smith (1979) distinguish an *L. pubescens* v. *betulae* (A.H. Sm.) Hesler & A.H. Sm. based on yellowing latex among other subtle features, however yellowing latex was not noted in our collections. Further investigation of *L. pubescens* in North America is warranted. The *Betula* associate *L. torminosus* is similar, and closely related (Figure 2B) but its basidiomes are typically more pink colored and it has larger basidiospores (7.5–9.6 × 5.6–6.9 µm) (Heilmann-Clausen et al. 1998). *Lactarius resimus* (Fr.) Fr. is also similar, however it has strongly yellowing latex and flesh and larger basidiospores (7.0–9.7 × 5.3–7.2 µm) (Heilmann-Clausen et al. 1998). See comments under *L. pseudodelicatus* for distinguishing features for that taxon.

14. *Lactarius zonarius* v. *riparius* Hesler & A.H. Sm.

Figure 16

Description. Pileus 50–80 mm in diameter, depressed–convex to broadly infundibuliform, viscid to dry, smooth to ± matted–tomentose toward the margin, zonate to faintly zonate, yellow–brown to orange–brown, ± lighter toward the margin; margin incurved and matted–tomentose to cottony–tomentose when young, becoming straight and glabrous in age. Lamellae subdecurrent to decurrent, crowded, cream, staining brownish where damaged. Stipe 20–40 × 15–25 mm, equal to tapering toward the base, smooth,

Figure 16. *Lactarius zonarius* v. *riparius*. Collection CLC2933 under *Populus trichocarpa*, Bozeman, Montana, USA. Scale bar: 2 cm. Photo by E. Barge.

dry, cream, ± with small pale brown scrobicules. Context very firm, cream. Latex white, unchanging, staining lamellae brownish. Odor sweet, fruity. Taste slowly acrid.

Basidiospores 7–9 × 5.5–7.5 µm, Q = 1.2–1.4, broadly ellipsoid to ellipsoid; ornamentation forming a highly broken reticulum. Pleuromacrocystidia 40–66 × 4.5–7.4 µm, scarce to scattered, narrowly subfusiform to fusiform; apex acute to moniliform. Cheilomacrocystidia 25–49 × 4.5–5.5 µm, numerous, narrowly subfusiform to fusiform; apex acute to moniliform.

Ecology and distribution. Originally described and reported from rich wet humus along small streams in hardwood forests in Michigan. There are very few subsequent reports. In the GYE, it occurs in rich, moist riparian areas with *Populus trichocarpa*, summer to fall.

Specimens examined. U.S.A. MONTANA: Gallatin County, Bozeman, along Sourdough Creek, under *Populus trichocarpa*, 2013, CLC2933 (MONT).

Discussion. Molecularly, this taxon is very close to the European *L. evosmus* Kühner & Romagn. (Figure 2B), which also associates with *Populus*, as well as *Quercus*, and occasionally *Salix* (Heilmann-Clausen et al. 1998). It is also close to but distinct from the European *L. zonarius* (Figure 2B). Neither *L. evosmus* or *L. zonarius* feature a bearded pileus margin at any point in sporocarp development. *Lactarius zonarius* v. *riparius* will likely need to be given species level status and a new name, although this hinges on examination of type material.

Similar taxa in western North America include *L. sanmiguelensis* Hesler & A.H. Sm., described from under cottonwood in southwestern Colorado that has a pileus with cinnamon–buff zones on a pinkish buff ground color, the role of felt along the margin is pinkish buff, it does not have a distinctive odor, it is instantly and very strongly acrid, the lamellae are strongly anastomosed, pinkish buff, and do not discolor where injured, and the stipe is longer and pale pinkish buff (Hesler and Smith 1979). Bessette et al. (2009) synonymize *L. sanmiguelensis* and *L. subvillosus* Hesler & A.H. Sm., the latter being undoubtedly different from the species described here. *Lactarius pseudodelicatus* is somewhat similar but it has a longer stipe, smaller basidiospores (6–8 × 5–6.5 µm), and much larger pleuromacrocystidia (60–100 × 7–12 µm). *Lactarius psammicola* A.H. Sm. and *L. yazooensis* Hesler & A.H. Sm. are similar species with a more Eastern North American distribution in *Quercus* forests (Hesler and Smith 1979).

15. *Lactarius alnicola* A.H. Sm.

Figure 17

Description. Pileus 60–170 mm in diameter, depressed–convex to infundibuliform, glutinous when wet, with matted fibrils beneath the gluten especially near the margin, ± faintly zonate, pale creamy yellow to pale yellow–brown to golden yellow–brown, discoloring orange–brown to brown where damaged; margin ± faintly tomentose, incurved when young, becoming straight to wavy. Lamellae subdecurrent to decurrent, some forked toward the stipe, crowded, pale cream to pale buff, ± slowly discoloring

Figure 17. *Lactarius alnicola*. Top and bottom collection EB0064-14 under *Picea engelmannii*, Gallatin Range, Montana, USA. Scale bars: 2 cm. Photos by E. Barge.

yellow and eventually orange–brown where damaged. Stipe 20–60 × 30–50 mm, equal to clavate to tapering toward the base, smooth, dry, conspicuously scrobiculate, white, discoloring orange–brown where damaged or in age, solid, becoming hollow. Context firm, white, ± slowly discoloring yellow to orange–brown where damaged. Latex scarce

to undetectable, white, ± becoming very pale yellow, and slowly staining damaged tissue yellow. Odor mild to sweet. Taste quickly very acrid.

Basidiospores 7.5–10 × 6–8.5 µm, Q = 1.2–1.5, broadly ellipsoid to ellipsoid; ornamentation forming a partial reticulum. Pleuromacrocystidia 60–90 × 3–8 µm, rare, mostly near the pileus and between the lamellae, cylindric to fusiform; apex acute to moniliform. Cheilomacrocystidia absent.

Ecology and distribution. In western North America and Mexico under conifers. Also reported from California with *Quercus*. In the GYE, *L. alnicola* occurs in wet areas, often along streams in the spruce-fir zone, possibly always in the presence of *Picea engelmannii*, summer and early fall.

Specimens examined. U.S.A. MONTANA: Gallatin County, Gallatin Range, Langhor Road, under *Picea engelmannii*, 27 Aug, EB0064-14 (MONT); Madison County, Tobacco Root Mountains, Branham Lakes, under *Picea engelmannii*, 1 Sept 2014, EB0067-14 (MONT).

Discussion. *Lactarius alnicola* is phylogenetically very closely related to the European *L. scrobiculatus* (Scop.) Fr., and may be conspecific, however more specimens need to be sequenced before making this determination final (Figure 2B). For morphological differences, *L. scrobiculatus* features a heavily bearded pileus margin, and produces white latex which rapidly turns yellow (Kytövuori 1984). *Lactarius alnicola*, and other members of subsection *Scrobiculati* Hesler & A.H. Sm. sensu Kytövuori (1984) form a strongly supported clade in the phylogeny (Figure 2B).

Two varieties of *L. alnicola* have been described: *L. alnicola* v. *pitkinensis* Hesler & A.H. Sm., described from Colorado under aspen and conifers, has cream colored to white basidiomes, an acrid taste, unchanging latex, and unchanging (non-yellowing) flesh; *L. alnicola* v. *pungens* Hesler & A.H. Sm., described from Michigan in mixed forest, has a dull ochraceous to ochraceous–tan, subviscid, glabrous pileus, an acrid taste, and white, unchanging latex, which stains white paper yellow (Hesler and Smith 1979). Neither appear to fit the taxon described here.

16. *Lactarius* aff. *tuomikoskii* Kytöv.

Figure 18

Description. Pileus to 80 mm in diameter, broadly convex with a depressed center, glutinous when wet, with matted fibrils beneath the gluten especially near the margin, azonate, pale yellow–cream to yellow–tan, discoloring brown in places; margin densely bearded, incurved at least when young. Lamellae subdecurrent, crowded, cream to pale yellow–cream, ± discoloring yellow and eventually rusty brown where damaged. Stipe 30 × 20 mm, tapering toward the base, smooth, dry, white to pale yellow–tan, with small, faint, dull yellow–tan scrobicules, hollow. Context white, ± slowly discoloring pale yellow to faintly tan where damaged. Latex scarce, white, becoming very pale yellow, and slowly staining damaged tissue pale yellow. Odor sweet. Taste acrid.

Figure 18. *Lactarius* aff. *tuomikoskii*. Top and bottom collection EB0052-14 under *Picea engelmannii*, Silver Gate, Montana, USA. Scale bars: 2 cm. Photos by E. Barge.

Basidiospores 7–10 × 5.5–7.5 µm, Q = 1.2–1.5, broadly ellipsoid to ellipsoid; ornamentation forming a broken to nearly complete reticulum. Pleuromacrocystidia 50–100 × 7–12 µm, abundant, strongly projecting, fusiform to lanceolate; apex acute to moniliform. Cheilomacrocystidia absent.

