# **Pacific Northwest Tricholomas:**

# Are We Using the **Right Names?**

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# **Pacific Northwest Tricholomas:** Are We Using the **Right Names?**

### Steven A. Trudell<sup>a, 1</sup>, P. Brandon Matheny<sup>b</sup>, Andrew D. Parker<sup>c</sup>, Matthew Gordon<sup>d</sup>, Diantha B. Dougil<sup>e</sup>, Erica T. Cline<sup>e</sup>

**SUMMARY:** Despite the fact that *Tricholoma* includes many large conspicuous woodland fungi, the genus historically has received very little attention in North America and is one of many genera of North American agarics for which identification and other taxonomic resources are largely lacking. More than 130 "Tricholoma" species have been reported to occur in the Pacific Northwest region of North America (PNW), including some no longer accepted in the genus and a large number being referred to, often incorrectly, by names based on European fungi. In light of this uncertainty, we made an initial attempt to clarify the application of *Tricholoma* species names in the PNW. This included (i) obtaining ITS barcode sequences from holotypes of Tricholoma species described from the PNW, selected other holotypes, and recent, excellent-condition, mostly well-photographed collections; (ii) phylogenetic analysis utilizing 142 sequences generated in this project along with 431

additional sequences obtained from GenBank and other researchers; and (iii) morphological study of selected collections. Our results provide evidence for the existence of at least 50 species of Tricholoma in the PNW. As expected, there are many undescribed species here and a number of European names have been misapplied to our fungi. We estimate that the total number of Tricholoma species in the PNW could be as high as 75 to 100.

**KEY WORDS:** Agaricales, Basidiomycota, biodiversity, Fungal Diversity Survey, fungi, ITS barcode, molecular phylogenetics, North American mycota, Tricholoma, Tricholomataceae.

NOTE TO READERS REGARDING **PEER REVIEW:** Although we have chosen to self-publish our study results, they have been reviewed by several knowledgeable peers with expertise in fungal systematics and the genus, Tricholoma, in particular. The reviewers are credited and thanked in the Acknowledgments section.

What we know as the genus, *Tricholoma*, originated with Elias Magnus Fries in his 1821–1828 publication, Systema Mycologicum. Fries defined Tricholoma as including fungi that produce white-spored terrestrial basidiomes that are fleshy and relatively robust. They lack a universal veil and either lack a partial veil or have one that is fibrillose or floccose and disappears early, sometimes leaving remnants on the margin of the pileus. The pileus is hemispherical or somewhat campanulate, often umbonate, and with a thin incurved (at least when young) margin. The lamellae are of unequal length and sinuate or rounded where they approach the stipe. The stipe is fibrillose, scaly, or has coarse longitudinal striations formed by aggregated fibrils, and its flesh is confluent with that of the pileus. The basidiomes exhibit diverse colors, especially in the pileus surface. Subsequent to Fries's initial circumscription of Tricholoma, many Friesian "tricholomas" have been transferred to other existing or newly created genera such as *Calocybe*, Leucopaxillus, Lyophyllum, Melanoleuca, and Tricholomopsis, most often based on differences in microscopic features. In addition, some Friesian "armillarias," which differed from his tricholomas mainly by having membranous partial veils, have been transferred to Tricholoma, resulting in species such as *T. focale* being accepted in the genus. *Tricholoma*, as now generally circumscribed, has been shown to represent a monophyletic group (Sánchez-García et al. 2014).

Despite the fact that Tricholoma includes many of the larger and more conspicuous of our woodland fungi, the genus historically has received very little attention in North America. Charles Horton Peck described over 60 Tricholoma species in the late

### **INTRODUCTION**

1800s and early 1900s, although many of them subsequently have been transferred to other genera. Between roughly 1910 and 1950, William Alphonso Murrill described slightly more than 100 Tricholoma species. Some of these originally were described in other genera, especially Melanoleuca, and, similarly to Peck's species, many have since been transferred to other genera. In what still is the only comprehensive treatment of the genus in North America, Murrill prepared the "Tricholoma" section of the North American Flora (Murrill 1914) under the genus names, Melanoleuca and Cortinellus.

More recent regional monographic treatments include Clark Ovrebo's (1973) survey of the tricholomas of the Pacific Northwest, his later (Ovrebo 1980) study of the genus in the Great Lakes area, and Kris Shanks's (1994, 1997) survey of the tricholomas of California, which resulted in the description of several new species (Shanks 1996). More recently Ovrebo et al. (2009) produced a preliminary phylogeny of the genus, with emphasis on eastern North American taxa. Bessette et al. (2013) published a popular guidebook to the genus in North America. It drew attention to numerous areas of taxonomic uncertainty and the need for study of nearly all infrageneric groups within Tricholoma.

Matheny and Vellinga (2009) called attention to the need for a centralized and updated version of the out-of-date North American Flora published by the New York Botanical Garden, an outstanding resource from the early 1900s that provided dichotomous keys and descriptions to mushroom-forming fungi from North America. To illustrate this need, they used the genus, Melanoleuca, as an example. In

their words, "Melanoleuca is step-motherly treated in guide books where descriptions and illustrations are few. There is no insight into the number of species in North America, nor their identity, and there are no keys to the 17 species recognized for the USA so far. Distribution and ecology of the species are mostly unknown. There are no combined molecular-phylogenetic/morphologictaxonomic treatments of the genus, nor is its position within the Agaricales sufficiently elucidated." Unfortunately, there are many genera of North American agarics for which resources are similarly sparse to nearly non-existent, and none that can be described as being well provided-for, including

Subsequent to Matheny and Vellinga's plea, the Fungal Diversity Survey ("FunDis," originally known as the North American Mycoflora Project) has gathered momentum and now involves a large number of participants, both individual and organizational, throughout the continent (https://fundis.org/). The growing success of this project has increased the need for resources to assist the participants in identifying collected specimens and understanding their biology and ecology.

More than 130 "Tricholoma" species (TABLES 1 and 2) have been reported to occur in the Pacific Northwest region of North America (PNW), here taken to include Oregon, Washington, Idaho, southern and westernmost British Columbia, and southeastern and south-central Alaska. Northernmost California and westernmost Montana share many environmental characteristics of the PNW but, for ease of reference, we have not attempted to formally include them. Many of the epithets that have been applied pertain to species now accepted in other genera or that are so little known

that it can't be certain what they are or, in some cases, even if they are tricholomas. Among the remaining ~100 names, many are based on European fungi, or on North American species whose protologues are very brief and usually unillustrated, so that it has been difficult to develop widely accepted concepts of the species involved. Thus, we hypothesized that many of the epithets were being misapplied when used for PNW fungi.

In order to begin to clarify the application of Tricholoma species names in the PNW and to contribute to future continentwide and world-wide understanding of the genus, our main objectives were to (i) obtain ITS barcode sequences from the holotypes of Tricholoma species described from the PNW, selected other holotypes, and recent, excellent-condition, mostly well-photographed collections; (ii) provide an initial assessment of the phylogenetic diversity of PNW tricholomas; and (iii) assess the degree to which names based on fungi from outside the PNW can correctly be applied to our species. Although our work was not intended as a systematic or monographic study, in the course of the project we generated evidence for the existence of a number of undescribed species of Tricholoma. In most cases, solidification of species concepts and study of additional well-documented collections will be required before their status as new species can be confirmed. However there was sufficient information to allow publication of five new species and two new combinations (Trudell & Parker 2021, Trudell 2022).

#### **MATERIALS AND METHODS**

Type specimens for 23 Armillaria and Tricholoma / Melanoleuca species were obtained from the herbaria / fungaria at Cornell University (CUP; herbarium

Epithet	Authority	Ovrebo (1973)	TNA <sup>a</sup>	PNWKC <sup>b</sup>	Myco Match <sup>c</sup>	Herbarium Records <sup>d</sup>
acerbum	(Bulliard) Quélet					OR
acre (-is)	Peck		Х	Х	Х	WA
aestuans	(Fries) Gillet			Х	Х	
albobrunneum	(Persoon) P. Kummer			Х	Х	OR, WA, ID, BC
album	(Schaeffer) P. Kummer					BC
apium	Jul. Schäffer		Х	Х	Х	WA, BC
arenarium (=equestre)	(Léveillé) Gillet					WA
argenteum	Ovrebo		Х	Х	Х	
argyraceum	(Bulliard) Gillet					ID
arvernense	Bon		Х		Х	OR, WA, ID
atrodiscum (-us)	Ovrebo			Х		
atrosquamosum	Saccardo		Х	Х	Х	OR, WA, BC
atroviolaceum	A.H. Smith	Х	Х	Х	Х	OR, WA, ID, BC
aurantio-olivaceum	A.H. Smith	Х	Х	Х	Х	OR, WA, BC
aurantium	(Schaeffer) Ricken	х	Х	Х	Х	OR, WA, ID, BC, AK
bisporigerum (=terreum)	J.E. Lange					WA
brunneosquamosa	Beeli					ID
bufonium	(Persoon) Gillet			Х	Х	WA, BC
californicum (=subannulatum)	(Murrill) Murrill					OR
caligatum	(Viviani) Ricken		Х	Х		OR, WA, BC, AK
cartilagineum	(Bulliard) Quélet					OR
cheilolaminum (=davisiae)	Ovrebo & Tylutki					OR, WA, ID
chrysites (=scalpturatum)	(Junghuhn) Quélet					WA
cingulatum	(Almfelt) Jacobasch	Х	Х	Х	Х	OR, WA, BC
columbetta	(Fries) P. Kummer					BC, AK
davisiae	Peck		Х	Х	Х	WA, ID, BC
dryophilum	(Murrill) Murrill		Х		Х	
dulciolens	Kytövuori				Х	
equestre/flavovirens	(Linnaeus) P. Kummer/ (Persoon) S. Lundell	Х	Х	Х	Х	OR, WA, ID, BC, AK
farinaceum	(Murrill) Murrill	Х	Х	Х	Х	OR
flavobrunneum (=fulvum)	(Fries) P. Kummer					OR, WA
focale	(Fries) Ricken		Х	Х	х	OR, WA, ID, BC, AK
fracticum (=batschii)	(Britzelmayr) Kreisel		Х			
fulvum	(Candolle) Bigeard & H. Guillemin		Х	Х	Х	OR, WA, BC, AK
fumosoluteum	(Peck) Saccardo					ID
gausapatum (=terreum)	a (=terreum) (Fries) Quélet		BC			

Tricholoma.

TABLE 1. Species of Tricholoma reported to occur in the Pacific Northwest region of North America.

Epithet	Authority	Ovrebo (1973)	TNAª	PNWKC <sup>b</sup>	Myco Match <sup>c</sup>	Herbarium Records <sup>d</sup>	
grande	Peck					WA	
griseoviolaceum	Shanks		Х			BC	
huronense	A.H. Smith			X	Х		
imbricatum	(Fries) P. Kummer	X	x	X	Х	OR, WA, ID, BC, AK	
impolitum (=acerbum? columbetta?)	(Lasch) P. Kummer					WA, ID	
inamoenum	(Fries) Gillet	Х	x	X	Х	OR, WA, ID, BC, AK	
intermedium	Peck		Х	X	Х	OR, WA, ID, BC	
joachimii	Bon & A. Riva					OR	
josserandii	Bon					WA	
leucophyllum (=intermedium)	Ovrebo & Tylutki	Х				ID, BC	
luteomaculosum	A.H. Smith		Х	X	Х	BC	
manzanitae	Baroni & Ovrebo		Х			OR	
marquettense	Ovrebo		Х			WA	
moseri	Singer		X		Х	OR, WA	
muricatum	Shanks		Х	X	Х	OR, WA, BC	
<i>murrillianum</i> [incl. as <i>magnivelare</i> ]	Singer	X	X	X	X	X OR, WA, ID, BO	
mutabile	Shanks		Х	X	Х	BC	
myomyces (=terreum)	(Persoon) J.E. Lange	Х	X	X	X OR, WA BC, A		
nictitans (=fulvum)	(Fries) Gillet					WA	
nigrocystidium	nom. prov. (Ovrebo 1973)	Х		X			
nigrum	Shanks & Ovrebo		Х	X	Х	OR, WA	
odorum	Peck	X	Х	X	Х	WA	
orirubens	Quélet	X		X	Х	OR, WA	
pardinum	(Persoon) Quélet	Х	Х	X	Х	OR, WA, ID, BC	
pessundatum	(Fries) Quélet	Х	X	X	Х	OR, WA, ID, BC, AK	
platyphyllum	(Murrill) Murrill	Х		X	Х	OR, WA, ID, BC, AK	
populinum	J.E. Lange	X	x	X	X X O		
portentosum	(Fries) Quélet	X	X	X	X OR, WA, BC, AF		
portentosum var. avellaneifolium (=mutabile)	(Murrill) A.H. Smith	Х				WA	
psammopus	(Kalchbrenner) Quélet			X		ID, BC	
pullum	Ovrebo					BC	
resplendens (=columbetta)	(Fries) P. Karsten					BC, AK	
robustum	(Albertini & Schweinitz) Ricken	Х	X X X OR, W		OR, WA, BC		

Epithet	Authority	Ovrebo (1973)	TNA <sup>a</sup>	PNWKC <sup>b</sup>	Myco Match <sup>c</sup>	Herbarium Records <sup>d</sup>	
saponaceum	(Fries) P. Kummer	X	Х	X X X O		OR, WA, ID, BC, AK	
scalpturatum	(Fries) Quélet		Х	X	Х	WA, BC	
sciodes	(Persoon) C. Martín					BC	
sejunctum	(Sowerby) Quélet	X X X X OR		OR, WA, ID, BC, AK			
silvaticum	Peck X						
spermaticum (=umbonatum?)	(Fries) Gillet					WA	
squarrulosum	Bresadola		Х	Х		WA, BC	
stans	(Fries) Saccardo			X	Х	OR, BC, AK	
striatum (=albobrunneum)	(Schaeffer) Quélet			X		BC	
subacutum	Peck					OR, WA	
subannulatum	(Peck) Zeller					OR	
subluridum	(Murrill) Murrill	Х		X	Х		
subluteum	Peck			X	Х	BC	
subsejunctum	Peck					OR, WA, ID, BC	
subumbrinum	A.H. Smith	Х		X	Х	K WA	
sudum	(Fries) Quélet					ID	
sulphurescens	Bresadola		Х	Х	Х	WA, ID, BC, AK	
sulphureum	(Bulliard) P. Kummer	X	X	X	Х	OR, WA, ID, BC, AK	
terreum	(Schaeffer) P. Kummer	Х	Х	X	Х	OR, WA, ID, AK	
transmutans	(Peck) Saccardo		Х		Х	OR, WA	
triste	(Scopoli) Quélet			X	Х	OR, WA, ID	
tumidum	(Persoon) Ricken		Х			OR	
umbonatum	Clémençon & Bon			X			
ustale	(Fries) P. Kummer		Х	Х	Х	OR, WA, ID, BC, AK	
ustaloides	Romagnesi					OR, BC	
vaccinum	(Schaeffer) P. Kummer	Х	Х	Х	Х	OR, WA, ID, BC, AK	
venenatum	G.F. Atkinson		Х	X	Х	OR, WA, BC	
vernaticum	Shanks		Х	X	Х	OR, WA	
virgatum	(Fries) P. Kummer	Х	Х	Х	Х	OR, WA, ID, BC, AK	
zelleri (=focale)	(D.E. Stuntz & A.H. Smith) Ovrebo & Tylutki	Х			Х	OR, WA, ID, BC, AK	
	No. Species:	31	49	58	56		
<sup>a</sup> TNA = Tricholomas of North A	merica (Bessette et al. 2013)						
<sup>b</sup> Leuthy C. 2019. A skeleton tria	l key to Tricholoma in the Pacij	fic Northwe	est. Prepa	ared for the P	Pacific Nort	hwest Key Council.	
<sup>c</sup> MycoMatch (MatchMaker). Mushrooms of the Pacific Northwest. Version 2.4. Copyright Ian Gibson 1999–2020.							
<sup>d</sup> State/province list based on herbarium specimen records accessed via MyCoPortal (15 June 2019).							

**TABLE 2.** Species reported from the PNW as tricholomas that are no longer accepted in *Tricholoma*.

Epithet	Authority <sup>a</sup>	Current name
alboflavidum	(Peck) Saccardo	Collybia alboflavida (Peck) Kauffman
amplum	(Persoon) Rea	Lyophyllum decastes (Fries) Singer
arcuatum	(Bulliard) Quélet	Melanoleuca arcuata (Bulliard) Singer
avellaneifolium	(Murrill) Murrill	Melanoleuca avellaneifolium Murrill
bicolor	(Murrill) Murrill	Melanoleuca bicolor Murrill
calathus	Never combined in <i>Tricholoma</i> ?	Lepista sordida (Schumacher) Singer? L. calathus (Fries) Bon?
chrysenteroides	Peck	Melanoleuca chrysenteroides (Peck) Murrill
cinerascens	(Bulliard) Gillet	Lyophyllum decastes (Fries) Singer
cognatum	(Fries) Gillet	Melanoleuca cognata (Fries) Konrad & Maublanc
crassifolium	Saccardo	Lyophyllum crassifolium (Saccardo) Singer
cystidiosum	A.H. Smith	Inocybe cystidiosa (A.H. Smith) Singer
decorum	(Fries) Quélet	Tricholomopsis decora (Fries) Singer
fallax	Quélet & Schulzer	Megacollybia fallax (A.H. Smith) R.H. Petersen & J.L. Mata?
fuligineum	Peck	Lyophyllum fuligineum (Peck) Singer
grammopodium	(Bulliard) Quélet	Melanoleuca grammopodia (Bulliard) Murrill
ionides	(Bulliard) P. Kummer	Calocybe ionides (Bulliard) Donk
irinum	(Fries) P. Kummer	Lepista irina (Fries) H.E. Bigelow
laterarium	(Peck) Saccardo	Leucopaxillus laterarius (Peck) Singer & A.H. Smith
melaleucum	(Persoon) P. Kummer	Melanoleuca melaleuca (Persoon) Murrill
memmingeri	(Murrill) Murrill	Melanoleuca memmingeri Murrill
naucoria	(Murrill) Murrill	Calocybe naucoria (Murrill) Singer
nudum	(Bulliard) P. Kummer	Lepista nuda (Bulliard) Cooke
onychinum	(Fries) Gillet	Calocybe onychina (Fries) Donk
panaeolus var. caespitosum	Bresadola	Clitocybe fasciculata H.E. Bigelow & A.H. Smith
personatum	(Fries) P. Kummer	Lepista personata (Fries) Cooke
rhizoideum	A.H. Smith	Clitocybe ramigena H.E. Bigelow
roseobrunneum	(Murrill) Murrill	Leucopaxillus gentianeus f. roseobrunneus sensu Singer & A.H. Smith
russula	(Schaeffer) Gillet	Hygrophorus russula (Schaeffer ex Fries) Kauffman
rutilans	(Schaeffer) P. Kummer	Tricholomopsis rutilans (Schaeffer) Singer
sclerotoideum	Morse	Clitocybe sclerotoidea (Morse) H.E. Bigelow
secedifolium	(Murrill) Murrill	Tricholomopsis secedifolia (Murrill) Singer
sordidum	(Schumacher) P. Kummer	Lepista sordida (Schumacher) Singer
subpessundatum	(Murrill) Murrill	Limacella subpessundata (Murrill) Singer
terriferum	Peck	Melanoleuca terrifera (Peck) Murrill
<sup>a</sup> Per Index Fungorum. In ma	ny reports, the authority has not bee	n included.

Are We Using the Right Names?

abbreviations follow those in Index Herbariorum [Thiers, continuously updated]), Field Museum (F), New York Botanical Garden (NY), and San Francisco State University (SFSU), as well as 46 additional specimens of interest from SFSU, University of British Columbia (UBC), University of California, Berkeley (UC), and University of Washington (WTU) (APPENDIX 1), including permission to sample the collections for DNA sequencing. Eighty-eight more recent exsiccates, subsequently deposited at WTU, also were included (APPENDIX 1). Not all of the samples yielded usable DNA despite multiple extraction attempts, so there are gaps in the TR### samplenumber sequence. Some specimens were sequenced twice, in separate labs (University of Washington, Tacoma, Washington and Molecular Solutions, LLC, Portland, Oregon) for quality assurance purposes.

In the sequencing, we targeted the two internal transcribed spacers in the nuclear rDNA region (ITS1–5.8S–ITS2 = "ITS"), which is commonly used for fungus species identification and represents the universal fungus barcode (Schoch et al. 2012). Details of the procedures followed for DNA extraction, amplification, and sequencing are provided in APPENDIX 2.

Four hundred thirty-one additional sequences, including many identified during review of previous studies (e.g., Heilmann-Clausen et al. 2017, Ovrebo & Hughes 2018, Ovrebo et al. 2019, Reschke et al. 2018), were obtained from GenBank or other researchers (APPENDIX 3) to assemble a geographically diverse dataset that broadly represents *Tricholoma*, in order to provide a framework within which to assess the PNW species. *Dermoloma magicum* was chosen as outgroup for the analyses. Sequences were aligned using MAFFT 7 (Katoh and Toh 2008; http://mafft.cbrc.jp/ alignment/server/) and edited and manually adjusted in AliView 1.11 (Larsson 2014). Regions of the dataset with ambiguous alignments were excluded. The aligned sequence set was analyzed using two methods: (i) maximum likelihood (ML) analyses using RAxML 8.2.9 (Stamatakis 2014), with 1000 rapid bootstrap replicates; (ii) Bayesian inference (BI) analyses using MrBayes 3.2.6 (Ronquist et al. 2012). Details of the phylogenetics analysis procedures are provided in APPENDIX 2.

We consider ML bootstrap values (MLBS)  $\geq$ 70% and BI posterior probabilities (BIPP)  $\geq$ 0.95 to indicate strong support.

#### **RESULTS** Species occurrences supported by our work

We successfully obtained 142 ITS sequences from 134 specimens, including 17 from 14 holotypes. Sequences from specimens that were processed twice, in separate labs, for quality assurance purposes were not always identical but, in all cases, grouped in the same terminal clade.

The ML and BI analyses returned tree topology quite similar to each other and to the ITS trees reported by previous workers (Heilmann-Clausen et al. 2017, Ovrebo et al. 2009, Reschke et al. 2018). The 573 sequences fell within 17 well-defined clades (FIG. 1), 16 of which are well supported (one of those in BI only) and most of which correspond approximately to section rank (cf. Heilmann-Clausen et al. 2017, Reschke et al. 2018): Clade 1 = Sect. *Tricholoma*; Clade 2 = Sect. Contextocutis / Rigida; Clade 3 = Sect. *Genuina*; Clade 4 = Sect. *Megatricholoma*; Clade 5 = T. apium; Clade 6 = Sect. Caligata; Clade 7 = Sect. Sericella; Clade 8 = Sect. *Lasciva*; Clade 9 = Sect. *Pardinicutis*;



FIG. 1. Fifty percent majority-rule consensus tree from the BI analysis of the ITS dataset. Node symbols: solid squares = BI posterior probability (BIPP)  $\geq$ 0.95 and ML bootstrap value (MLBS)  $\geq$ 70%; solid circles = BIPP  $\geq$ 0.95, MLBS <70%; open circles = MLBS  $\geq$ 70%, BIPP <0.95. Major clades have been collapsed and root length reduced to facilitate graphical presentation. Details of each of the 17 major clades are provided in subsequent figures.

Clade 10 in part = Sect. *Muscaria*; Clade 11 = Sect. *Atrosquamosa* (relatively weak support, especially in ML); Clade 12 = T. *subumbrinum* – *T. mutabile* group; Clade 13 = *T. borgsjoeënse* + *T. atroviolaceum*; Clade 14 = *T. vernaticum* + "*T. turpescens*"; Clade 15 = *T. luridum*; Clade 16 = *T. melleum*; Clade 17 = Sect. *Terrea*. The PNW species are discussed by clade, below.

Clade 1: Section Tricholoma. Our Clade 1 corresponds to Sect. Tricholoma sensu Heilmann-Clausen et al. (2017) and Reschke et al. (2018). The PNW mycota includes representatives of most of the principal groups within the section including (i) T. subacutum, sister species to the European T. virgatum; (ii) T. griseoviolaceum / T. "portentosum" specimens in a T. portentosum complex; (iii) T. subsejunctum and T. *atrofibrillosum* in the *T. sejunctum* complex; (iv) T. intermedium and a number of probably undescribed T. "equestre" / "flavovirens" and T. "frondosae" species in the large T. equestre complex; and (v) *T. megalophaeum*, a new species, closely related to T. guldeniae.

#### Clade 1a. Sect. Tricholoma in part (FIG. 2)

## *Tricholoma atrofibrillosum* S.A. Trudell, A.D. Parker & E.T. Cline and *T. subsejunctum* Peck

Tricholoma sejunctum (Sowerby) Quélet is a European species associated with deciduous angiosperm trees such as beech, oak, hazel, and hornbeam. It is most common in southern and central Europe and declines in abundance northward (Christensen & Heilmann-Clausen 2013). Our analyses returned a wellsupported broad "T. sejunctum" complex, including T. sejunctum sensu stricto (Europe), T. subluteum (eastern North America), T. viridilutescens (Europe, two separate clades), T. olivaceoluteolum (China), T. rufenum (Europe), T. sinoportentosum (China), and two groups of North American "sejunctum" / "subsejunctum" / "viridilutescens" collections. The first of the latter two groups is a well-supported (ML only) clade consisting of specimens from Ontario, North Carolina, and Alaska (TR002). We consider it likely that this represents T. subsejunctum. The second well-supported North American

clade contains specimens from California, Idaho, and Alaska and represents the new species *T. atrofibrillosum*.

Tricholoma subsejunctum was described from New York, where the holotype was collected in a mixed forest of conifers and deciduous angiosperms. Peck stated that it differs from T. sejunctum primarily in the darker more pronounced radial fibrils on the pileus surface and, probably, in the association with conifers. After studying the holotype, Ammirati and Ovrebo (1979) concluded that, with respect to micromorphology, T. subsejunctum is almost identical to T. sejunctum. Peck considered it a rare species. Although the macromorphology of our collection TR002 closely fits Peck's type description, the spores of TR002 are larger (mean =  $7.6 \times 5.9 \mu m$ , n = 70) than those reported by Peck ( $5-6 \times 4-5 \mu m$ ) and Ammirati & Ovrebo  $(5.7-6.7 \times 4.8-5.7 \ \mu m)$ Thus, it would be desirable to obtain an ITS sequence from the holotype or a designated epitype collection to confirm the occurrence of T. subsejunctum in the PNW.

*Tricholoma atrofibrillosum* differs from *T. sejunctum* by the much darker radial fibrils on the cap surface, its occurrence with conifers, and by geographic distribution. Based on the samples studied so far, there are no obvious morphological or ecological features to distinguish *T. atrofibrillosum* from *T. subsejunctum*. However, as shown in FIG. 2, the degree of ITS divergence is high among these two species and *T. viridilutescens* Type II.

We are not aware of any evidence that would support the occurrence of *T. sejunctum* sensu stricto in the PNW and consider past reports to be misapplications of the name.

*Illustrations and descriptions*: FIG. 3A; Baroni 2017; Bessette et al. 2013, p. 141(A– Pacific Northwest Tricholomas:



FIG. 2. Detail of Clade 1a, Section *Tricholoma* in part. Symbols as in FIG. 1. PNW sequences shown in blue.