Ecology and distribution. In montane, rich, moist habitats with *Picea engelmannii*, late summer.

Specimens examined. U.S.A. MONTANA: Park County, Silver Gate, under *Picea engelmannii*, 13 Aug 2014, EB0052-14 (MONT).

Discussion. This species, along with *L. alnicola*, and *L.* aff. *olivinus* Kytöv. described below, fall in subsection *Scrobiculati* as recognized by Kytövuori (1984). Morphologically, it is quite close to the European *L. tuomikoskii* Kytöv. It is also very close to some interpretations of *L. scrobiculatus* v. *canadensis* A.H. Sm., and *L. gossypinus* Hesler & A.H. Sm., except it has larger basidiospores and pleuromacrocystidia. *Lactarius payettensis* A.H. Sm. is also similar, but differs by having a more robust, heavily scrobiculate stipe and apparently unchanging latex (Hesler and Smith 1979). Both *L. gossypinus* and *L. payettensis* have been previously reported from the GYE (McKnight 1982), however neither were examined for this treatment. Overall, the complex of species surrounding *L. scrobiculatus* in North America, which includes *L. alnicola*, *L. gossypinus*, *L. payettensis*, *L. scrobiculatus* v. *canadensis*, *L. scrobiculatus* v. *montanus* Methven, and the two taxa described here (*L.* aff. *tuomikoskii*, and *L.* aff. *olivinus*) appears to be in need of revision, especially in relation to European taxa such as *L. auriolla* Kytöv., *L. leonis* Kytöv., *L. olivinus*, *L. scrobiculatus*, and *L. tuomikoskii* (Kytövuori 1984).

17. *Lactarius* aff. *olivinus* Kytöv.

Figure 19

Description. Pileus 30–110 mm in diameter, depressed–convex to infundibuliform, viscid when wet, with appressed, agglutinated scales of confluent hairs, especially near the margin, more or less azonate, cream to olive–buff to yellow–tan to orange–tan, ± darker toward the center; margin incurved and wooly–tomentose when young, often forming a cottony rim, becoming straight and more or less glabrous. Lamellae subdecurrent, crowded, cream, staining yellow where damaged and then fading or eventually becoming pale ochraceous. Stipe 30–45 × 10–25 mm, equal to clavate to tapering toward the base, smooth, dry, cream to pale yellow–tan to orange–tan, ± with pale yellow–tan scrobicules, often with a white ring near the apex, solid, becoming hollow. Context white, staining pale yellow at first and then fading. Latex scarce to undetectable, white, becoming yellow, staining tissue yellow and then fading. Odor faintly sweet to faintly spermatic. Taste mild.

Basidiospores 7.5–10 × 5.5–7 µm, Q = 1.3–1.5, ellipsoid; ornamentation forming a partial reticulum. Pleuromacrocystidia 51–100 × 9–14 µm, abundant, strongly projecting, fusiform to lanceolate; apex acute to moniliform. Cheilomacrocystidia absent.

Ecology and distribution. In montane, rich, moist habitats with *Picea engelmannii*, mid to late summer.

Figure 19. *Lactarius* aff. *olivinus*. Top collection EB0051-14 and bottom collection EB0050-14 under *Picea engelmannii*, Silver Gate, Montana, USA. Scale bars: 2 cm. Photos by E. Barge.

Specimens examined. U.S.A. MONTANA: Park County, Silver Gate, under *Picea engelmannii*, 13 Aug 2014, EB0050-14 (MONT), EB0051-14 (MONT).

Discussion. This species is morphologically close to the European *L. olivinus* except for the mild rather than acrid taste. Molecularly (Figure 2B), and ecologically, it is also

close, however we refrain from calling it that species until more collections are examined and compared with European material. It is also very close to some interpretations of the North American taxa *L. scrobiculatus* v. *canadensis*, and *L. gossypinus*, except it has larger basidiospores and pleuromacrocystidia. *Lactarius payettensis* is also similar, but it has unchanging latex, and a strongly acrid taste. See comments under *L.* aff. *tuomikoskii* for additional information.

18. *Lactarius barrowsii* Hesler & A.H. Sm.

Figure 20

Description. Pileus 30–140 mm in diameter, depressed–convex to broadly infundibuliform, viscid to dry, smooth, azonate, cream to dingy pinkish orange to pale yellow–brown to straw yellow, discoloring red and eventally green in age or where damaged; margin incurved with a white bloom when young, becoming straight to upturned and wavy in age. Lamellae adnate to subdecurrent, crowded to subdistant, dingy pinkish orange to creamy yellow–orange, discoloring red and eventually green where damaged. Stipe 15–50 × 10–30 mm, equal to tapering toward the base, dry, smooth, at first with a white bloom, becoming dingy pinkish orange to yellow–brown in places, staining red and eventually green where damaged, solid, becoming hollow. Context whitish, staining red. Latex scarce to undetectable, watery, red, staining flesh red and eventually green. Odor faintly sweet to spermatic in age. Taste mild.

Basidiospores 8.5–10 × 6–7.5 µm, Q = 1.3–1.5, ellipsoid; ornamentation forming a broken reticulum. Pleuromacrocystidia none observed (absent in Hesler and Smith 1979). Cheilomacrocystidia 30–50 × 2–6 µm, scattered, fusoid; apex acute.

Ecology and distribution. In Western North America, previously reported with ponderosa and pinyon pine. In the GYE, it occurs in foothills to low montane dry scrubland, so far reported only from under *Pinus flexilis*, spring and early summer. This is the first report of this species with *Pinus flexilis*.

Specimens examined. U.S.A. MONTANA: Gallatin County, Story Hill, under *Pinus flexilis*, 30 May 2015, EB008-15, EB015-15, EB028-15 (all at MONT); Madison County, Revenue Flats, under *Pinus flexilis*, 1 June 2015, EB037-15 (MONT).

Discussion. This is the first report of *L. barrowsii* from the GYE. *Lactarius barrowsii*, and other members of section *Deliciosi* (Fr.:Fr.) Redeuilh, Verbeken & Walleyn, such as *L. deliciosus* (L.) Gray, *L. deterrimus* Gröger, and *L. rubrilacteus* Hesler & A.H. Sm. form a monophyletic group (Figure 2B), previously shown by Nuytinck et al. (2007). *Lactarius barrowsii* is morphologically close to the western North American *L. rubrilacteus*. However, in *L. barrowsii*, the lamellae are more orange, the pileus is lighter and more yellow, the margin has a white bloom when young, and the stipe is often whiter. Phylogenetically, *L. barrowsii* is very close to the hypogeous, spring fruiting, pine associated *L. rubriviridis* Desjardin, H.M. Saylor & Thiers, which occurs in similar dry habitats in western North America (Nuytinck et al. 2007).

Figure 20. *Lactarius barrowsii*. Top collection EB008-15 (left and right) and bottom collection EB015-15 under *Pinus flexilis*, Story Hill, Bozeman, Montana, USA. Scale bars: 2 cm. Photos by E. Barge.

19. *Lactarius rubrilacteus* Hesler & A.H. Sm.

Figure 21

Description. Pileus 45–90 mm in diameter, shallowly depressed–convex to broadly infundibuliform, smooth, viscid, zonate, light brown to orange–cream to yellow–orange to orange–brown to carrot to dingy orange, often with green stains; margin incurved when young becoming straight. Lamellae adnate to subdecurrent, crowded to

Figure 21. *Lactarius rubrilacteus*. Collection EB13-040 under *Pseudotsuga menziesii*, Bridger Range, Montana, USA. Scale bar: 2 cm. Photo by E. Barge.

subdistant, cream to pinkish cinnamon to dull pink, discoloring wine red and eventually green where damaged. Stipe 20–40 × 10–25 mm, equal to tapering toward the base, dry, smooth, at first with a light glaucous coating, ± scrobiculate, cream to dull pink to orange–cream, discoloring wine red and eventually green where damaged, solid, becoming hollow. Context white, immediately staining deep wine–red to burgundy. Latex scarce, wine red, staining tissue wine–red to burgundy and eventually green. Odor mild. Taste mild.

Basidiospores 7.5–9.5 × 5–7.5 µm, Q = 1.3–1.5, ellipsoid; ornamentation forming a partial reticulum. Pleuromacrocystidia 40–80 × 4–6 µm, sparse, fusoid; apex acute. Cheilomacrocystidia 30–65 × 6–9 µm, scattered, fusoid; apex acute.

Ecology and distribution. In western North America with *Pseudotsuga menziesii* and *Pinus*. In the GYE this species occurs in foothills to low montane areas, near *Pseudotsuga menziesii*, spring and early summer.