B), 142(C); McNeil 2006 (*T. subsejunctum*). FIG. 3B–E, 4; Bessette et al. 2013, p. 142(E); Trudell & Parker 2021 (description) (*T. atrofibrillosum*).

#### Tricholoma portentosum (Fries) Quélet

Tricholoma portentosum generally is considered a relatively large species with a gravish somewhat viscid pileus, whitish lamellae and stipe that often develop yellowish tones, mildly farinaceous odor and taste, and association with conifers. Our analyses returned a well-supported "*T. portentosum*" clade that includes the *T. portentosum* neotype and the *T.* griseoviolaceum holotype, however, there is little support for *T. griseoviolaceum* (BIPP = 0.81; MLBS = 45%) and for other PNW / California "T. portentosum" specimens. For now, we accept *T. portentosum* sensu lato as occurring in the PNW, pending future work to better resolve the relationships in this group.

After study of the holotype, Shanks (1994) concluded that *T. avellaneifolium* (Murrill) Murrill actually represents a species of *Lyophyllum*. Thus, *T. portentosum* var. *avellaneifolium* (Murrill) A.H. Smith, described from Olympic National Park, Washington, required a new name, which Shanks (1996) provided — *T. mutabile*. It appears in our Clade 12 (FIG. 31) with other species that do not fall in one of the traditional sections and was included in Shanks (1994) under the provisional name, *T. smithii*.

*Illustrations and descriptions*: FIG. 3F–H; Bessette et al. 2013, p. 127(D); Breitenbach & Kränzlin 1991; Christensen & Heilmann-Clausen 2013; Ludwig 2012; Læssøe & Petersen 2019; McKenny et al. 1987; Shanks 1997; Siegel & Schwarz 2016.

#### Tricholoma subacutum Peck

Misapplied names: Tricholoma virgatum, T. argenteum

Tricholoma subacutum was described from New York where it was reported to occur with spruce and fir. Peck (1903) stated that it is easily recognized by its prominent pointed, often darkly colored, umbo, by the radiating brown or blackish lines or fibrils on its dry cap, and by the white color of its flesh and stem. The taste was described as sometimes acrid and sometimes mild (perhaps because the taste can be slow to develop). In both the protologue and the later description (Peck 1903), Peck commented on the close similarity of T. subacutum and T. virgatum, saying "The species is so closely related to the European virgate tricholoma, Tricholoma *virgatum*, that it is with some hesitation that I have kept it distinct." Both Ovrebo (1989) and Shanks (1994) considered the two species to be synonymous. In our analysis, all North American "T. virgatum" specimens and one "T. argenteum" specimen formed a wellsupported clade sister to the European T. virgatum clade, the latter of which includes the neotype. The morphology and ecology of the collections we have examined agree well with the description of T. subacutum and we accept that name for our PNW taxon. According to Ovrebo (1989), T. argenteum is distinguished by a light gray to silvery gray pileus, innate, radially arranged pileus surface fibrils, and bitter taste, and differs from T. virgatum in lacking an acute umbo or at most having a rounded subacute umbo, lighter pileus surface, and by lacking a distinctly virgate pileus surface. ITS or other DNA sequences from the holotype do not appear to be available. For now, we interpret the "T. argenteum" specimen in our analyses as a misapplication of the name. However, further work, including DNA sequence analysis of the type collections and recent welldocumented material, would be desirable to



FIG. 3. Photographs of Tricholoma collections studied in this project. A. T. subsejunctum (TR002). B-E. T. atrofibrillosum (B: TR046. C: TR074. D: TR089. E: NS1908). F-H. T. portentosum s.l. (F: TR047. G: TR010. H: TR015). Collection details can be found in APPENDIX 1 (TR### collections) and APPENDIX 3 (others). E. Photograph courtesy of Noah Siegel.



FIG. 4. Photograph of holotype collection for Tricholoma atrofibrillosum (TR118). Collection details can be found in APPENDIX 1.

clarify the relationship between T. subacutum and T. argenteum.

*Illustrations and descriptions*: FIG. 5A–F; Baroni 2017; McNeil 2006; Shanks 1997; Siegel & Schwarz 2016; Trudell & Ammirati 2009 (all as "*T. virgatum*.").

#### Clade 1b. Sect. Tricholoma in part (FIG. 6) Tricholoma equestre (Linnaeus) P. Kummer

Synonyms: Tricholoma arenarium (Léveillé) Gillet, T. auratum (Paulet) Gillet, T. flavovirens (Persoon) S. Lundell

"Tricholoma equestre" represents a complex of many species that will require considerable future work to resolve. For instance, Heilmann-Clausen et al. (2017), Moukha et al. (2013), and Reschke et al. (2018) recognized multiple clades within the complex with little correspondence to the epithets applied to the specimens, which included auratum, equestre, flavovirens, and

frondosae. We observed a similar pattern, including sequences labeled with those epithets, but also others labeled ulvinenii, intermedium, leucophyllum, and joachimii. Consistent with the findings of Horton (2002), it is clear that we have multiple (perhaps as many as six or more) "equestre" / "frondosae" species in the PNW, but establishing the species boundaries and how the PNW taxa relate to those in Europe and elsewhere will require revision, beginning with solidifying the concepts for the previously described European species. For now, it will probably be best to refer to PNW collections as "*T*. equestre group."

Illustrations and descriptions: FIG. 5G-H, 7A-E; Bessette et al. 2013, (p. 62[C] *T. frondosae* s.l., [D–E] *T. equestre* s.l.); Breitenbach & Kränzlin 1991 (T. frondosae s.l., as T. equestre); Christensen & Heilmann-Clausen 2013, p. 101, 103 (T.



FIG. 5. Photographs of *Tricholoma* collections studied in this project. A–F. *T. subacutum* (A: TR005. B: TR007. C: TR012. D: TR072. E. TR073. F: AKFF-076-14). G–H. *T. equestre* group (G: TR009. H: TR079). Collection details can be found in APPENDIX 1 (TR### collections) and APPENDIX 3 (others).

FIG. 6. Detail of Clade 1b, Section *Tricholo* shown in blue.





FIG. 6. Detail of Clade 1b, Section Tricholoma in part. Symbols as in FIG. 1. PNW sequences



FIG. 7. Photographs of *Tricholoma* collections studied in this project. A–E. *T. equestre* group (A: TR124. B: TR137. C: AKFF-078-14. D: AKFF-087-14. E: SAT-16-237-24). F–G. *T. intermedium* (F: TR016. G: TR051). H. *T. megalophaeum* (TR081). Collection details can be found in APPENDIX 1 (TR### collections) and APPENDIX 3 (others). C–D. Photographs courtesy of Noah Siegel.

*equestre* s.l.), 102, 105 (*T. frondosae*); Desjardin et al. 2015; Ludwig 2012; Læssøe & Petersen 2019; McKenny et al. 1987 (as *T. flavovirens*); Siegel & Schwarz 2016; Trudell & Ammirati 2009.

#### Tricholoma intermedium Peck

*Synonym: Tricholoma leucophyllum* Ovrebo & Tylutki

Tricholoma intermedium was described from a "thin woods" of unspecified tree species composition in New York. The epithet reflects Peck's interpretation of the species as intermediate between *T*. equestre and T. sejunctum. It resembles some forms of T. equestre in its slightly viscid, greenish-yellow cap but differs in having whitish gills. It differs from *T. sejunctum* principally in having a glabrous, rather than fibrillose, cap. Ovrebo (1980) concluded that *T. leucophyllum* was a synonym of *T*. intermedium and we follow his interpretation here (although note in FIG. 6 the GenBank sequence from British Columbia labelled *"leucophyllum"* that clusters with our TR137, labelled "arvernense cf."). The morphology of two PNW collections of T. intermedium (TR016 and TR051) closely matches descriptions and photographs of eastern North American collections (McNeil 2006; Bessette et al. 2013) as well as Peck's original description, and their occurrence with conifers agrees with that of the recent eastern reports. In our analyses, sequences from those collections grouped with French samples labelled "equestre," and "frondosae," so *T. intermedium* belongs in the *T. equestre* complex and is more distantly related to the T. *sejunctum* complex.

*Illustrations and descriptions*: FIG. 7F–G; Bessette et al. 2013; McNeil 2006.

**Clade 1c. Sect.** *Tricholoma* in part (FIG. 8) In our analyses, this small group was sister

to Clades 1a and 1b within Sect. *Tricholoma*. Three European specimens of *T. guldeniae* formed a well-supported clade sister to a well-supported clade consisting of TR081 and TR154, which represents the new species, *T. megalophaeum*.

## *Tricholoma megalophaeum* N. Siegel, S.A. Trudell & A.D. Parker

Tricholoma megalophaeum is mediumsized to large with a dry umbonate cap that is appressed-fibrillose or faintly virgate and very dark olivaceous gray over a yellowish ground color. The gills are pale cream with a grayish cast to dingy grayish yellow and slightly eroded. The stipe is equal or somewhat clavate with an abruptly rounded to bulbous base, dry, fibrillose-scaly, and off-white to pale yellowish. The odor is slightly farinaceous, sometimes somewhat like green corn and the taste is mild to slightly farinaceous. All known collections to date have come from coastal conifer forests that contain abundant Sitka spruce. Tricholoma guldeniae is a very similar species described from Norway that also occurs primarily with spruce in near-coastal environments. Based on the illustrations we have seen, its cap is considerably lighter in color, at least at maturity.

*Illustrations and descriptions*: FIG. 7H, 9A, 10; Trudell & Parker 2021 (description).

Clade 2. Sect. *Contextocutis / Rigida* (FIG. 11). Our Clade 2 corresponds to Sect. *Contextocutis* sensu Heilmann-Clausen et al. (2017) and Sect. *Rigida* sensu Reschke et al. (2018). As in the former study, our analyses supported the existence of at least four European taxa, viz. *T. "saponaceum," T. sudum, T. rapipes*, and *T. boudieri*. European specimens labelled *"T. saponaceum"* were paraphyletic with respect to *T. rapipes* and might represent two different species. Unfortunately, there is no type material



for T. saponaceum so it remains unclear just what the "real" T. saponaceum is. In addition, specimens of T. olivaceum and T. viridiolivaceum, from China and New Zealand, respectively, fell within the clade that includes specimens labelled T. boudieri, so the latter epithet may encompass more than one species, as was noted by Heilmann-Clausen et al. (2017). All North American specimens, including those from the PNW, clustered separately from specimens from other continents in a paraphyletic assemblage. It appears that several lineages are represented but more work will be needed to resolve the relationships among them and determine appropriate names.

#### Tricholoma saponaceum (Fries) P. Kummer

*Tricholoma saponaceum* sensu lato is a highly variable species and many varieties have been described (Christensen & Heilmann-Clausen 2013). However, those authors concluded that many of the varieties were based on characters that are highly variable and have limited taxonomic

value. Nonetheless, at least T. rapipes and T. boudieri are sufficiently distinct to warrant recognition at species rank (Heilmann-Clausen et al. 2017). Our analyses returned a well-supported broad "T. saponaceum" clade, with two large groups sister to T. forteflavescens (China). The first group consists of European "T. saponaceum" specimens that, together, are paraphyletic with respect to *T. rapipes*. The second group consists of a number of North American specimens that, together, are paraphyletic with respect to species from other continents, including T. sudum (Europe), T. boudieri (Europe, multiple specimens likely representing more than one species), T. olivaceum (China), and T. viridiolivaceum (New Zealand). It appears that the North American collections could represent a number of distinct lineages, three of which occur in the PNW. Further work, including designation and sequencing of a type specimen for T. saponaceum sensu stricto, will be necessary to resolve the relationships within this group. For now, we accept the occurrence of T.



(others). A, D. Photographs courtesy of Noah Siegel.

megalophaeum (TR154). B-F. T. saponaceum group (B: TR123. C: TR130. D: AKFF-082-14. E: SAT-16-237-07. F: SAT-16-237-14). G-H. T. ammophilum (G: TR017. H: TR096). Collection details can be found in APPENDIX 1 (TR### collections) and APPENDIX 3

#### Are We Using the Right Names?

saponaceum sensu lato in the PNW.

*Illustrations and descriptions*: FIG. 9B–F; Bessette et al. 2013, p. 137(H); McKenny et al. 1987; Siegel & Schwarz 2016.

Clade 3: Section Genuina. Our Clade 3 corresponds to Sect. Genuina sensu Heilmann-Clausen et al. (2017) and Reschke et al. (2018) and, as in those studies, we observed two subclades, both well supported. The first includes the species with reddish brown colors and a usually viscid to glutinous pileus surface such as T. focale, T. fulvum, and T. subannulatum. It includes a clade formed exclusively by a large number of Southern Hemisphere specimens. The second subclade includes species with a dry, often scaly, pileus surface such as T. vaccinum. The PNW T. aurantio-olivaceum groups with the European T. imbricatum and closely related West Coast "T. imbricatum" specimens (FIG. 19) and does not appear to be very closely



FIG. 10. Photograph of holotype collection for *Tricholoma megalophaeum* (Noah Siegel NS4666 / WTU-F-073091 / MW597305 [ITS]). Photograph courtesy of Noah Siegel.

related to *T. fucatum* (in our Clade 12, FIG. 31), as conjectured by Heilmann-Clausen et al. (2017). TR159 (FIG. 19) could represent an undescribed species in this group but the specimen was obtained at an exhibition and so important information about it is lacking.

Clade 3a. Sect. Genuina in part, viscid-



■ = BIPP ≥ 0.95 and MLBS ≥ 70% ■ = BIPP ≥ 0.95, MLBS < 70%</p> focale FJ845447 BC ○ = MLBS ≥ 70%, BIPP < 0.95</p> focale KJ705238 QC Blue font = PNW sequence focale NS1831 AK focale TR022 WA focale TR034 CA focale TR088 OR zelleri TR029 BC zelleri TR029b BC zelleri TR032 BC zelleri TR032b BC aurantium LT000012 DNK aurantium LT000100 ITA aurantium AF377233 CA aurantium DQ367919 BC aurantium TR023 WA populinum KC146366 CAN populinum SAT-16-237-12 AK populinum TR017 WA populinum TR096 AK populinum EF493259 SWE populinum JV08398 EST populinum LT000143 SVN pessundatum LT000032 DNK Epitype "ustaloides" AF377240 CA cedrotorum MC99049 FRA tridentinum LT000076 FRA batschi populinum cf EU819446\_WI fulvum s.l. ustaloides fulvum aff KU058505 NC ustale LT000064 DNK quercetorum LT000125 PRT Clade 3b - Sect. Genuina - Dry Caps

0.2

capped species (FIG. 12, 13)

*Tricholoma ammophilum* A.D. Parker, Grubisha & S.A. Trudell

Misapplied name: Tricholoma populinum



FIG. 12. Detail of Clade 3a in part, Section *Genuina*—viscid caps, Part 1. Symbols as in FIG. 1. PNW sequences shown in blue.

*Tricholoma populinum* was described from Denmark and is generally considered to be ectomycorrhizal exclusively with *Populus* species. In our analyses, "*T. populinum*" specimens formed a moderately supported



group with the *T. pessundatum* epitype (FIG. 12). Within this group, specimens from Europe and specimens from the PNW formed two well-supported, mutually exclusive clades. This is consistent with the results of

Grubisha et al. (2012) who found substantial divergence between North American and Fennoscandian populations of T. populinum, and estimated that reproductive isolation began 1–1.7 million years ago. Thus, the PNW



FIG. 14. Photograph of holotype collection for T. ammophilum (SAT-16-237-12). Collection details can be found in APPENDIX 3.

"T. populinum" represents a separate species, T. ammophilum ("sand-loving"), reflecting the taxon's regional common name of "the sandy." It is medium-sized, often occurring in dense groups under black cottonwood. The cap is broadly convex, viscid when moist, pale pinkish brown to reddish brown, darker over the disc, and paler or whitish toward the edge. The flesh is thick and the odor and taste are farinaceous. The whitish gills stain reddish brown in age, especially along the edge. The thick stem is white at first, then colored like the cap at maturity.

Illustrations and descriptions: FIG. 9G-H, 14; Bessette et al. 2013 (as *T. populinum*); McKenny et al. 1987 (as *T. populinum*); Trudell & Parker 2021 (description).

#### Tricholoma aurantium (Schaeffer) Ricken

Tricholoma aurantium is a European species that occurs with both coniferous and

angiosperm trees. In our analyses, sequences from Washington, British Columbia, and California collections of "T. aurantium" fell in a well-supported (ML only) clade with sequences from two well-documented European collections (FIG. 12). In addition, the macromorphology of North American specimens closely matches that of European material, so we accept T. aurantium sensu lato as occurring in the PNW. However, we are unaware of DNA sequence data from type material (it appears that designation of an epitype would be necessary) and, in our analyses, the North American group is paraphyletic with respect to the European collections, so further work, at least including ITS comparison with type material would be desirable to resolve the group.

Illustrations and descriptions: FIG. 15A; Bessette et al. 2013; Breitenbach & Kränzlin 1991; Christensen & Heilmann-Clausen 2013;



FIG. 15. Photographs of *Tricholoma* collections studied in this project. A. *T. aurantium* (TR023). B–H. *T. badicephalum* (B: TR011. C: TR026. D: TR049. E: TR099. F: TR115. G: TR116. H: NS1894). Collection details can be found in APPENDIX 1 (TR### collections) and APPENDIX 3 (others). C, H. Photographs courtesy of Paul Kroeger and Noah Siegel, respectively.



FIG. 16. Photograph of epitype collection for *Tricholoma badicephalum* (NS1006 / WTU-F-073095 / MW597309 [ITS]). Photograph courtesy of Noah Siegel.

Ludwig 2012; Læssøe & Petersen 2019; Shanks 1997; Siegel & Schwarz 2016.

*Tricholoma badicephalum* (Zeller) N. Siegel, S.A. Trudell & M.J. Gordon

Misapplied names: Tricholoma focale, T. robustum

A large number of "*T. focale*," "*T. focale* group," and "*T. robustum*" samples comprise a well-supported clade sister to the *T. focale* clade, which includes the neotype (FIG. 12). It had been recognized that these collections looked different from other *T. focale* and some had been informally referred to as the "other *focale*." Siegel and Schwarz (2016) called attention to *Armillaria badicephala* Zeller, noting that it belongs in *Tricholoma* and that it "is like a brown-colored version of *T. focale*." They considered it to be rare in California, occurring only on the northernmost coast on sand dunes under spruce and pine. *Armillaria badicephala* was described from a small collection made near Newport, Oregon on sand-dune soil under scrubby Sitka spruce trees. Our collections TR049, TR099, TR115, and TR116 fit the macroscopic and microscopic description of *A. badicephala* and ITS sequences (not included in our tree) from two Oregon collections of *A. badicephala* made by Noah Siegel cluster within the "other *focale*" clade (analysis results not shown). Therefore the new combination, *Tricholoma badicephalum*, was made and an epitype collection designated (Trudell & Parker 2021).

*Tricholoma badicephalum* differs from *T. focale* by the usually dry cap (although it clearly is a member of the "viscid-capped" group), greater tendency of the cap to be squamulose, the duller brown and gray-brown colors, and lack of prominent orange and green tones, although orangish brown fibrils may be present on cap and stipe. The two species share a similar stature, with a tapered

APPENDIX 3 (others).

stipe similar to that of T. murrillianum, and ecological occurrence with conifers in sandy nutrient-poor soils. We have observed them to fruit near each other at times.

In the PNW, the name T. robustum sometimes has been applied to this taxon (e.g., TR011, TR026, TR027, and TR030) and two "robustum" sequences from Japan fall in our badicephalum clade. Photographs in Japanese publications (e.g., Imazeki and Hongo 1957, Imazeki et al. 1977, Imazeki et al. 1988) are very similar to images of collections from the PNW. However, T. *robustum* is a European species, the concept of which has not been solidified, and is considered a synonym of *T. focale* by many European mycologists (e.g., Christensen & Heilmann-Clausen 2013, Galli 1999, Riva 2003). In addition, Albertini and Schweinitz's image of "Armillaria robusta" (as presented by Riva 2003) clearly does not represent the same fungus as our PNW taxon.

Illustrations and descriptions: FIG. 15B-H, 16; Bessette et al. 2013, p. 69; Trudell & Ammirati 2009, p. 102, lower figure (all as T. focale).

#### Tricholoma focale (Fries) Ricken

Synonyms: Armillaria zelleri D.E. Stuntz & A.H. Smith, Tricholoma zelleri (D.E. Stuntz & A.H. Smith) Ovrebo & Tylutki

Tricholoma focale was described from Europe, where it commonly occurs with pines on sandy soils. ITS sequences from several PNW specimens, including the holotype of T. zelleri and Shanks's (1994) voucher collection for T. focale (TR034), fall in a group with sequences from several European specimens, including the neotype of T. focale. Morphology of the PNW specimens and their occurrence with conifers, often including pine, on nutrient-poor, often sandy, soils is consistent with the European concept of the

species. Therefore, we currently accept T. focale as occurring in the PNW. However, support for the group (BIPP = 0.78; MLBS = 63%) was not high.

Illustrations and descriptions: FIG. 17A-D; Bessette et al. 2013, pp. 67(B)–68(C-D); Christensen & Heilmann-Clausen 2013; Desjardin et al. 2015; Ludwig 2012; Læssøe & Petersen 2019; McKenny et al. 1987 (as T. zelleri); Shanks 1997; Siegel & Schwarz 2016; Trudell & Ammirati 2009, p. 102 upper figure.

#### Tricholoma fulvum (DC.) Bigeard & H. Guillemin

Synonyms: Tricholoma flavobrunneum (Fries) P. Kummer, T. nictitans (Fries) Gillet, *T. pseudonictitans* Bon, *T. transmutans* (Peck) Saccardo?

Tricholoma fulvum is a European species that has been subject to different interpretations. We follow the concept presented by Christensen and Heilmann-Clausen (2013), which includes gill colors from cream to yellow and occurrence with conifers as well as birch. Our BI analysis returned a well-supported "T. fulvum" group, including PNW, eastern North American, and European sequences labeled "pessundatum (group)," "fulvum," "muricatum," "nictitans" (Shanks [1994] voucher collection), and "transmutans." A number of PNW "pessundatum group" sequences from conifer forests that include spruce and lack birch form a well-supported clade that appears to represent a distinct species, derived within *T. fulvum* s.l. However the collections do not differ obviously in macromorphology or micromorphology from the others in the broad T. fulvum group. Further work will be required to resolve the taxonomy of this group, including T. transmutans, and clarify the name(s). Until such time, we accept that T. fulvum sensu lato occurs, probably



SAT-16-244-03). Collection details can be found in APPENDIX 1 (TR### collections) and

representing more than one taxon, and is fairly widespread and common, in the PNW.

*Illustrations and descriptions*: FIG. 17E–H, 18A–B; Bessette et al. 2013, pp. 73–75, 162 (as *T. transmutans*); Breitenbach & Kränzlin 1991; Christensen & Heilmann-Clausen 2013; Ludwig 2012; Læssøe & Petersen 2019; Shanks 1997 (as *T. nictitans*); Siegel & Schwarz 2016 (as *T. nictitans* sensu California).

#### Tricholoma subannulatum (Peck) Zeller

Synonyms: Armillaria subannulata Peck, Melanoleuca subannulata (Peck) Murrill, M. californica Murrill, Tricholoma californicum (Murrill) Murrill

non *Tricholoma subannulatum* (Batsch) Bresadola (*=T. batschii* Gulden ex Mort. Christensen & Noordeloos)

#### Misapplied names: Tricholoma dryophilum, T. ustale, T. ustaloides

Charles Peck's description of *A*. subannulata in general reflects a typical member of the "*T. pessundatum* group," with a viscid reddish brown cap and farinaceous odor and taste. However, unlike most of the species in that group, he cited it as having "veil thick, soft, white, evanescent; spores elliptic,  $10-12 \times 8-9 \mu m$ " (large for the group). The type collection originated from southern California under oaks so, as noted by Zeller (1922), Peck saw only dried material.

Shortly thereafter, Murrill (1913) described *Melanoleuca californica / T. californicum* from the vicinity of Stanford University in California, where it was found under oaks. In his description, which is similar to that of Peck's species, Murrill commented that "This large and handsome species resembles specimens determined as *Armillaria subannulata* Peck" and, indeed, in the *North American Flora* (Murrill 1914), he combined Peck's species in *Melanoleuca* (using his description of *M. californica* rather than Peck's original) and synonymized *M. californica* with it, despite apparent differences in the presence of a partial veil and spore size (Murrill reported  $5-7 \times 4-5$  µm for his species). Subsequently Zeller (1922) combined Peck's species in *Tricholoma*.

Shanks (1994) studied the type collections for both Peck's and Murrill's species although without acknowledging Murrill's considering them to be one species. With respect to subannulatum, she commented "there is no evidence of a veil on the holotype material, and notes included with the holotype by the collector do not describe the annulus in any detail." Further, she reported the spore size as 5.3–6.  $7 \times 3.8$ –4.8 µm, much smaller than Peck's measurements. As for *californicum*, she stated that "inamyloid spores, absence of clamp connections and parallel lamellar trama hyphae indicate the holotype is a *Tricholoma*. The status of *T*. californicum is difficult to assess. The stature of the preserved specimens is similar to T. dryophilum, with very long stipes relative to the pileus diameter, but T. californicum has smaller spores, lacks cheilocystidia, and is reported to have a slightly bitter taste. It is possible that T. californicum is a synonym of T. ustale (which Shanks accepted as occurring in California), although the spores are slightly smaller than common for *T. ustale*." Singer (1942) also studied the holotype of T. californicum and suggested that it represents a species close to T. ustale.

Given Shanks's observations on the *A. subannulata* holotype, we believe that Peck erred in his description, both with respect to the presence of a well-developed partial veil and spore size. Thus we accept Murrill's synonymy of *M. subannulata* (*T.* 



FIG. 18. Photographs of *Tricholoma* collections studied in this project. A–B. *T. fulvum* s.l. (A: TR106. B: TR139). C–D. *T. subannulatum* (C: TR114. D: TR129). E–F. *T. aurantio-olivaceum* (E: TR108. F: TR133). G–H. *T.* cf. *imbricatum* (G: TR021. H: TR080). Collection details can be found in APPENDIX 1. D. Photograph courtesy of Michael Beug.

subannulatum) and M. californica (T. *californicum*), with the former having priority, although the latter would appear to be a more fitting epithet.

Our BI analysis returned a small wellsupported clade that included two oakassociated collections from Oregon and Washington (TR114 and TR129) labelled "dryophilum" and "pessundatum group," respectively, along with Shanks's voucher specimen for T. ustale (cited in her 1997 publication and labelled "T. ustaloides" in GenBank and FIG. 12). Habitat, macromorphology, and micromorphology of our two collections, plus an additional Oregon collection with matching ITS sequence not included in our analyses are consistent with T. subannulatum, as is Shanks's (1994, 1997) description of "T. ustale." Therefore we accept the former as the correct name for this oak-associated "pessundatum group" species. However, we have not been able to study the holotype of T. subannulatum and, despite several attempts, we were unable to obtain an ITS sequence from the holotype of T. californicum. Therefore an attempt should be made to obtain at least an ITS sequence from the T. subannulatum holotype to confirm a match with the recent samples.

Illustrations and descriptions: FIG. 18C-D; Shanks 1997. Review of numerous online images at sites such as Mushroom Observer suggest that many of the "T. dryophilum" collections represent this species.