Specimens examined. U.S.A. MONTANA: Gallatin County, Bridger Range, Fairy Lake Road, under *Pseudotsuga menziesii*, 25 June 2013, EB13-040 (MONT); Park County, Absaroka Mountains, George Lake Trailhead, under *Pseudotsuga menziesii*, 27 June 2014, EB900-14 (MONT).

Discussion. The European *L. sanguifluus* (Paulet) Fr. is morphologically similar, however, its lamellae are typically more violet tinged and its stipe is often scrobiculate. Western North American members of the "*L. deliciosus*" group can appear similar, however, their latex does not start out red as in *L. rubrilacteus*. The western North American *Lactarius barrowsii* also has reddish latex, however, it features a whitish to straw colored pileus and ochraceous to pinkish orange lamellae.

20. "*Lactarius deliciosus*" (L.) Gray (group)
Figure 22

Description. Pileus 30–100 mm in diameter, convex to broadly infundibuliform, smooth to faintly areolate, viscid to dry, ± faintly zonate, pale cream to pale yellow to carrot orange, often with green stains especially in age; margin striate when wet, incurved when young and becoming straight. Lamellae adnate to subdecurrent, crowded to subdistant, creamy orange to carrot orange, discoloring orange to reddish and eventally green where damaged. Stipe 30–70 × 5–25 mm, equal to clavate to tapering toward the base, viscid to dry, smooth, creamy orange to carrot orange with a white band toward the apex; discoloring carrot orange to dull reddish and eventually green where damaged, hollow. Context yellowish, immediately staining carrot orange to dull reddish and eventally green. Latex scarce, carrot orange, staining tissue carrot orange to dull reddish and eventually green. Odor mild. Taste mild.

Basidiospores 7.5–10.5 × 5.5–7.5 µm, Q = 1.3–1.5, ellipsoid; ornamentation forming a partial reticulum. Pleuromacrocystidia 40–55 × 3–6 µm, very sparse, subfusiform; apex moniliform. Cheilomacrocystidia 45–60 × 4–9 µm, scarce to numerous, subfusiform; apex moniliform.

Ecology and distribution. In North America with conifers. In the GYE, members of this group occur in montane mixed lodgepole/spruce-fir forests, the spruce-fir zone, and the krummholz zone, summer to fall; there are also reports specifically with *Pinus flexilis* (Cripps and Antibus 2011) and *Pinus albicaulis* (Mohatt et al. 2008, Cripps and Antibus 2011), and one collection is reported here with *Arctostaphylos uva-ursi*, well-separated from any conifers.

Specimens examined. U.S.A. MONTANA: Carbon County, Hellroaring Plateau, Hellroaring Creek, among *Arctostaphylos uva-ursi*, 9 Aug 2015, EB107-15 (MONT); Gallatin County, Gallatin Range, East Fork Hyalite Creek, under *Picea engelmannii*, 24 Aug 2014, EB0063-14 (MONT); Madison County, Madison Range, Taylor Creek, under *Abies lasiocarpa*, *Picea engelmannii* and *Pinus contorta*, 25 July 2015, EB089-15 (MONT).

Discussion. While section *Deliciosi* (Fr.:Fr.) Redeuilh, Verbeken & Walleyn has been resolved as monophyletic (Nuytinck et al. 2007) (Figure 2B), the complex of species surrounding *L. deliciosus* (L.) Gray in North America is poorly resolved. Using molecular techniques, Nuytinck et al. (2007) showed that *L. deliciosus* and *L. deterrimus* Gröger likely do not occur in North America. The collections of the North American varieties of *L. deliciosus* described by Hesler and Smith (1979) that they analyzed formed a clade separate from the European *L. deliciosus* and *L. deterrimus*, but were poorly resolved, with the exception of *L. deliciosus* v. *areolatus* A.H. Smith, which formed a monophyletic group. For descriptions of North American members of this group see Hesler and Smith (1979) and Methven (1997).

Lactarius deliciosus and all of its North American varieties, as well as *L. deterrimus* have been previously reported from the GYE (McKnight 1982, Mohatt et al. 2008,

Figure 22. "*Lactarius deliciosus*" group. Top collection EB107-15 among *Arctostaphylos uva-ursi*, Hell-roaring Plateau, Montana, USA. Bottom collection EB089-15 under *Picea engelmannii*, *Pinus contorta*, and *Abies lasiocarpa*, Madison Range, Montana, USA. Scale bars: 2 cm. Photos by E. Barge.

Cripps 2011, Cripps and Antibus 2011). Specimens from the GYE included in the phylogenetic analysis in the present study fall in the poorly resolved North American "*L. deliciosus*" group including "*L. deliciosus* v. *deterrimus*" (Gröger) Hesler & A.H.

Sm. and *L. deliciosus* v. *olivaceosordidus* Hesler & A.H. Sm. (Figure 2B). Previous reports of *L. thyinos* from the GYE (McKnight 1982), a northeastern North American member of sect. *Deliciosi* that occurs in *Thuja* bogs may refer to the "*L. deliciosus*" group described here. Overall, this group is in need of revision.

21. *Lactarius badiosanguineus* Kühner & Romagn.

Figure 23

Description. Pileus 15–70 mm in diameter, broadly convex to depressed–convex to broadly infundibuliform, ± umbonate, subviscid to dry, smooth to wrinkled–veined, typically darker when young, liver colored to deep scarlet red to red–brown to orange–brown to dingy orange, conspicuously lighter (to yellow–orange) toward the margin in age; margin ± striate when wet, slightly incurved to straight when young, remaining straight or becoming slightly wavy in age. Lamellae subdecurrent, crowded to subdistant, cream to creamy yellow to pale tan to pale orange–tan. Stipe 20–70 × 8–13 mm, equal to slightly clavate, smooth, dry, faintly white–pruinose when young, dingy orange to red–orange, solid, becoming hollow. Context pale tan to red–orange. Latex scarce to abundant, white, unchanging. Odor mild. Taste mild to slightly bitter.

Basidiospores 7–9.5 × 6–8 μm, Q = 1.1–1.4, subglobose to ellipsoid; ornamentation forming a broken to nearly complete reticulum. Pleuromacrocystidia 40–90 × 5–10 μm, scattered to numerous, subfusiform; apex obtuse to broadly acute. Cheilomacrocystidia 20–50 × 5–9 μm, scattered to numerous, subfusiform; apex obtuse to broadly acute.

Ecology and distribution. In Eurasia and North America with *Picea*. In the GYE, this species occurs in moist areas and along streams (although it can also occur on drier upland sites) in the montane spruce-fir zone, possibly always in the presence of *Picea engelmannii*, summer to fall.

Specimens examined. U.S.A. MONTANA: Gallatin County, Gallatin Range, East Fork Hyalite Creek, under *Abies lasiocarpa* and *Picea engelmannii*, 25 Sept 2013, EB200-13 (MONT); under *Abies lasiocarpa*, *Picea engelmannii* and *Pinus contorta*, 24 Aug 2014, EB0062-14 (MONT); Madison County, Tobacco Root Mountains, Branham Lakes, under *Picea engelmannii*; 1 Sept 2014, EB0069-14 (MONT); Sweet Grass County, Crazy Mountains, Big Timber Creek, under *Abies lasiocarpa* and *Picea engelmannii*, 1 Aug 2015, EB094-15 (MONT).

Discussion. This is the first report of this species from the GYE under the name *L. badiosanguineus*. In North American treatments (e.g. Hesler and Smith 1979, Bessette et al. 2009), this species may have gone under the name *L. hepaticus* Plowr. Previous reports of *L. subdulcis* (Pers.) Gray from the GYE (McKnight 1982) likely refer to *L. badiosanguineus*. The European *L. hepaticus* has a duller, browner pileus (although it can be deep red), yellowing latex and flesh, an acrid taste, and it associates with *Pinus* in nutrient-poor, acidic soils (Kränzlin 2005). The European *L. subdulcis* has a more orange–brown to brown pileus (although it can be reddish), a mild to unpleasant

Figure 23. *Lactarius badiosanguineus*. Top collection EB0069-14 under *Picea engelmannii*, Tobacco Root Mountains, Montana, USA. Bottom collection EB200-13 under *Picea engelmannii* and *Abies lasiocarpa*, Gallatin Range, Montana, USA. Scale bars: 2 cm. Photos by E. Barge.

smell, a bitter–acrid taste, and an association with *Fagus* (Heilmann-Clausen et al. 1998, Kränzlin 2005). Phylogenetically, *L. badiosanguineus* appears to be fairly closely related to but distinct from both *L. subdulcis* and *L. hepaticus* (Figure 2C).

Lactarius badiosanguineus is closely related to *L. subviscidus* Hesler & A.H. Sm., *L. sphagneti* (Fr.) Neuhoff, and *L. fulvissimus* Romagn. *Lactarius subviscidus* features typically smaller, more fragile basidiomes with a more uniformly orange pileus, and latex that stains white paper yellow (Hesler and Smith 1979); *L. subviscidus* appears to be confined to the coastal forests of the Pacific Northwest of North America. According to Heilmann-Clausen et al. (1998), the European *L. sphagneti* features a more distinctly two-toned pileus with a paler margin and darker center (although *L. badiosanguineus* also often displays this character at least in the GYE) as well as more densely reticulate spores with a stronger amyloid reaction. The European *L. fulvissimus* typically features basidiomes which are more orange overall, white latex which often turns yellow, basidiospores with an ornamentation of small pointed warts, and an ecology with deciduous trees such as *Fagus*, *Quercus*, *Tilia*, *Populus*, and *Corylus*, more rarely with conifers (Heilmann-Clausen et al. 1998, Kränzlin 2005).

Lactarius badiosanguineus is also very similar to *L. atrobadius* Hesler & A.H. Sm., reported from the Pacific coastal *Picea sitchensis* belt in North America. *Lactarius atrobadius* appears to have darker basidiomes, however, a more in depth molecular and morphological comparison between the two taxa is warranted. *Lactarius lanceolatus* O.K. Mill. & Laursen is also similar, however it typically produces basidiomes which are overall more orange with larger pleuromacrocystidia (73.5–127 × 6.5–10 µm), and it occurs above tree line with *Salix*. See comments under *L. luculentus* v. *laetus* Hesler & A.H. Sm. for features distinguishing it from *L. badiosanguineus*.

22. *Lactarius rufus* (Scop.) Fr.
Figure 24

Description. Pileus 45–110 mm in diameter, convex to ± depressed–convex to broadly infundibuliform, smooth, at first covered with a fine bloom becoming ± faintly areolate in age, subviscid when wet, becoming dry, azonate, deep red–brown to orange–brown, sometimes with gray–brown bands or blotches; margin incurved when young, becoming straight. Lamellae adnate to subdecurrent, subdistant to crowded, cream to dingy orange–tan in age, discoloring dingy brown where damaged. Stipe 40–90 × 10–15 mm, equal to subclavate, smooth, at first with a fine bloom, dry, cream to tan–pink to red–brown, typically remaining cream toward the base, solid, becoming hollow. Context white to vinaceous–buff. Latex scarce to abundant, white, unchanging. Odor mild. Taste acrid.

Basidiospores 6.8–9.2 × 5.1–7.1 µm, Q = 1.3–1.5, ellipsoid; ornamentation forming a complete reticulum. Pleuromacrocystidia 26–70 × 6–12 µm, scattered to abundant, subfusiform to fusiform; apex obtuse to mucronate. Cheilomacrocystidia 20–50 × 5–9 µm, scattered, subfusiform to fusiform; apex obtuse to broadly acute.

Ecology and distribution. Widely distributed in the northern hemisphere with conifers and *Betula*. In the GYE, it occurs in montane mid-elevation mixed lodgepole/spruce-fir forests up through to high elevation mixed lodgepole/spruce-fir/whitebark pine forests, typically on drier, upland sites, summer to fall.

Figure 24. *Lactarius rufus*. Collection EB0076-14 under *Pinus contorta* and *Picea engelmannii*, Gallatin Range, Montana, USA. Scale bar: 2 cm. Photo by E. Barge.

Specimens examined. U.S.A. MONTANA: Gallatin County, Gallatin Range, Fox Meadow, under *Abies lasiocarpa*, *Picea engelmannii* and *Pinus albicaulis*, 7 Sept 2013, EB125-13 (MONT); Gallatin County, Gallatin Range, Blackmore Trailhead, under *Abies lasiocarpa* and *Pinus contorta*, 15 Sept 2015, EB301-15 (MONT); Gallatin County, Gallatin Range, Lick Creek, under *Picea engelmannii* and *Pinus contorta*, 27 Aug 2014, EB0076-14 (MONT). WYOMING: Park County, Washburn Range, Dunraven Pass, under *Pinus albicaulis* and *Pinus contorta*, 10 Sept 2005, CLC2205 (MONT).

Discussion. *Lactarius rufus* appears to be an extremely morphologically and ecologically variable species, although more research is needed to see if this is backed up molecularly. At the ITS region, specimens from the GYE are molecularly identical to European specimens (*RPB2* data missing for European collections) (Figure 2C). Similar species in the Rocky Mountains include *L. badiosanguineus* and *L. luculentus* v. *laetus*, both of which are less robust and not acrid.

23. *Lactarius luculentus* v. *laetus* Hesler & A.H. Sm.

Figure 25

Description. Pileus 30–50 mm in diameter, broadly convex to broadly infundibuliform, ± umbonate, smooth, viscid when wet but soon dry, yellow–orange to dull orange to brilliant orange to orange–brown; margin straight when young to wavy in age. Lamellae

Figure 25. *Lactarius luculentus* v. *laetus*. Collection EB097-15 under *Abies lasiocarpa* and *Picea engelmannii*, Crazy Mountains, Montana, USA. Scale bar: 2 cm. Photo by E. Barge.

adnate to decurrent, crowded to subdistant, cream to pale yellow–orange. Stipe 20–60 × 5–10 mm, equal to slightly clavate to tapering toward the base, smooth, subviscid to dry, lighter than to concolorous with the pileus, typically getting lighter toward the apex, sometimes with scattered small scrobicules present, solid, becoming hollow. Context cream to pale yellow. Latex scarce, white, unchanging. Odor mild. Taste mild to slightly bitter.

Basidiospores 7–10 × 5.5–8 µm, Q = 1.2–1.5, broadly ellipsoid to ellipsoid; ornamentation forming a very broken reticulum. Pleuromacrocystidia 60–98 × 8–12 µm, scattered to numerous, strongly projecting, subfusiform to fusiform; apex acute. Cheilomacrocystidia none observed, possibly absent.

Ecology and distribution. In western North America with conifers. In the GYE it occurs in the montane spruce-fir zone, summer.

Specimens examined. U.S.A. MONTANA: Sweet Grass County, Crazy Mountains, Big Timber Creek, under *Abies lasiocarpa* and *Picea engelmannii*, 1 Aug 2015, EB097-15 (MONT).

Discussion. This is the first report of this taxon from the GYE under the name *L. luculentus* v. *laetus*. Previous reports of *L. aurantiacus* (Pers.) Gray from subalpine areas in the GYE (McKnight 1982) may refer to *L. luculentus* v. *laetus*.

Variety *laetus* is distinguished from var. *luculentus* by a brighter orange pileus as opposed to orange–brown and a mild to slightly bitter taste as opposed to slightly acrid (Hesler and Smith 1979). At the molecular level, there is some divergence within *L. luculentus* (Figure 2C, see also Barge et al. 2016) and there may be more than one species hiding under the name, although more specimens need to be examined and sequenced before making any nomenclatural changes.

Lactarius luculentus v. *laetus* is very closely related to *L. aurantiacus* and *L. lanceolatus* (Figure 2C) and morphological differences between them are subtle. *Lactarius lanceolatus* appears to have longer and more numerous cheilomacrocystidia (35.5–89 × 5–10 µm), longer pleuromacrocystidia (73.5–127 × 6.5–10 µm), as well as an alpine ecology with *Salix*. *Lactarius aurantiacus* also appears to have slightly longer pleuromacrocystidia (68.6–119.4 × 7.6–12.7 µm), and, while it occupies similar habitats to *L. luculentus* v. *laetus*, it may be absent from western North America outside of Alaska (Barge 2015).

The closely related *Betula* associate *L. lapponicus* Harmaja (syn.: *L. duplicatus* A.H. Sm.) (Figure 2C) has yellowing latex as opposed to white, unchanging latex, and appears to have a more boreal to arctic distribution (Heilmann-Clausen et al. 1998); it has not been reported from the Rocky Mountains. The closely related *L. substriatus* A.H. Sm. and *L. subflammeus* Hesler & A.H. Sm. (Figure 2C) have slightly smaller basidiospores (6.5–9 × 6–8 µm, 7.5–9 × 6.5–7.5 µm respectively), a slightly acrid taste, and are scarlet when young (Hesler and Smith 1979). The latex of *L. substriatus* also slowly stains pale yellow. Phylogenetic analyses suggest *L. substriatus* and *L. subflammeus* are conspecific, and that yellowing latex is a variable feature within the combined species, although more specimens should be sequenced before making this determination final. Neither of these taxa have been reported from the GYE and their distribution seems to be centered along the Pacific Northwest coast. The morphologically similar *L. subviscidus*, also centered along the Pacific Northwest coast, typically has smaller and more fragile basidiomes, a slightly acrid taste and unchanging latex which stains white paper yellow (Hesler and Smith 1979). In the Rocky Mountains, *L. luculentus* v. *laetus* and *L. badiosanguineus* occur in the same habitat and can easily be confused. However, the latter has slightly smaller basidiospores (7–9.5 × 6–8 µm) and typically has a more red–brown pileus which is often darker toward the center and lighter toward the margin.