#### Clade 3b. Sect. Genuina in part, drycapped species (FIG. 19)

#### Tricholoma aurantio-olivaceum A.H. Smith

Tricholoma aurantio-olivaceum was described from mixed conifer forest on the Olympic Peninsula of Washington and appears to occur widely in the PNW. However, it is not common or at least not frequently reported. Sequences from two recent PNW collections formed a wellsupported clade with the holotype sequence.

Illustrations and descriptions: FIG. 18E-F; Bessette et al. 2013; Shanks 1997; Siegel & Schwarz 2016.

#### Tricholoma imbricatum (Fries) P. Kummer

Tricholoma imbricatum is a European species that typically occurs with pines on sandy soil. In our analyses, one "T. intermedium" and three "T. imbricatum" sequences are closely related to a wellsupported *T. aurantio-olivaceum*. This group of western North American sequences is sister to well-supported European T. imbricatum, including the neotype. However the entire "T. imbricatum" group is not strongly supported, especially in the ML analysis. These results suggest that western North American "*T. imbricatum*" collections do not belong to that species and that future study will be required to resolve the relationships in this group. For now we refer to the PNW collections as T. cf. imbricatum.

Illustrations and descriptions: FIG. 18G-H; Bessette et al. 2013; Desjardin et al. 2015; Siegel & Schwarz 2016 (as T. imbricatum sensu California); Trudell & Ammirati 2009.

#### Tricholoma vaccinum (Schaeffer) P. Kummer

*Tricholoma vaccinum* is a widely distributed species that is associated with conifers, especially spruce. In our analyses, a number of Washington and Alaska specimens fell in a well-supported clade with T. vaccinum specimens from Sweden and Slovenia. Thus, we accept the occurrence of T. vaccinum in the PNW.

Illustrations and descriptions: FIG. 20A-F; Bessette et al. 2013; Breitenbach & Kränzlin 1991; Christensen & Heilmann-Clausen 2013; Ludwig 2012; Læssøe &



Petersen 2019; McKenny et al. 1987; Shanks 1997; Siegel & Schwarz 2016; Trudell & Ammirati 2009.

#### Tricholoma sp.

Our specimen TR159 was found on the drop-off tables at the Mt. Pisgah Arboretum's annual Mushroom Festival in Springfield, Oregon. The name of the collector and the location where the collection was found are unknown. In our analyses it appeared by itself sister to a well supported T. psammopus clade consisting only of European samples. Based on inspection of a number of illustrations of T. psammopus, TR159 appears much darker in color, exhibits much greater color contrast between cap and gills, and has a more scaly stipe than *T. psammopus*. It also is unlikely that TR159 was collected in an area with larch (T. psammopus is primarily a larch associate). Thus TR159 could represent an undescribed species. However, study of additional well-documented collections will be necessary to determine whether description as a new species is warranted.

Clade 3a - Sect. Genuina - Viscid Caps

■ = BIPP ≥ 0.95 and MLBS ≥ 70% ● = BIPP ≥ 0.95, MLBS < 70%</p> ○ = MLBS ≥ 70%, BIPP < 0.95</p> Blue font = PNW sequence

cf. imbricatum

FIG. 19. Detail of Clade 3b, Section *Genuina*—dry caps. Symbols as in FIG. 1. PNW sequences shown in blue.

#### Illustration: FIG. 20G.

Clade 4. Sect. Megatricholoma (FIG. 21). Our Clade 4 corresponds to Sect. Megatricholoma sensu Heilmann-Clausen et al. (2017), which, in their analysis, comprised T. colossus, T. acerbum, and T. roseoacerbum / japonicum. Although Reschke et al. (2018) could not confirm inclusion of the *T*. acerbum clade (sensu Heilmann-Clausen et al. 2017, = T. acerbum + T. roseoacerbum + T. japonicum), it is well supported in our analyses. Specimens from the PNW and California all fall within the *T. acerbum* group, including T. manzanitae and TR147, which we assign to T. japonicum, pending better resolution of T. roseoacerbum / japonicum.

#### Tricholoma japonicum Kawamura

Tricholoma japonicum was described from Japan where it occurs most commonly with pine. Heilmann-Clausen et al. (2017) noted its close relationship to the European *T. roseoacerbum* (as well as to specimens from North America) and commented that, if a single species is involved, the epithet,



FIG. 20. Photographs of Tricholoma collections studied in this project. A-F. T. vaccinum (A: TR071. B: TR091. C: TR120. D: TR122. E: TR128. F: TR152). G. Tricholoma sp. (TR159). H. *T. japonicum* (TR147). Collection details can be found in APPENDIX 1.



Clade 1 - Sect. Tricholoma Clade 3 - Sect. Genuina japonicum AB036900 JPN iaponicum japonicum AF204810 JPN sp NS3319 TR147 WA roseoacerbum LT000072 FIN roseoacerbum LT000073 FIN manzanitae TR057 CA Holotype manzanitae TR057b CA Holotype acerbum LT000005 DNK acerbum LT000134 SVN colossus LT000137 SVN colossus LT000164 SWE ■ = BIPP ≥ 0.95 and MLBS ≥ 70% ● = BIPP ≥ 0.95, MLBS < 70%</p> ○ = MLBS ≥ 70%, BIPP < 0.95</p> Blue font = PNW sequence FIG. 21. Detail of Clades 4–6, Section Megatricholoma, T. apium, and Section Caligata. Symbols as in FIG. 1. PNW sequences shown in blue. murrillianum Arm-caligata v glaucescens AF309522 NC Arm-caligata v glaucescens KU058510 NC "caligatum" AF309520 CRI Arm-caligata v occidentalis TR054 ID Holotype Arm-caligata v occidentalis TR054b ID Holotype dulciolens dulciolens AB738883 SWE Holotype ilkkae LT222029 SWE Holotype Clade 7 - Sect. Sericella Clade 8 - Sect. Lasciva Clade 9 - Sect. Pardinicutis Clade 10 - Sect. Muscaria et al. Clade 12 - Section Undetermined

Clade 13 - Section Undetermined

*japonicum* (from 1954), would have priority over roseoacerbum (from 1984). Our analyses returned a well-supported clade including T. roseoacerbum, TR147, and two T. japonicum specimens. In addition, the separation of TR147 and T. japonicum also is well supported, so it is possible that there are three species represented in the group. However, given the short branch lengths involved and the fact that we have only two PNW collections (a sequence from a second collection, obtained subsequent to the phylogenetic analyses, matches that of TR147), for now we use *T. japonicum* for the PNW specimens, pending possible future work to clarify the relationships in this group, including sequencing of type material of *T*. roseoacerbum and T. japonicum.

Illustrations and descriptions: FIG. 20H, 22A; Imazeki & Hongo 1957; Imazeki et al. 1970; Imazeki et al. 1988.

Tricholoma manzanitae T.J. Baroni & Ovrebo

Tricholoma manzanitae was described from northern California where it is associated with manzanita shrubs, which form arbutoid mycorrhizas. We are aware of three reports of *T. manzanitae* occurring in Oregon made by Dr. James Trappe. Although we have not studied the collections, habitat notes from two of them indicate that madrone, a close relative of manzanita and also an arbutoid mycorrhizaformer, was present. Thus, it appears likely that *T. manzanitae* occurs in at least the southern portion of the PNW and possibly beyond as madrone occurs north as far as southern British Columbia.

*Illustrations and descriptions*: Bessette et al. 2013; Shanks 1997; Siegel & Schwarz 2016 (collection associated with madrone).

Clade 5. Tricholoma apium (FIG. 21). Our Clade 5 comprises a single species, T. apium.

#### Tricholoma apium Jul. Schäffer

Tricholoma apium is a European species that is typically associated with pine on sandy soil. Although it is a relatively distinctive species, it appears that no type material has been designated to help solidify the species concept. Our analyses returned a wellsupported "T. apium" clade, which did not fall into any of the traditional sections. Within that clade are two well-supported lineages — one from the PNW and the other (wellsupported only in ML) from well-documented European collections. Based on the short branch lengths and close morphological and ecological similarity of PNW and European specimens, we accept T. apium as occurring in the PNW pending designation of, and critical comparison with, type material.

Illustrations and descriptions: FIG. 22B-C; Bessette et al. 2013; Breitenbach & Kränzlin 1991: Christensen & Heilmann-Clausen 2013; Ludwig 2012; Læssøe & Petersen 2019.

Clade 6. Sect. Caligata (FIG. 21). Our Clade 6 corresponds to Sect. Caligata sensu Heilmann-Clausen et al. (2017) and Reschke et al. (2018). PNW species include T. murrillianum, described from coastal Oregon, and T. dulciolens, which has usually been referred to as T. caligatum in western North America.

#### Tricholoma dulciolens Kytövuori

Synonym: Armillaria caligata var. occidentalis A.H. Smith

Tricholoma dulciolens is a close relative of the matsutake group. It was described from Fennoscandia where it occurs with spruce. Two sequences from the holotype of Armillaria caligata var. occidentalis, described from Idaho, fall in a wellsupported clade that includes several PNW "T. caligatum" specimens as well as the



T. aff. bryogenum (TR001). Collection details can be found in APPENDIX 1 (TR### collections). D, E. Photographs courtesy of Chris Herrera and Noah Siegel, respectively.

holotype of T. dulciolens. Thus, we accept T. dulciolens as the correct name for the PNW "T. caligatum."

Illustrations and descriptions: FIG. 22D-E; Christensen & Heilmann-Clausen 2013; Ludwig 2012; Shanks 1997 (as T. caligatum); Trudell & Ammirati 2009 (as T. caligatum).

#### Tricholoma murrillianum Singer

Misapplied names: Armillaria ponderosa, Tricholoma ponderosum, T. magnivelare

Tricholoma murrillianum is the common, well-known, PNW matsutake species, originally described as Armillaria arenicola by Murrill. Tricholoma magnivelare is its eastern North American counterpart.

Illustrations and descriptions: FIG. 22F-G; Bessette et al. 2013; Desjardin et al. 2015; Shanks 1997; Siegel & Schwarz 2016; Trudell & Ammirati 2009 (all as T. magnivelare).

Clade 7. Sect. Sericella (FIG. 23). Our Clade 7 corresponds to Sect. Sericella sensu Heilmann-Clausen et al. (2017) and Reschke et al. (2018). In Europe, this section includes T. bryogenum, T. hemisulphureum, T. inamoenum, and a complex of "T. sulphureum" species. Several PNW specimens appear to be closely related to T. bryogenum and could represent a separate species. A number of specimens can be assigned to T. inamoenum and T. *platyphyllum*. Representatives of the *T*. sulphureum complex also occur in the PNW. All of these are characterized by a strong "coal tar" odor.

#### Tricholoma aff. bryogenum

Tricholoma bryogenum Mort. Christensen, Heilmann-Clausen & Vauras is a member of the *T. sulphureum* complex, small to medium in size with yellowish coloration, white basal mycelium, and strong coal tar odor. It is known from a small number

of locations in Fennoscandia where it is, possibly exclusively, a spruce associate. Given the uncertainty in species concepts within the T. sulphureum complex and the fact that it has only recently been described, *T. bryogenum* could well be more widely distributed. In our analyses, a well-supported group of specimens from Washington, British Columbia, and Alaska labeled "sulphureum" and "cf. inamoenum" appears to represent one, or possibly two, distinct species, closely related to T. bryogenum. Until sufficient welldocumented collections have been made to study the matter closely, we refer the PNW collections to T. aff. bryogenum.

Illustrations and descriptions: FIG. 22H, 24A; Christensen & Heilmann-Clausen 2013 (holotype).

#### Tricholoma inamoenum (Fries) Gillet

Tricholoma inamoenum is a creamy whitish European species that typically occurs with spruce and has relatively wide-spaced gills, large spores, and a strong coal tar odor like that of T. sulphureum. Our analyses returned a well-supported "T. inamoenum" clade that, in turn comprises two wellsupported subclades, each containing a mix of "T. inamoenum" and "T. platyphyllum" sequences. One clade contains northern specimens from Alaska, British Columbia, Ontario, and Sweden and includes the European neotype. Therefore, it can be taken to represent T. inamoenum sensu stricto. The second contains specimens from Washington, Oregon, and California, including Shanks's (1994) voucher collection for *T. inamoenum*, and we accept these as representing T. platyphyllum (below).

Illustrations and descriptions: FIG. 24B; Breitenbach & Kränzlin 1991; Christensen & Heilmann-Clausen 2013; Ludwig 2012; Læssøe & Petersen 2019.



#### FIG. 23. Detail of Clade 7, Section Sericella. Symbols as in FIG. 1. PNW sequences shown in blue.

#### Tricholoma platyphyllum (Murrill) Murrill

Tricholoma platyphyllum was described from the vicinity of Seattle, Washington. From Murrill's description of the type specimen (a single fruitbody) it is clear that his species is very similar to T. inamoenum. However, his specimen was rather small, he made no mention of odor (T. inamoenum has a very strong coal tar odor that is difficult to ignore), and he reported the spore size as  $8.5 \times 6 \mu m$ , which would be at

0.3

the low end of the range for *T. inamoenum*. Ovrebo (1973) noted the similarity of T. *platyphyllum* to *T* inamoenum. Although he reported spore size for the T. platyphyllum holotype as  $11.3-12(-12.8) \times 6-7.5(-9)$ um, consistent with T. inamoenum, he chose to recognize T. platyphyllum as a separate species, emphasizing its smaller fruitbodies, pending future study. As part of her study of the T. platyphyllum holotype, Shanks (1994) measured the spores as 9.6–12  $\times$ 



FIG. 24. Photographs of *Tricholoma* collections studied in this project. A. *T.* aff. *bryogenum* (TR084). B. *T. inamoenum* (TR140). C–F. *T. platyphyllum* (C: TR003. D: TR077. E: TR078. F: TR087). G–H. *T. sulphureum* s.l. (G: TR020. H: TR148). Collection details can be found in APPENDIX 1.