24. *Lactarius lanceolatus* O.K. Mill. & Laursen

Figure 26

The following description is based on Barge et al. (2016)

Description. Pileus 10–45 mm in diameter, convex to depressed–convex at first, becoming plane to infundibuliform, with or without a small papilla, smooth, sometimes faintly scaly toward the center, viscid to dry, azonate, deep orange–brown to deep orange when immature becoming light to deep orange, often blotchy; margin incurved to straight when immature, becoming straight to upturned and often slightly wavy when mature, ± slightly crenulate. Lamellae adnate to subdecurrent, slightly crowded, pale cream to pale yellow to pale orange, discoloring brownish orange in age or where damaged. Stipe 10–20 × 2.5–7.5 mm, equal to clavate, smooth, dry, at first covered by faint whitish pubescence, pale orange, discoloring dingy orange to dingy light brown where damaged, hollow. Context pale orange. Latex scarce to undetectable, watery, white, unchanging. Odor mild. Taste mild.

Figure 26. *Lactarius lanceolatus*. Top collection EB103-15 under shrubby *Salix* spp. and *Betula glandulosa*, Hellroaring Plateau, Montana, USA. Bottom collection EB105-13 among *Salix arctica*, *S. reticulata*, and *S. planifolia*, Beartooth Plateau, Wyoming, USA. Scale bars: 2 cm. Photos by E. Barge.

Basidiospores 8–10 × 6–8 µm, Q = 1.1–1.4, broadly ellipsoid; ornamentation forming a broken reticulum. Pleuromacrocystidia 73.5–127 × 6.5–10 µm, scattered to abundant, strongly projecting, fusiform to lanceolate; apex acute to moniliform. Cheilomacrocystidia 35.5–89 × 5–10 µm, sparse to abundant, strongly projecting, conical to fusiform; apex acute to moniliform.

Ecology and distribution. Widespread in arctic-alpine areas in the northern hemisphere with *Salix*. In the GYE, it occurs above tree line in alpine areas with *Salix reticulata*, *S. arctica*, and *S. planifolia*, late summer.

Specimens examined. U.S.A. MONTANA: Carbon County, Beartooth Plateau, Highline Trail, among dwarf and shrubby *Salix* spp., 1 Aug 1997, ZT6214 (MONT); among *Salix* spp. 7 Aug 1998, ZT6412 (MONT); among *Salix reticulata*, 20 Aug 1999, CLC1389 (MONT); 5 Aug 2008, CLC2358 (MONT); 27 July 1997, CLC1139 (MONT); Carbon County, Hellroaring Plateau, Hellroaring Creek, among *Dryas octopetala* and shrubby *Salix* spp., 8 Aug 2015, EB104-15 (MONT); among *Dryas octopetala*, shrubby *Salix* spp. and *S. reticulata*, 8 Aug 2015, EB105-15 (MONT); among *Betula glandulosa* and shrubby *Salix* spp., 9 Aug 2015, EB103-15 (MONT). WYOMING: Park County, Beartooth Plateau, Solifluction Terraces, among *Salix reticulata*, 20 July 2001, CLC1578 (MONT); 13 Aug 2007, CLC2319 (MONT); among *Salix arctica*, *S. planifolia* and *S. reticulata*, 17 Aug 2013, EB 105-13 (MONT).

Discussion. *Lactarius lanceolatus* is closely related to *L. aurantiacus*, and *L. luculentus*/*L. luculentus* v. *laetus* (Figure 2C). It can be distinguished from *L. luculentus*/*L. luculentus* v. *laetus* in having longer cheilomacrocystidia and an alpine ecology with *Salix*, whereas the latter occur with conifers. Currently, we are unaware of any solid morphological differences between *L. lanceolatus* and *L. aurantiacus*. *Lactarius lapponicus* (syn.: *L. duplicatus*), which occurs in boreal and arctic-alpine areas in the Northern Hemisphere with *Betula*, and possibly other hosts, is also closely related, yet it features strongly yellowing latex (Heilmann-Clausen et al. 1998). Other similar orange taxa in western North America such as *L. substriatus, L. subflammeus*, and *L. subviscidus* all occur below tree line with conifers, and their distributions seem to be centered along the Pacific Northwest coast (Hesler and Smith 1979). See comments under *L. badiosanguineus* for features differentiating *L. lanceolatus* from that species.

Discussion

This study reports 20 *Lactarius* species, three varieties, and one unresolved species group from the GYE. *Lactarius alpinus* v. *mitis* with *Alnus incana*, *L. barrowsii* with *Pinus flexilis*, *L.* aff. *brunneoviolaceus* with *Salix reticulata*, *L. luculentus* v. *laetus* under mixed conifers, *L.* aff. *olivinus* with *Picea engelmannii*, *L. pseudodelicatus* with *Populus tremuloides*, and *L.* aff. *tuomikoskii* with *Picea engelmannii* are reported from the GYE for the first time. *Lactarius badiosanguineus* is also reported from the GYE for the first time, and it appears to fairly common throughout the Rockies with *Picea*, however, it has likely been misidentified in past treatments as *L. hepaticus* (Hesler and Smith 1979, Bessette et al. 2009) and *L. subdulcis* (McKnight 1982).

Several taxonomic problems in need of clarification were encountered. In the Rocky Mountains and North America in general, the group of species surrounding *L. scrobiculatus* (*L. alnicola*, *L. gossypinus*, *L.* aff. *olivinus*, *L. payettensis*, *L. scrobiculatus* v. *canadensis*,

L. scrobiculatus v. *montanus*, and *L.* aff. *tuomikoskii*) requires clarification with respect to European taxa such as *L. auriolla*, *L. leonis*, *L. olivinus*, and *L. tuomikoskii* as was already highlighted by Kytövuori (1984). The "*L. deliciosus*" group, whose members are commonly encountered under conifers during the summer and fall in the GYE and elsewhere in western North America is also in need of clarification (Nuytinck et al. 2007). Species delimitation in the *L. aurantiacus–L. lanceolatus–L. luculentus* complex bares further scrutiny (Barge et al. 2016). The varieties *L. alpinus* v. *mitis*, and *L. zonarius* v. *riparius* may need to be raised to the species level. Potential conspecificity between the North American *L. olympianus* and the European *L. zonarioides* should be investigated. Further, the presence of *L. helvus*, *L. resimus*, *L. torminosus*, and *L. trivialis* in the GYE (McKnight 1982) and North America in general needs clarification (Hesler and Smith 1979).

Barge et al. (2016) reinforced the traditional concept of broad intercontinental distributions for alpine species associated with *Salix* (*L. lanceolatus*, *L. nanus*, *L. salicis-reticulatae*) and *Betula* (*L. glyciosmus*, *L. pubescens*). Based on the results of the present study, broad intercontinental distributions are also suggested for some *Picea* associates (e.g. *L. badiosanguineus*, *L. repraesentaneus*), some aspen associates (*L. controversus*, *L. pubescens*), and *L. rufus*, whose range of host affinities within the GYE remain difficult to untangle. However, it has been shown that at least some regions of the *Lactarius* genome, particularly the ITS region, are relatively slowly evolving (Verbeken and Nuytinck 2013, Barge et al. 2016), thus inclusion of more loci and individuals in phylogenetic analyses would likely reveal finer biogeographic patterns for these taxa. Broad intercontinental distributions have also been confirmed for some western North American arctic-alpine and subalpine members of the ectomycorrhizal genus *Inocybe* (Cripps et al. 2010, Larsson et al. 2014) as well as for some members of the ectomycorrhizal genus *Cortinarius* subg. *Phlegmacium* associated with *P. tremuloides* in western North America (Cripps et al. 2015).

Lactarius species reported from the GYE such as *L. barrowsii* with *Pinus flexilis*, *L. rubrilacteus* with *Pseudotsuga menziesii*, and *L. caespitosus* with *Abies lasiocarpa*, appear to be restricted to western North America. The distribution and host affinities of some species is not clear due in part to taxonomic problems (e.g. "*L. deliciosus*" group) or the relative rarity with which they have been collected and reported (e.g. *L. pallidomarginatus*, *L. pseudodelicatus*, *L. zonarius* v. *riparius*). Interestingly, nearly every major ectomycorrhizal host plant in the GYE has at least one *Lactarius* species associated with it, with some species appearing to be highly host specific (Table 2), highlighting the importance of this genus in the GYE.