4.8–6.7 μm and noted the existence of European *T. inamoenum* specimens similar in size to Murrill's specimen. Consequently, she considered *T. platyphyllum* to be a later synonym of *T. inamoenum*.

Our analyses returned a well-supported "T. inamoenum" clade that includes two groups, one of which consists of northern specimens and includes the neotype of *T*. *inamoenum*. This group thus represents *T*. inamoenum sensu stricto. The second group contains specimens from California, Oregon, and Washington and likely represents T. platyphyllum. Repeated attempts to obtain an ITS sequence from the holotype were unsuccessful. Based on a small number of observations, consistent differences in macromorphology are not immediately obvious. Ecologically, T. inamoenum is generally considered to associate primarily with spruce, whereas it is likely that the holotype of T. platyphyllum came from a forest dominated by Douglas-fir and western hemlock. Four of the five samples in our *T. platyphyllum* clade came from forests that lack spruce, however the California specimen came from an area where spruce is present. Thus, habitat might provide a useful, but not fool-proof, differentiator. Limited observations suggest that spore size differs between T. platyphyllum and T. inamoenum — the four *T. platyphyllum* collections we studied (TR003, TR077, TR078, and TR087) had mean spore size  $11.4 \times 6.5 \,\mu\text{m}$ whereas those from two T. inamoenum sensu stricto collections (TR140 and an additional collection sequenced after completion of the phylogenetic analyses) had mean spore size  $10.0 \times 5.8 \ \mu m$  (n = 20 for each collection). Mean Q-values were 1.78 and 1.75, respectively. Observations on additional collections would be highly desirable but, for now, we accept that the specimens in our T.

*platyphyllum* clade represent that species. For a possible additional consideration, see the discussion of *T. silvaticum* below under *Other reported species, not confirmed from PNW but considered possible to occur here.* 

*Illustrations and descriptions*: FIG. 24C–F; Bessette et al. 2013, p. 87(A); Trudell & Ammirati 2009 (both as *T. inamoenum*).

#### Tricholoma sulphureum (Bulliard) P. Kummer

*"Tricholoma sulphureum"* represents a species complex within Sect. Sericella. Heilmann-Clausen et al. (2017) recognized three "types" within the complex. Type I is sister to T. hemisulphureum (Kühner) A. Riva, Type II is sister to T. bryogenum sensu lato, and Type III is sister to the Type I + T. hemisulphureum + TR148 clade. "Tricholoma sulphureum" from the PNW was not well represented in our analyses. One Washington specimen appears to be closely related to Type III, and a well-supported group from Washington, British Columbia, and Alaska appears to represent a distinct species, closely related to T. bryogenum (see above). Until such time as the taxonomy of this complex is worked out, we accept T. aff. bryogenum and T. sulphureum sensu lato as occurring in the PNW.

*Illustrations and descriptions*: FIG. 24G–H; Christensen & Heilmann-Clausen 2013; Ludwig 2012; Læssøe & Petersen 2019.

Clade 8. Sect. *Lasciva* (FIG. 25). Our Clade 8 corresponds to Sect. *Lasciva* sensu Heilmann-Clausen et al. (2017). Consistent with that study, in our tree, the section is split in two well-supported subclades. The first includes the European species *T. album*, *T. lascivum*, and *T. stiparophyllum*, and the second includes the European species *T. boreosulphurescens* (including two samples labelled "*T. sulphurescens*") and *T. sulphurescens* (the



latter apparently representing two species). All of the PNW specimens in our analyses form a well-supported clade, sister to *T. boreosulphurescens*, and representing a new species, *Tricholoma lutescens*.

*Tricholoma lutescens* S.A Trudell, A.D. Parker & E.T. Cline

Misapplied name: Tricholoma sulphurescens

Tricholoma sulphurescens is a whitish, yellow-staining, strongly odorous European species that typically is associated with beech and oak. It is much more common in southern Europe than in more northerly areas (Christensen & Heilmann-Clausen 2013). Tricholoma boreosulphurescens Mort. Christensen & Heilmann-Clausen is a macroscopically and microscopically very similar species described from Fennoscandia. It differs from T. sulphurescens in its boreal and high-mountain occurrence in birch and birch-spruce forests. In our analyses, all of the PNW "T. sulphurescens" specimens fell in a well-supported group, sister to T. boreosulphurescens, and representing *T. lutescens*. Our collections all came from forests with abundant spruce, often accompanied by birch. In addition to the geographic separation, the PNW collections have smaller basidiospores (mean  $5.4 \times 4.0$  $\mu$ m [n = 130, from five collections] versus average 5.6–6.4  $\times$  4.2–5.1 µm [Christensen & Heilmann-Clausen 2013]), although the difference may be too small to apply in determining individual collections. Otherwise, we have found no obvious correlated morphological or ecological differences between T. lutescens and T. boreosulphurescens.

*Illustrations and descriptions*: FIG. 26A–D, 27; Christensen & Heilmann-Clausen 2013 (*T. boreosulphurescens*); Trudell &

Parker 2021 (description, as *T. leucoxanthum* sp. nov., an illegitimate name).

**Clade 9. Sect.** *Pardinicutis* (FIG. 25). Our Clade 9 corresponds to Sect. *Pardinicutis* sensu Heilmann-Clausen et al. (2017) and Reschke et al. (2018) and the "*Pardinicutis* complex" of Ovrebo and Hughes (2018). As noted in the previous studies, western North American (including PNW) "*T. pardinum*" specimens appear to represent an undescribed species closely related to *T. pardinum* and from which *T. smithii* and a clade of West Coast "*T. venenatum*" specimens (*T. venenatum*" specimens (*T. venenatoides*) are derived.

#### Tricholoma aff. pardinum

Tricholoma pardinum (Persoon) Quélet was described from France. In Europe, it is considered a widespread, but not common, usually montane species associated principally with beech and fir (Bon 1991; Galli 1999; Christensen & Heilmann-Clausen 2013). In our analyses, two well-documented European specimens of *T. pardinum* formed a well-supported clade. "Tricholoma pardinum" specimens from California, Oregon, Washington, and British Columbia and a "T. huronense" specimen from California (T. huronense is an apparently rare, or at least rarely reported, species described from a single collection from Michigan in association with oak), formed a group that is paraphyletic with respect to well-supported clades of Rocky Mountain T. smithii and West Coast "T. venenatum" specimens (=T. venenatoides, see below). Ovrebo and Hughes (2018) reported essentially the same result. Although the paraphyletic West Coast "T. pardinum" samples appear to represent at least one undescribed species, the relationships within the overall T. pardinum group need to be better resolved before describing new taxa involving those specimens. Therefore, until



FIG. 26. Photographs of Tricholoma collections studied in this project. A-D. T. lutescens (A: TR052. B: TR093. C: TR097. D: TR150). E-F. T. aff. pardinum (E: TR069. F: TR144). G. T. smithii (TR146). H. T. arvernense (TR004). Collection details can be found in APPENDIX 1.



FIG. 27. Photograph of the holotype collection for T. lutescens (TR151). Collection details can be found in APPENDIX 1.

future studies, including sequencing of T. pardinum type material, are conducted, we refer to PNW "T. pardinum" specimens as T. aff. pardinum.

Illustrations and descriptions: FIG. 26E-F; Desjardin et al. 2015; Shanks 1997; Siegel & Schwarz 2016; Trudell & Ammirati 2009 (all as T. pardinum).

Tricholoma venenatoides S.A. Trudell, A.D. Parker & M.J. Gordon

Misapplied name: Tricholoma venenatum

Tricholoma venenatum was described in 1908 from Michigan where it was collected under deciduous angiosperm trees. We were able to obtain a partial ITS sequence from the holotype and, in our analyses, it was matched at 141 of 142 positions by an oak ectomycorrhiza from North Carolina. These two samples formed a well-supported clade, sister to a well-supported broad "T. pardinum" clade. Within the latter clade, Rocky Mountain collections of "T. venenatum" are now assigned to T. smithii (Ovrebo & Hughes 2018, TR146—our FIG. 26G). West Coast collections of "T. venenatum" represent a new species, T. venenatoides. It is very similar to *T. smithii*—medium to large in size, whitish with tan to brownish scales on the pileus,



FIG. 28. Photograph of the holotype collection for T. venenatoides (SAT-19-298-14 /WTU-F-073089/MW597303 [ITS]).

farinaceous odor and taste, relatively large spores, abundant clamp connections, and occurrence in montane forests.

Illustrations and descriptions: FIG. 28. Trudell & Parker 2021 (description).

Clade 10. Sect. Muscaria plus additional species (FIG. 29). Our Clade 10 includes Sect. Muscaria, which was recently described by Reschke et al. (2018) and, in their circumscription, comprised the Asian species T. aurantiipes, T. muscarium, and T. muscarioides, plus the North American species T. davisiae. Our analyses, which included the latter two species, strongly support the placement of T. luteomaculosum in the section in a narrow sense and also suggest that expanding the section to include T. nigrum and T. arvernense should be considered.

#### Tricholoma arvernense Bon

Tricholoma arvernense is a European species, which, on that continent, is primarily associated with pine on sandy soil. In our analyses, sequences from several PNW and European collections fell in a wellsupported, but paraphyletic (with respect to a group of species including *T. davisiae* and T. luteomaculosum), "T. arvernense"



FIG. 29. Detail of Clades 10–11, Section *Muscaria*, additional species, and Section *Atrosquamosa*. Symbols as in FIG. 1. PNW sequences shown in blue.



FIG. 30. Photographs of *Tricholoma* collections studied in this project. A *T. arvernense* (AKFF-004-14). B–C. *T. davisiae* (B: TR018. C: TR050). D–F. *T. nigrum* (D: TR019. E: TR070. F: TR143). G. *T.* aff. *olivaceotinctum* (TR111). H. *T. mutabile* (TR109). Collection details can be found in APPENDIX 1 (TR### collections) and APPENDIX 3 (others). A. Photograph courtesy of Noah Siegel.

group. Although the PNW collections were associated with a variety of conifers, including spruce and hemlock, and were not restricted to sandy soils, we accept T. arvernense as occurring in the PNW, pending better resolution of the group.

Illustrations and descriptions: FIG. 26H, 30A; Bessette et al. 2013; Breitenbach & Kränzlin 1991; Christensen & Heilmann-Clausen 2013; Ludwig 2012; Læssøe & Petersen 2019; Siegel & Schwarz 2016.

#### *Tricholoma davisiae* Peck

Synonym: Tricholoma cheilolaminum Ovrebo & Tylutki

Tricholoma davisiae was described from a collection made under conifers in Maine. In our analyses, ITS sequences from two Idaho collections form a well-supported clade with sequences from two Québec specimens and morphology of the Idaho specimens closely matches the current concept of the species (that of Ovrebo 1980). We are unaware of any molecular data from the holotype but, for now, we accept T. davisiae as occurring in the PNW. Tricholoma cheilolaminum was described from Oregon by Ovrebo and Tylutki in 1975 and noted to occur in Idaho. However, subsequently Ovrebo (1980) concluded that this name is a later synonym of T. davisiae.

Illustrations and descriptions: FIG. 30B-C; Bessette et al. 2013; McNeil 2006.

#### Tricholoma nigrum Shanks & Ovrebo

Tricholoma nigrum was described from Oregon and, in our analyses, sequences from three collections (TR019, TR070, and TR143) that match the holotype (the latter sequence not shown) formed a well-supported clade sister, with very short branch lengths, to a clade comprising four "T. luteomaculosum" sequences from coastal Oregon and

Vancouver, British Columbia. Although detailed information concerning the latter four specimens was not readily available, they do not cluster with other T. luteomaculosum sequences, and it is likely that they represent misdeterminations of T. nigrum.

Illustrations and descriptions: FIG. 30D-F; Shanks 1996.

Clade 11. Sect. Atrosquamosa (FIG. 29). Although only weakly supported in both BI and ML, our Clade 11 corresponds closely to Sect. Atrosquamosa as presented by Heilmann-Clausen et al. (2017). It includes five well-circumscribed European species, viz. T. atrosquamosum, T. orirubens, T. basirubens, T. squarrulosum and T. olivaceotinctum, and these species fall in two distinct subclades. The single PNW specimen, TR111 labelled "T. squarrulosum," occurs as sister to a well-supported T. olivaceotinctum. For now, we refer to it as T. aff. olivaceotinctum. Two Colorado collections of T. atrosquamosum appear to be closely related to European material of that species (sensu Heilmann-Clausen et al 2017) and a California collection labelled "T. cf. atrosquamosum" could represent a new species, closely related to T. squarrulosum.

Illustration: FIG. 30G.

Clade 12. Tricholoma subumbrinum – T. mutabile group (FIG. 31). Our Clade 12 comprises a well-supported group of species that, at least in terms of ITS barcodes, do not fit within any of the currently recognized sections of Tricholoma. Included are the European taxa, T. fucatum and T. josserandii and the American T. felschii, T. marguettense, T. mutabile, and T. subumbrinum. The PNW report of T. josserandii likely represents a misdetermination of either T. mutabile or T. marquettense.



#### Tricholoma marquettense Ovrebo

Tricholoma marquettense was described from jack pine forests in Michigan. In our analyses, a sequence from an Olympic Peninsula, Washington collection clustered (well supported in ML) with a collection from Alabama that Ovrebo et al. (2019) accepted as representing T. marquettense. Consequently, we accept the occurrence of *T. marquettense* in the PNW, although additional study would seem desirable in light of the unusual apparent distribution.