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The Flora Mycologica Iberica Project fungi occurrence dataset

Francisco Pando[1], Margarita Dueñas[1], Carlos Lado[1], María Teresa Telleria[1]

1 *Real Jardín Botánico-CSIC, Claudio Moyano 1, 28014, Madrid, Spain*

Corresponding author: *Francisco Pando* (pando@rjb.csic.es)

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Abstract

The dataset contains detailed distribution information on several fungal groups. The information has been revised, and in many times compiled, by expert mycologist(s) working on the monographs for the Flora Mycologica Iberica Project (FMI). Records comprise both collection and observational data, obtained from a variety of sources including field work, herbaria, and the literature. The dataset contains 59,235 records, of which 21,393 are georeferenced. These correspond to 2,445 species, grouped in 18 classes. The geographical scope of the dataset is Iberian Peninsula (Continental Portugal and Spain, and Andorra) and Balearic Islands. The complete dataset is available in Darwin Core Archive format via the Global Biodiversity Information Facility (GBIF).

Key words

Gasteromycetes, Myxomycetes, Agaricales, Boletales, Aphyllophorales, Dothideales, Gomphales, Helotiales, Laboulbeniales, Tremellales, Ustilaginales, Cantharellaceae, Andorra, Balearic Islands, Portugal, Spain, fungi, mitosporic fungi, fungi and lichens, occurrence, observation

Introduction

The "Flora Mycologica Iberica Project dataset" is one of the main results produced by the "Flora Mycologica Iberica", a research project that stood from 1988 to 2008 and involved over 30 researchers from Spain and Portugal. This dataset contains information on 2,445 species of fungi recorded from The Iberian Peninsula and Balearic Islands. As an online resource, it is a valuable source of information on fungi growing in that area, with a high reuse potential, given its coverage, taxonomic scrutiny --carried out by taxonomic experts in the different groups-- and validation processes of the associate information (location, habitat). The other major outcome of the project were the monographs of the studied groups: Aphyllophorales [p.p.] (Telleria and Melo 1995), Myxomycetes [p.p.] (Lado and Pando 1997), Gasteromycetes [p.p.] (Calonge 1998), Laboulbeniales (Santamaria 1998, 2003) and Dictyosporic Dothideales (Checa 2004). These publications provide descriptions, illustrations, identification keys and additional information on many of the species and taxa included in this dataset.

General description

Purpose: This dataset was conceived within the Flora Mycologica Iberica Project (FMI).

The ultimate objective of the FMI project was to make a critical flora which enables the identification of fungi naturally growing in the Iberian Peninsula and Balearic Islands (excluding parasites of humans and other mammals).

The purpose of the dataset was:

1. To gather the available information on Iberian fungi as published in the scientific literature, and to establish baseline knowledge for the project and the project's monographs, among other aims.

2. To incorporate the primary data produced and compiled during the project to the previously available information, and thus providing updated and validated data on Iberian fungi. These data were gathered or verified by professional researchers, many of whom also authored the project's monographs (Calonge 1998, Checa 2004, Lado and Pando 1997, Santamaria 1998, 2003, Telleria and Melo 1995) and/or check-lists (Calonge 1990, Castro 1998, Checa 1997a, 1997b, 1998, Dueñas, 2002, Garcia-Blazquez et al. 2007, Justo and Castro 2007, 2010, Lado 1991, Melo et al. 2007, Telleria 1990). Primary data added in this way mostly came from studied herbarium specimens and field surveys. Targeted field surveys on sites poorly known and of ecological or conservation relevance were carried out within the framework of the project. Unpublished records gathered within the project, along with those found in the literature, were also made available as publications in the "Cuadernos de Trabajo de Flora Micológica" series (see References). This is reflected in the 'AssociatedReference' column of the dataset.

Project details

Project personnel: Telleria, M.T. (Principal Investigator), Dueñas, M. (Principal Investigator), Blanco, M.N., Calonge, F., Cardoso, J., Castro Cerceda, M.I., Checa, J., Daniëls, P.P., Descals, E., Esteve-Raventós, F., Galán, R., F., Girbal, J., Heykoop, M., Illana, C., Jiménez Rico, V., Lado, C., Listosella, J., Melo, I., Moreno, G., Pando, F., Salcedo, I., Santamaria, S. & Hernández, J.C.

Project title: Flora Mycologica Iberica

Funding: Funded by Spanish Government under its National Science Plan through its Competitive Grant Programs. Awards:

Flora Mycologica Iberica I
DGCYT PB87-0370 (1987-1991)
Flora Mycologica Iberica II
DGCYT PR92-0012 (1992-1994)
Flora Mycologica Iberica III
DGES PB95-0129-C03 (1995-1997)
Flora Mycologica Iberica IV
PB98-0538-C04 (1998-2001)
Flora Mycologica Iberica V
REN2002-04068-C02-01 (2002-2004)
Flora Mycologica Iberica VI
CGL2006-12732-C02-01 (2005-2008)

Data capture was carried out mostly by an agreement between CSIC and National Institute of Employment of Spain (INEM). Program: Módulo de documentación Botánica INEM-CSIC.

Study area descriptions/descriptor: Terrestrial biomes and freshwater environments in the Iberian Peninsula and Balearic Islands.

Design description: The final objective of the FMI project was to make a critical flora which enables the identification of fungi naturally growing in the Iberian Peninsula and Balearic Islands (excluding parasites of humans and other mammals).

One of the pillars in pursuing this objective was the compilation of the literature-based information about Iberian fungi. This was planned as a two-step process:

The first one was to compile a bibliography of all published works recording fungi from the Iberian Peninsula (Pando et al. 1990, Cardoso and Melo 1992, Pando 1996). This in itself is a very robust resource for carrying out all kinds of studies involving fungi in the Iberian Peninsula.

The second phase was to enter chorological records (species occurrences) contained in those publications into a database. After some trial and error, we aimed to compile a dataset of all genera cited in all publications. That task was accomplished surprisingly quickly (c. 79,000 genus-in-publication entries for c. 10,000 works in less than two years, by two full time data entry persons and one part-time scientific supervisor). With

that information at hand, we could target the specific publications and occurrences needed for the check-lists and monographs to be prepared within the FMI project.

Data entry management and publication were carried out using the Bibmaster software v. 3.7 (Pando et al 2004).

Manuals and guidelines were prepared to establish a clear standard basis regarding data entry and quality control procedures (Pando 1991, Pando et al. 1999).

Data published through GBIF: http://www.gbif.es/ipt/resource?r=floramicologicaiberica

Taxonomic coverage

General taxonomic coverage description: Dataset comprising distribution records of fungal species belonging to selected groups (Agaricomycetes, Dothideomycetes, Mycetozoa, Laboulbeniomycetes, Ustilaginomycetes and aquatic Hyphomycetes) found in the Iberian Peninsula and Balearic Islands (Western Europe). Sources included literature, herbaria and field surveys.

Taxonomic ranks

The consensus classification provided by Index Fungorum in Catalogue of Life (Kirk 2016) has been followed for taxonomic categories above genus.

It is worth mentioning that recent and profound changes in fungal classification have rendered some categories used in the project such as "Gasteromycetes" or "Aphyllophorales" obsolete. These groups, now referred informally as Gasteroid and Corticioid fungi, are especially well-covered, but scattered across a number of orders (cf. Pegler et al. 1995, Kirk et al. 2008, Larsson 2007).

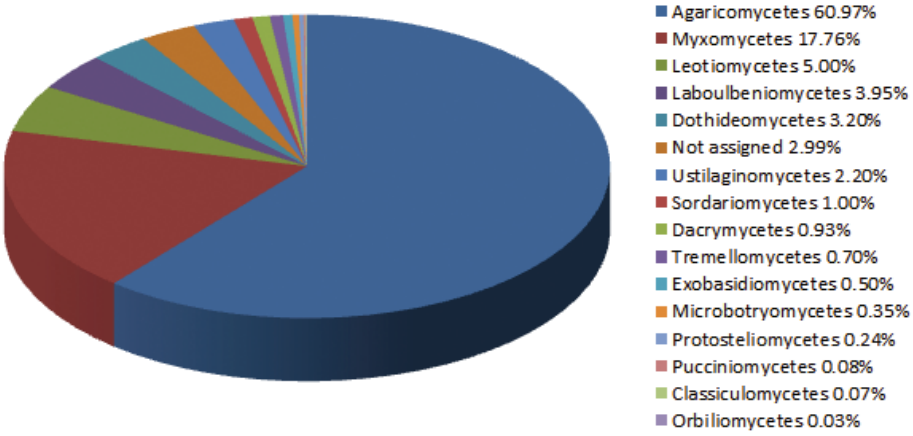

Figure 1. Taxonomic distribution of the dataset (percentage of specimens per classes).

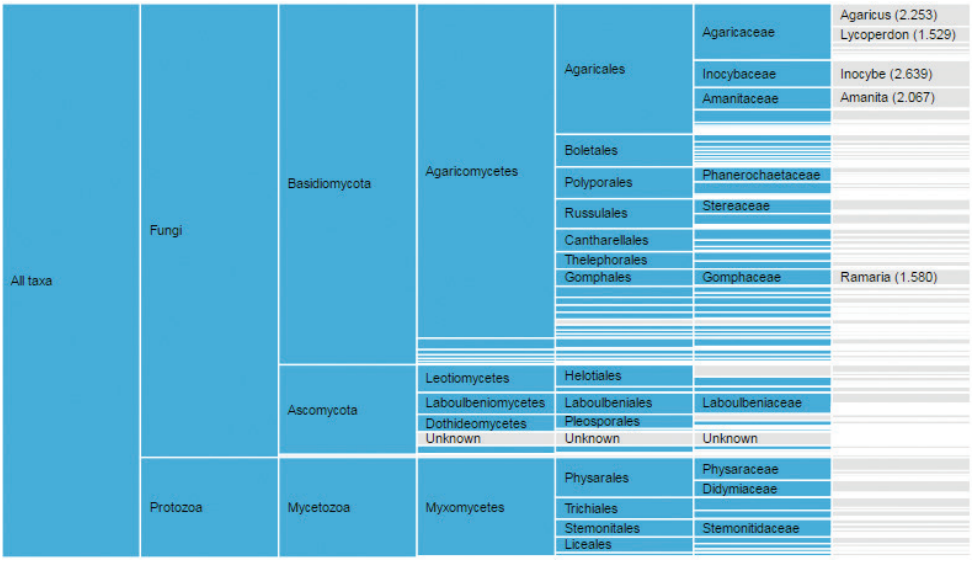

Figure 2. Visual representations of taxon record abundance in the dataset.

Classes and orders included in the dataset follow:

Classes	**Orders**
Agaricomycetes	Agaricales*†, Atheliales†, Auriculariales, Boletales*†, Cantharellales†, Corticiales†, Geastrales*, Gloeophyllales†, Gomphales*†, Hymenochaetales†, Hysterangiales*, Phallales*, Polyporales†, Russulales*†, Sebacinales, Stereaceae, Thelephorales†, Trechisporales†
Atractiellomycetes	Atractiellales
Classiculomycetes	Classiculales
Dacrymycetes	Dacrymycetales
Dothideomycetes	Capnodiales, Hysteriales, Mytilinidiales, Pleosporales
Eurotiomycetes	Not assigned
Exobasidiomycetes	Doassansiales, Entylomatales, Exobasidiales, Tilletiales
Laboulbeniomycetes	Laboulbeniales
Leotiomycetes	Helotiales, Leotiales
Microbotryomycetes	Microbotryales
Myxomycetes	Echinosteliales, Liceales, Physarales, Stemonitales, Trichiales
Not assigned	Zoopagales
Orbiliomycetes	Orbiliales
Pezizomycetes	Pezizales
Protosteliomycetes	Ceratiomyxales
Pucciniomycetes	Helicobasidiales, Platygloeales, Septobasidiales
Sordariomycetes	Chaetosphaeriales, Hypocreales, Microascales, Sordariales, Xylariales
Tremellomycetes	Tremellales
Ustilaginomycetes	Urocystidales, Ustilaginales

* Orders containing gasteroid taxa. † Orders containing corticioid taxa.

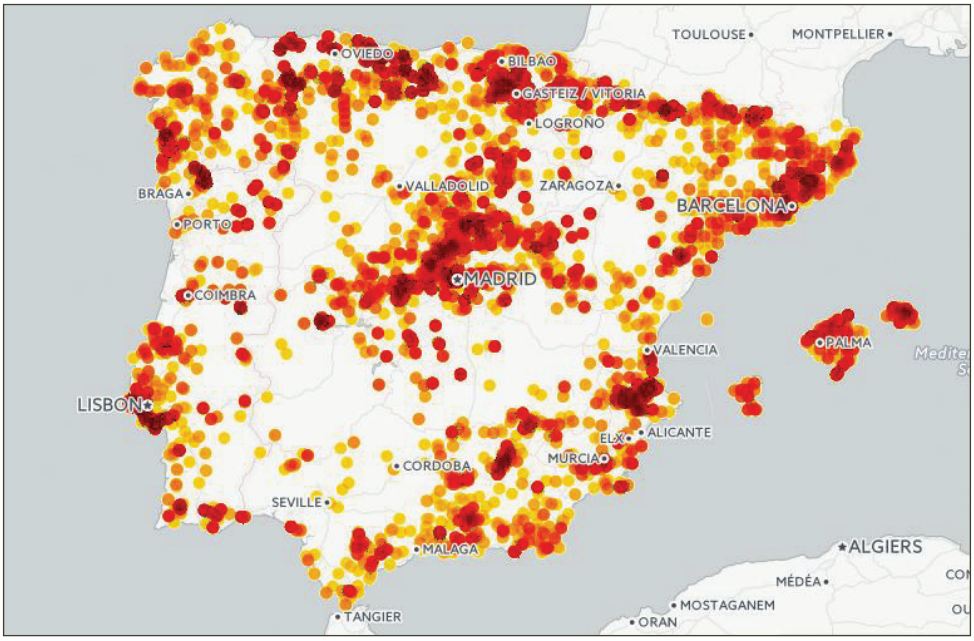

Figure 3. Geographic distribution of the georeferenced records. The darker the color, the higher is the record density.

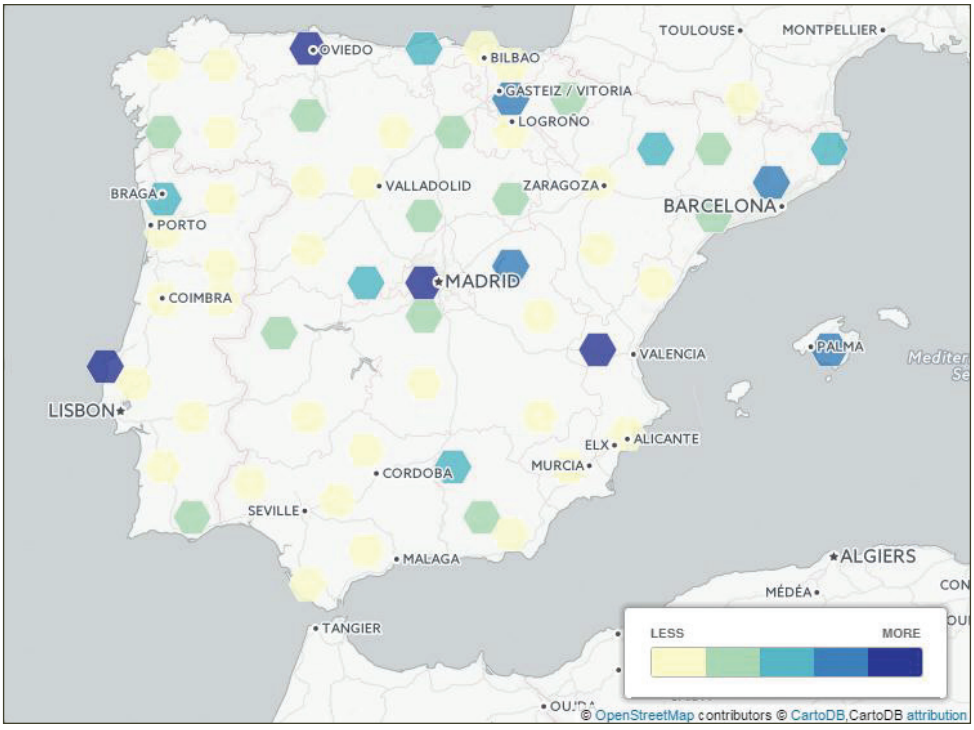

Figure 4. Geographic distribution. Records grouped by provinces, georeferenced only.