Clade 1 - Sect. Tricholoma Clade 3 - Sect. Genuina Clade 4 - Sect. Megatricholom Clade 6 - Sect. Caligata Clade 7 - Sect. Sericella Clade 8 - Sect. Lasciva Clade 10 - Sect. Muscaria et al. mutabile aff MH704860 TX nigrum" TR109 WA ■ = BIPP ≥ 0.95 and MLBS ≥ 70% mutabile AF349703 CA ● = BIPP ≥ 0.95, MLBS < 70%</p> mutabile AF458444 OR mutabile AF458445 OR ○ = MLBS ≥ 70%, BIPP < 0.95</p> mutabile TR040 CA Holotype Blue font = PNW sequence mutabile TR110 ID fucatum LT000121 NOR fucatum LT000170 SWE Neotyp subumbrinum JQ711805 Root-tip BC atroviolaceum KU058509 WA

atroviolaceum TR132 ID sp TR126b ID atroviolaceum AY750166 WA atroviolaceum TR055 OR Holotype atroviolaceum TR131b WA sp TR126 ID

0.3

FIG. 31. Detail of Clades 12–16, all comprising species not aligned with any of the traditional sections of Tricholoma. Symbols as in FIG. 1. PNW sequences shown in blue.

melleum MF034210 CHN Holotype

#### Illustration and description: Ovrebo 1986.

#### Tricholoma mutabile Shanks

Synonym: Tricholoma portentosum var. avellaneifolium (Murrill) A.H. Smith

Tricholoma mutabile was described from California with reference to multiple specimens from Washington. It was earlier proposed as T. smithii (Shanks 1994) but never validly published under that name. Shanks (1994, 1996) determined that her California collections represented the same taxon as

Smith's *T. portentosum* var. *avellaneifolium*, a PNW taxon based on collections from Olympic National Park, Washington. However, the latter taxon required a new name ("*T. mutabile*") as Shanks (1994) had determined that the holotype of *M. avellaneifolia / T. avellaneifolium* was not a tricholoma and more properly belonged in ("probably") *Lyophyllum* based on the presence of siderophilous granules in the basidia. In our analyses, sequences from Oregon and Idaho *T. mutabile* specimens and a Washington "*T. nigrum*" specimen fell in a well-supported clade that includes the *T. mutabile* holotype sequence.

*Illustrations and descriptions*: FIG. 30H, 32A; Shanks 1996.

#### Tricholoma subumbrinum A.H. Smith

*Tricholoma subumbrinum* is a poorly known species described from Olympic National Park, Washington, where it was collected in a mixed conifer forest. Our analyses returned a well-supported clade that includes the T. subumbrinum holotype, the T. felschii Ovrebo, Hughes & Halling holotype, and other "subumbrinum" and "felschii" specimens from British Columbia, Arkansas, and Tennessee. This suggests that T. felschii is a later synonym of T. subumbrinum. Although there are many similarities in the type descriptions for the two species, there also are points of difference. If they do represent a single species, it would be one with a particularly wide distribution (Washington and British Columbia to eastern North America to Costa Rica) and broad ecological amplitude (with conifers in the PNW, in mixed forests in eastern North America, and with oaks in Costa Rica). Additional study is necessary before accepting the putative synonymy.

Clade 13. *Tricholoma borgsjoeënse* + *T. atroviolaceum* (FIG. 31). Our Clade 13

comprises a well-supported group of species that, at least in terms of ITS barcodes, do not fit within any of the currently recognized sections of *Tricholoma*. Included are the European species, *T. borgsjoeënse* and the very similar North American *T. atroviolaceum*.

#### Tricholoma atroviolaceum A.H. Smith

*Tricholoma atroviolaceum* was described from southern Oregon. It is a distinctive, fairly common, species that occurs in conifer forests in many parts of the PNW and appears to be relatively easy to identify, as all "*T*. *atroviolaceum*" specimens we obtained yielded sequences that fell in a well-supported clade with the holotype sequence. It is closely related, and rather similar in appearance, to the European species, *T. borgsjoeënse*.

*Illustrations and descriptions*: FIG. 32B– E; Bessette et al. 2013; Siegel & Schwarz 2016; Shanks 1997; Trudell & Ammirati 2009.

Clade 14. Tricholoma vernaticum + "T. turpescens" (FIG. 31). Our Clade 14 comprises a well-supported group of species that, at least in terms of ITS barcodes, do not fit within any of the currently recognized sections of Tricholoma. Included are T. vernaticum and an apparently undescribed whitish species from California, given the informal field name, "T. turpescens."

#### Tricholoma vernaticum Shanks

Synonym: Armillaria olida Thiers & Sundberg

*Tricholoma vernaticum* is a spring to early summer montane species described from California as *Armillaria olida*. In our analyses, specimens from California, Oregon, and Washington formed a well-supported clade with the holotype. The results of our analyses are consistent with the observation of



FIG. 32. Photographs of *Tricholoma* collections studied in this project. A. *T. mutabile* (TR110). B–E. *T. atroviolaceum* (B: TR131. C–D: TR126. E: TR132). F–G. *T. vernaticum* (F: TR024. G: TR095). H. *T. argyraceum* s.l. (TR107). Collection details can be found in APPENDIX 1.





*Tricholoma*. The closest relative to it in our analyses (TR100 and TR101) is an apparently undescribed whitish species from California.

Illustrations and descriptions: FIG. 32F–G; Bessette et al. 2013; Desjardin et al. 2015; Shanks 1997.

Clade 15—Tricholoma luridum and Clade 16—*T. melleum* (FIG. 31). Our Clade 15



FIG. 34. Photographs of Tricholoma collections studied in this project. A–B. *T. argyraceum* s.l. (A: TR121. B: TR149). C-E. T. moseri (C: TR090. D: TR117. E: TR127). Collection details can be found in APPENDIX 1.

consists of three European specimens of T. luridum (Schaeffer) P. Kummer, which is a montane species that occurs in mixed forests with beech, fir, and spruce. Our Clade 16 consists of the holotype of T. melleum K. Reschke, F. Popa, Z.L. Yang & G. Kost, which was described from a spruce-oak forest in China and seems to be an oak associate. The relationships of these two species to the rest of the genus are unresolved and we have no evidence for the occurrence of either in



#### Tricholoma moseri Singer

Misapplied names: Tricholoma myomyces, T. terreum

Tricholoma moseri was described from montane pine forests in Mexico. In our analyses, all T. moseri sequences fell within a well-supported "T. triste" complex. Tricholoma triste specimens, mostly from Europe and including the neotype, but also one Colorado collection, formed a group that is paraphyletic with respect to T. moseri and T. bonii. In turn, T. moseri specimens, including the holotype, formed a group that is paraphyletic with respect to a wellsupported T. bonii clade, which includes the holotype. A clade consisting of *T. bonii* plus T. moseri sample TR090 also is well supported, as is a clade consisting of T. bonii plus T. moseri samples TR090 and TR117 (BI only). Christensen and Heilmann-Clausen (2013) discussed the difficulty in separating *T. triste* and *T. bonii* using morphological characteristics and also noted the similarity of *T. moseri* to the two European species. Clearly more work is needed to resolve the relationships within the *T. triste* complex. For now, we accept the existence of *T. moseri* in the PNW.

*Illustrations and descriptions*: FIG. 34C–E; Bessette et al. 2013; Desjardin et al. 2015; Shanks 1997.

## Poorly known species of uncertain status, described from the PNW

The following three species were described, one provisionally, from the PNW. However, their current status is unknown.

#### Tricholoma farinaceum (Murrill) Murrill

Synonym: Melanoleuca farinacea Murrill

*Tricholoma farinaceum* is a little-known white, strongly farinaceous-smelling species described from the vicinity of Seattle,



FIG. 35. Photograph of epitype collection for *Tricholoma dryophilum* (TR125). Collection details can be found in APPENDIX 1.

#### the PNW.

Clade 17. Sect. Terrea (FIG. 33). Our Clade 17 corresponds to Sect. Terrea sensu Heilmann-Clausen et al. (2017) and Reschke et al. (2018). Our analyses returned two well-supported subclades. The first includes the European species T. argyraceum, T. cingulatum, T. inocybeoides, and T. scalpturatum. Three specimens in our study formed part of a T. argyraceum group that is paraphyletic with respect to T. cingulatum. The second subclade included the European species T. bonii, T. terreum, and T. triste. PNW specimens labelled "T. moseri," along with the holotype of that species, formed a paraphyletic group with respect to a well-supported T. bonii within a larger T. triste complex.

#### Tricholoma argyraceum (Bulliard) Gillet

Tricholoma argyraceum is a European

species that is ectomycorrhizal with both deciduous angiosperm and coniferous trees (Jargeat et al. 2010). In our analyses, sequences from "*T. terreum*" and "Stanford gray" (Siegel & Schwarz 2016) collections from Washington and California, respectively, fell in a well-supported, but paraphyletic (with respect to *T. cingulatum*) "*T. argyraceum*" group. Morphology of the North American specimens is a close match to that of *T. argyraceum*. Thus, until further studies can be done to resolve the relationships within this group, we accept *T. argyraceum* sensu lato as occurring in the PNW.

*Illustrations and descriptions*: FIG. 32H, 34 A–B; Bessette et al. 2013 ("Stanford Gray" as "NAT-11"); Christensen & Heilmann-Clausen 2013; Ludwig 2012; Læssøe & Petersen 2019; Siegel & Schwarz 2016 (as "Stanford Gray").

Washington. Singer (1942) studied the type collection and concluded that T. farinaceum is closely related to *T. mongolicum* in Sect. Leucorigida of Subg. Contextocutis. Shanks (1994) accepted that section placement after her examination of the type collection and suggested a possible relationship to T. album. However, Singer characterized the species in Leucorigida as not occurring with forest trees, which is the norm for species of Tricholoma. Rather the former species occur in grassland and semi-desert habitats and so, presumably, would not be ectomycorrhizal. In part because of this difference, T. mongolicum, the type species of Sect. Leucorigida, has been transferred to Leucocalocybe (Yu et al. 2011) and, earlier, other species in the section were transferred to Macrocybe (Pegler et al. 1998). If Singer's placement of T. farinaceum was justified, then it is likely that it does not belong in Tricholoma. However, despite multiple attempts, we were unable to obtain an ITS sequence from the holotype. For now, it seems best to consider T. farinaceum as a nomen ambiguum.

#### *Tricholoma nigrocystidium* nom. prov. Ovrebo 1973

This putative species was based on study of three collections from Idaho. It was never validly published and we have no new information to add here.

#### Tricholoma subluridum (Murrill) Murrill

#### Synonym: Melanoleuca sublurida Murrill

The type collection (a single fruitbody) originated from the Oregon Coast Range. Based on his study of the type specimen, Singer (1942) suggested that it was close to, or the same as, *T. sudum* sensu Lange, which would suggest it is a member of the broad *T. saponaceum* complex. The type collection includes an annotation label from Howard Bigelow that refers to the specimen as *Melanoleuca sublurida* and provides no indication that he disagreed with that name. We have found no well-documented reports of this species since Murrill's original publication.

## Species that occur in California and are likely to extend into the PNW

These four species include three that were described from California plus a European species that appears to occur there. Although we did not confirm their occurrence in the PNW, it is likely that they occur here based on their typical habitats.

#### *Tricholoma batschii* Gulden ex Mort. Christensen & Noordeloos

#### Misapplied name: Tricholoma fracticum

Tricholoma batschii is a European species that is usually associated with pine. It has a slight annulus and the sharply defined stipe apex is whitish. An ITS sequence from Shanks's (1994) California voucher specimen of T. fracticum formed a well-supported clade with that from a Croatian specimen of T. batschii studied by Heilmann-Clausen et al. (2017). Macromorphology of the California collection is consistent with the European concept (Shanks 1994, Christensen & Heilmann-Clausen 2013) and ecology also appears consistent. Shanks's (1997) photograph (not of the voucher collection, which was obtained at an exhibition) includes needles of pine. Consequently, we accept the occurrence of *T. batschii* in California but its possible occurrence in the PNW remains to be confirmed.

Illustrations and descriptions: Bessette et al. 2013 (as *T. fracticum*); Breitenbach & Kränzlin 1991 (as *T. fracticum*); Christensen & Heilmann-Clausen 2013; Desjardin et al. 2015 (as *T. fracticum*); Shanks 1997 (as *T. fracticum*); Ludwig 2012; Siegel & Schwarz

#### 2016 (as T. fracticum).

#### Tricholoma dryophilum (Murrill) Murrill

Synonym: Melanoleuca dryophila Murrill

Tricholoma dryophilum was described from a collection occurring under coast live oak in the San Francisco Bay Area of California. In our study, multiple attempts to obtain an ITS sequence from the holotype were unsuccessful. However, a sequence from California specimens we collected formed a well-supported clade with two collections made by Shanks (1994), including her designated voucher for the species. The species appears to be sister to T. stans (Fries) Saccardo, a European species that most often occurs with pines. Oregon and Washington collections made under Garry oak during our study (TR114 and TR129, respectively) and originally thought to be T. dryophilum instead represent T. subannulatum (see above), as do many online observations from outside California. Thus, the occurrence of *T. dryophilum* in the PNW remains to be confirmed.

*Illustrations and descriptions*: FIG. 35; Shanks 1997; Siegel & Schwarz 2016.

#### Tricholoma griseoviolaceum Shanks

Tricholoma griseoviolaceum was described from California where it associates with coast live oak and tanoak. Our ITS sequence from the holotype, along with a British Columbia "*T. saponaceum*" sequence, formed one of four minimally diverged groupings (but without strong support) within a well-supported "*T. portentosum*" clade, along with European *T. portentosum* specimens, including the neotype, and western North American "*T. portentosum*" specimens. The common occurrence with oak, typically stocky fruitbody stature, violet tones in the cap, and lack of yellow in the gills and stipe have been used to distinguish *T. griseoviolaceum* from the other members of the "*T. portentosum*" clade and we recognize the species pending future resolution of the relationships within the group. Because the grouping of a British Columbia collection with the *T. griseoviolaceum* holotype was not supported we feel the occurrence of *T. griseoviolaceum* in the PNW remains to be confirmed.

*Illustrations and descriptions*: Bessette et al. 2013; Desjardin et al. 2015; Shanks 1997; Siegel & Schwarz 2016.