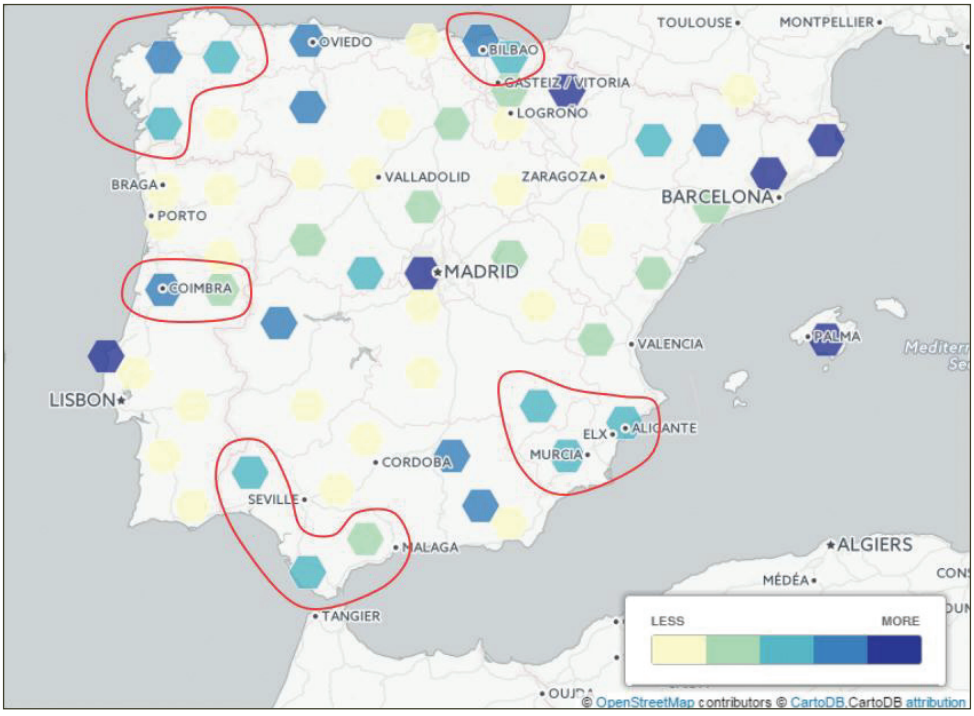

Figure 5. Geographic distribution. Records grouped by provinces, not georeferenced. Provinces where non-georeferenced records provide substantial information missing in georeferenced records are encircled in red.

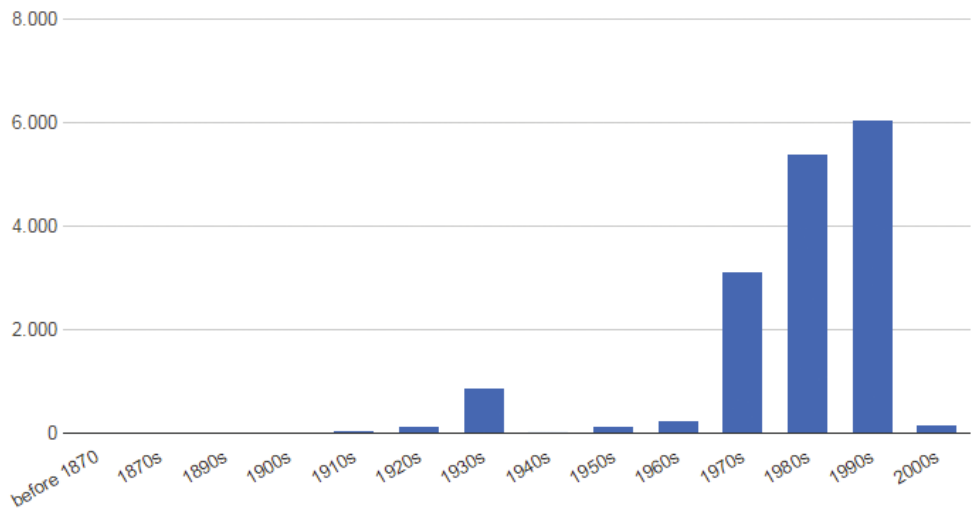

Figure 6. Temporal distribution of the records.

Spatial coverage

General spatial coverage: Iberian Peninsula, Balearic Islands, South-Western Europe

Coordinates: 35°45'36"N and 44°2'60"N Latitude; 9°56'60"W and 4°54'36"E Longitude

This comprises: Continental Portugal and Spain, Andorra and Balearic Islands. No records from Gibraltar (UK) have been included. A map showing georeference records and its density is provided (Fig. 3). Two additional maps showing records aggregated by province are presented here to show how records with coordinates provide only a partial view of the actual knowledge on Iberian fungi (Figs 4, 5). This highlights the importance of retrospective georeferencing when carrying on species distribution models and other geospatial analyses.

Temporal coverage: January 1, 1870 - February 20, 2012

Methods

Study extent description: Scientific literature was the main source for fungal occurrence records. Herbarium revisions, which included published and unpublished records, supplemented literature information. Additionally, targeted field campaigns were carried out within the framework of the project to fill gaps on sites poorly known and of ecological or conservation relevance such as national parks, and other protected areas. Unpublished relevant data were published as the "Bases Corológicas series in "Cuadernos de Trabajo" and reflected in the AssociatedReference field.

Sampling description: These two data avenues were subjected to different methodologies, as explained below.

Data collation from literature references. Three procedures are defined in this area:

1) Identifying and obtaining relevant publications.

A set of explicit criteria to determine whether a publication was eligible to be included into the database was defined. These were published by Pando (1996: 215-217). The Library of the Real Jardín Botánico-CSIC was the main source for literature. When an eligible publication was identified and not found in this library, a copy was obtained by the usual procedures (library exchange, colleagues, etc.) and deposited in that Library.

2) Treated genus data entry.

Genus names were extracted in a systematic way from the publications and entered into the database. Publications and genus names compiled up to, and including, 1995 were published in three volumes of the "Cuadernos de Trabajo" series (Pando et al. 1990, Cardoso and Melo 1992, Pando 1996). At this point, the database contained data from c. 5,000 publications, at the end of the project this gathered data pertaining to c. 10,000 publications. Although teleomorph nomenclature is used in the dataset, literature collation was made for anamorphic as well as teleomorphic genera.

3) Occurrence data entry.

A protocol in which occurrence records were entered targeting specific taxonomic groups --on the basis of the project's priorities and the schedule for the publication of the monographs-- was implemented at the early stages of the project. An effort was made to record all information associated to each occurrence, following an established schema, as described by Pando (1991). Besides scientific name, date and locality details, habitat – including host – is provided for the 78% of the records.

These works were mostly carried out by a small team of data entry technicians and supervisors, with the support of the Project's scientific team.

Primary data produced and compiled as part of the research conducted within the project, by researchers involved in the project, were also incorporated into the database. These come from studied specimens held in herbaria or fields surveys carried out within the framework of the project. These data, when relevant, were published as the "Bases Corológicas series in "Cuadernos de Trabajo" (14 volumes published between 1991 and 2008. See References). No species have been retrieved from molecular data.

Quality control description: Quality control and assurance comprises a number of procedures, references and tools along the data life cycle. These can be summarized as follows:

- A data-entry manual on what to capture and what not and how to capture the information was developed and published (Pando 1991).
- International standards approved or endorsed by the "Biodiversity Information Standards/TDWG). Specifically, the following were used: Brummitt and Powell (1992), Lawrence et al. (1968), and TL-2 (Stafleu and Cowan 1976–1985, Stafleu and Mennega 1992–2000, Dorr and Nicolson 2008, 2009).
- When herbarium information was available, this was recorded under column "otherCatalogNumbers" following "Index Herbariorum" (Thiers 2016) standard abbreviations.
- Additionally, the following works were used as a reference for taxonomic names: Farr et al. (1979a, b, c, 1986), and the Dictionary of the Fungi (Hawksworth et al. 1983, 1995, Kirk et al. 2001, 2008), Saccardo (1882–1931).
- The database management system used (Pando et al. 2004) had many of these standards build-in as dictionaries and controlled vocabularies.
- All newly entered records were checked against the actual publications by the supervisors as part of the database work flow.
- A final check was done by the "Bases Corológicas" authors and editors as part of the publication process.
- Dataset publication in the GBIF network include data transformation to comply with the Darwin Core specification (Wieczorek et al. 2012) and further validation procedures (geographic coordinate format, coordinates within country/provincial boundaries, absence of ASCII anomalous characters in the dataset) using DARWIN_TEST (v3.3) software (Ortega-Maqueda and Pando 2008).

Host information as well as geographic coordinates have been taken from the sources. Obvious errors and typos have been corrected, but no in-depth interpretation of these details nor retrospective georeferencing was carried out. This approach guarantees fidelity to the sources, but also results in some unavoidable heterogeneity in the information made available.

Datasets

Dataset description

Object name: Darwin Core Archive Flora Mycologica Iberica Project fungi occurrence dataset
Character encoding: UTF-8
Format name: Darwin Core Archive format
Format version: 1.0
Distribution: http://www.gbif.es/ipt/archive.do?r=floramicologicaiberica
Publication date of data: 2016-02-02
Language: Spanish
Records: 59,235, of which 21,393 are georeferenced.
Licences of use: This work is licensed under a Creative Commons Attribution (CC-BY) 4.0 License (http://creativecommons.org/licenses/by/4.0/legalcode).

External datasets

Dataset description

Object name: Flora Mycologica Iberica
Character encoding: UTF-8
Format name: Darwin Core Archive
Format version: 0
Distribution: http://www.gbif.es
Metadata language: English
Date of metadata creation: 2009-11-30
Hierarchy level: Dataset

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