#### Tricholoma muricatum Shanks

Tricholoma muricatum was described from California. Its species epithet reflects its typical association with *Pinus muricata* (Bishop pine). In our analyses, the holotype sequence fell in a well-supported clade with two T. albobrunneum (Persoon) P. Kummer (*=Tricholoma striatum* [Schaeffer] Quélet) sequences from Europe. Shanks's type description is very similar to Christensen and Heilmann-Clausen's (2013) description of *T*. albobrunneum, which also is ectomycorrhizal with pines. However, we are unaware of an ITS sequence from type material of the latter species (it appears that designation of an epitype would be necessary). Thus, we are hesitant to accept T. muricatum as synonymous with T. albobrunneum until confirmed by critical comparison with type material of the latter species. No PNW sequences grouped with the T. muricatum / T. *albobrunneum* sequences, so the occurrence of T. muricatum (or T. albobrunneum) in the PNW remains to be confirmed, although it appears likely.

*Illustrations and descriptions*: Desjardin et al. 2015; Shanks 1997 (however, the photograph, made by Ms. Catherine Ardrey, likely shows a collection from Oregon and there is no indication in Shanks's publications (1994, 1996, 1997) that she studied the material).

#### Other reported species, not confirmed from the PNW but considered possible to occur here

These 12 species include 4 that were described from eastern North America and 8 from Europe. Although we did not confirm their occurrence in the PNW, it is possible that they occur here based on their typical habitats.

#### Tricholoma aestuans (Fries) Gillet

Tricholoma aestuans is a European species with a conical to umbonate yellowish brown cap, yellowish gills, and an association with spruce and pine. Tricholoma palustre is a very similar northeastern North American species that is typically associated with beech and oak. After completion of our phylogenetic analyses, we became aware of a collection from shore pine woodland near Sand Lake, Oregon determined as "T. aestuans," with ITS sequence very close to that of European specimens that were included in our analyses (LT000007 and LT000153 [neotype], FIG. 2). Study of the morphological features of the Oregon collection will be required before the existence of T. aestuans in the PNW can be confirmed.

#### Tricholoma atrosquamosum Saccardo

*Tricholoma atrosquamosum* belongs to a taxonomically difficult group (Sect. *Atrosquamosa*) and Christensen and Heilmann-Clausen (2013) consider it to be most closely related to *T. orirubens* and to occur with a variety of tree species, including birch, hazel, linden, and spruce. Its occurrence in the PNW remains to be confirmed, although it (sensu Christensen & Heilmann-Clausen 2013), or a very close relative, occurs in the Colorado Rocky Mountains (FIG. 29).

#### Tricholoma bufonium (Persoon) Gillet

Tricholoma bufonium is a member of the T. sulphureum complex, traditionally considered to differ by its vinaceous brown pileus and association with conifers. However, Comandini et al. (2004) concluded that *T. bufonium* should be considered an intraspecific variant of T. sulphureum based on fruitbody morphology, ecological data, and analysis of ITS sequences from fruitbodies of different ecological and geographic origin. Christensen and Heilmann-Clausen (2013) and Heilmann-Clausen et al. (2017) agreed that cap color was not a reliable character for differentiating species in the complex but concluded that multiple species exist within *T. sulphureum* sensu lato that will require further work to sort out. Our study included a "T. sulphureum" specimen with reddish pileus (TR020, FIG. 24G) that fell within the broad T. sulphureum complex (FIG. 23). The possible occurrence of *T. bufonium* in the PNW cannot be assessed until the taxonomy of the complex is worked out and the status of the species is resolved.

#### *Tricholoma cingulatum* (Almfelt ex Fries) Jacobasch

*Tricholoma cingulatum* is an annulate species that, in Europe, occurs with willow (Bon 1991, Kibby 2012, Christensen & Heilmann-Clausen 2013). After completion of our phylogenetic analyses, we learned that the photograph of *T. cingulatum* in Shanks (1997) shows a collection made at Fort Casey State Park in Washington. It matches European material in macromorphology. The few other herbarium specimens of PNW "*T. cingulatum*" of which we are aware all appear to have been made under conifers and none include photographs of the fresh material. Siegel & Schwarz (2016) describe and illustrate a California collection that matches European material in macromorphology and host association.

However, we are unaware of ITS sequence data from either the PNW or California collections. Therefore we consider that the occurrence of *T. cingulatum* in the PNW, although likely, remains to be confirmed.

#### Tricholoma fumosoluteum (Peck) Saccardo

*Tricholoma fumosoluteum* is an eastern North American species associated with conifers. Although we are aware of only one PNW report (from Idaho), the conifer habitat (we have seen it in a mixed forest with spruce, fir, and larch in eastern Canada) suggests it might occur here.

#### Tricholoma joachimii Bon & A. Riva

*Tricholoma joachimii* was described from France and, although most common in southern Europe, it also extends into Fennoscandia. It is mycorrhizal with pines, often on sandy soils. We are aware of a single report of *T. joachimii* from coastal Oregon where pines and sandy soils are common. However, we have not studied that collection and, in our analyses, no PNW or other North American sequences appeared near the clade that includes two well-documented European *T. joachimii* sequences, so the report of that species remains to be confirmed.

#### Tricholoma odorum Peck

*Tricholoma odorum* is a member of the *T. sulphureum* complex, described from Washington D.C. under broad-leaved trees. Ovrebo et al. (2009) obtained ITS sequences from several "*T. odorum*" collections from eastern North America. All fell within the bounds of the *T. sulphureum* complex but they did not form a monophyletic group. ITS data apparently are not available for the holotype. Much work remains to be done to resolve the relationships within the *T. sulphureum* complex, including clarifying the concept of *T. odorum*. Thus, the possible

occurrence of *T. odorum* in the PNW cannot be reliably assessed until the species concept is solidified.

#### *Tricholoma psammopus* (Kalchbrenner) Quélet

*Tricholoma psammopus* is a coniferassociated species (mostly with larch) described from Europe. Its occurrence in the PNW remains to be confirmed.

#### Tricholoma silvaticum Peck

Tricholoma silvaticum is a little-known, small, white species with broad subdistant gills and large elliptical spores described from North Elba, New York. Peck compared it with T. inamoenum and T. leucocephalum (now Tricholomella constricta), differing from both of them primarily in lacking a strong odor. The overall description is very similar to that of *T. platyphyllum*. Should Peck's T. silvaticum and Murrill's T. platyphyllum prove to be the same, the former name would have priority. We have not studied the holotype and there appear to be no subsequent well-documented records so, pending future work, the occurrence of *T. silvaticum* in the PNW remains to be confirmed.

#### Tricholoma subluteum Peck

*Tricholoma subluteum*, a close relative of *T. sejunctum*, was described from New York and occurs widely in northeastern North America under conifers. Its occurrence in the PNW remains to be confirmed.

#### Tricholoma terreum (Schaeffer) P. Kummer

Synonyms: Tricholoma gausapatum (Fries) Quélet, T. myomyces (Persoon) J.E. Lange

*Tricholoma terreum* is a European species that has been interpreted in various ways by different authors. In order to solidify the species concept, Christensen and Noordeloos (1999) designated an epitype from Germany. During their study of more than 100 collections of T. terreum sensu lato, Christensen and Heilmann-Clausen (2013) observed gradational variation in characters such as cap color and presence of a partial veil, and little correlation among the characters. Thus, they interpret T. terreum as a variable species that includes T. gausapatum, T. myomyces, and T. leucoterreum. Our analyses returned a well-supported T. terreum clade, consisting entirely of European specimens (FIG. 33). Within it are two wellsupported clades, one containing the epitype. The most closely related PNW samples in our analyses are T. moseri collections that are more closely related to *T. triste* and *T.* bonii. Neither of the two PNW "T. terreum (cf.)" samples clustered with the European T. terreum samples. One (a British Columbia sequence from GenBank) fell in the North American T. subacutum clade and the other (TR107, from Washington) in T. argyraceum sensu lato. Consequently, the occurrence of T. terreum in the PNW remains to be confirmed.

#### Tricholoma triste (Scopoli) Quélet

*Tricholoma triste* is a European species that is associated with conifers and, perhaps, deciduous angiosperm trees. It is very similar in both macro- and micromorphology to T. bonii (Christensen & Heilmann-Clausen 2013). Christensen and Noordeloos (1999) stabilized the species concept and designated a neotype from southern Germany. In our analyses, T. triste specimens from Europe (including the neotype) and Colorado formed a paraphyletic group from which a paraphyletic group of T. moseri was derived and that from which, in turn, a well-supported T. bonii was derived (FIG. 33). Until further studies are conducted to resolve the taxonomy and application of names in the *T. triste* complex, we accept the occurrence of *T*. moseri in the PNW and that there could be

other closely related species here as well. The occurrence of *T. triste* sensu stricto remains to be confirmed.

#### Other reported species, not confirmed from the PNW and considered unlikely to occur here

Most of the following species were described from Europe or eastern North America, usually in association with beech, oak, or other deciduous angiosperm tree species that do not occur naturally or are rare in the PNW. Heilmann-Clausen et al. (2017) noted that at least 12 species in their analyses appeared to occur in North America and/ or Asia as well as in northern Europe and that all of them were associated with widely distributed boreal host tree genera, especially Picea, Populus, and Salix. None of the intercontinental species associated exclusively with lower-latitude deciduous angiosperm trees such as beech and oak. The results of our analyses are consistent with those observations. Therefore we consider the following species unlikely to occur in the PNW.

Tricholoma acerbum (Bulliard) Quélet Tricholoma acris (acre) Peck Tricholoma album (Schaeffer) P. Kummer Tricholoma atrodiscus (atrodiscum) Ovrebo Tricholoma bisporigerum J.E. Lange

Tricholoma brunneosquamosa Beeli

Tricholoma caligatum (Viviani) Ricken

*Tricholoma cartilagineum* (Bulliard) Quélet

*Tricholoma columbetta* (Fries) P. Kummer (Synonyms: *T. resplendens* [Fries] P. Karsten, *T. subresplendens* [Murrill] Murrill)

*Tricholoma grande* Peck

Tricholoma huronense A.H. Smith

Tricholoma impolitum (Lasch) P. Kummer Tricholoma josserandii Bon Tricholoma luteomaculosum A.H. Smith Tricholoma orirubens Quélet

*Tricholoma pessundatum* (Fries) Quélet. *Tricholoma pessundatum* is a European species that occurs with spruce, pine, and fir, often on sandy soil. Christensen and Heilmann-Clausen (2013) designated an epitype and solidified the species concept. In our analyses, sequences from PNW and European "*T. populinum*" collections were the closest relatives to the epitype of *T. pessundatum* (FIG. 12). Other variously labeled PNW *T. pessundatum* group collections all appear to represent different taxa.

Tricholoma pullum Ovrebo Tricholoma scalpturatum (Fries) Quélet Tricholoma sciodes (Persoon) C. Martín Tricholoma spermaticum (Fries) Gillet Tricholoma squarrulosum Bresadola Tricholoma sudum (Fries) Quélet Tricholoma sulphurescens Bresadola

*Tricholoma tumidum* (Persoon) P. Karsten. *Tricholoma tumidum* is a little-known European species. The epithet was applied by Shanks (1994, 1997) to specimens from California, however her description differs considerably from European descriptions (e.g., Bon 1984, 1991, Riva 1988, 2003), being a better fit for *T. arvernense*. Notes accompanying the single PNW record of "*T. tumidum*" of which we are aware also are a much better fit for *T. arvernense*.

*Tricholoma umbonatum* Clémençon & Bon

*Tricholoma ustale* (Fries) P. Kummer *Tricholoma ustaloides* Romagnesi Are We Using the Right Names?

Tricholoma venenatum G.F. Atkinson

### **DISCUSSION** Tricholoma diversity in the PNW

The results of our work provide evidence for the existence of at least 50 species of Tricholoma in the PNW; undoubtedly, there are more. Unambiguous or highly probable names can be assigned to 30 of the 50. Another 16 are closely related to, but appear to differ somewhat from, existing species or can be tentatively accommodated within broadly circumscribed, mostly European, species. Nearly all of these likely represent undescribed species or ones whose names have been forgotten and there are at least 2 additional putatively undescribed species. Many epithets clearly have been misapplied, mostly ones based on European or eastern North American fungi.

In a number of cases, considerable work will be needed before names can be assigned to PNW species, especially in the *T. equestre*, *T. saponaceum*, and *T. sulphureum* complexes. In most cases this will require solidifying the existing species concepts, often including designation and sequencing of type material, study of new well-documented collections, and sequencing DNA loci beyond the ITS barcode region.

## Association of PNW species with traditional sections

As would be expected from analyses using the same marker (ITS), our ML and BI analyses returned overall tree topology that, for most species, closely reflects existing infrageneric classifications as interpreted by Heilmann-Clausen et al. (2017) and Reschke et al. (2018). Nonetheless, we did observe some differences in placement of particular species within those groups. In addition, similar to their results, we found that several species do not fit comfortably in the existing section-level taxa. Consistent with the results of Heilmann-Clausen et al. (2017) and Reschke et al. (2018), the species in the following clades cannot be readily assigned to an existing section based on ITS data: Clade 5 (T. apium), Clade 12 (T. mutabile, T. marquettense, T. josserandii, T. fucatum, and T. subumbrinum / T. felschii), Clade 13 (T. borgsjoeënse and T. atroviolaceum), Clade 14 (T. vernaticum plus an apparently undescribed California species), Clade 15 (T. luridum), and Clade 16 (T. melleum). In addition, T. arvernense and T. nigrum appeared in a wellsupported Clade 10 with Sect. Muscaria sensu stricto and possible expansion of the section to include them should be investigated.

#### **Observations on species distributions**

Both Heilmann-Clausen et al. (2017) and Reschke et al. (2018) reported that a number of Tricholoma species occur in northern Europe as well as in North America and/ or Asia. These include T. albobrunneum, T. argvraceum, T. aurantium, T. batschii, T. bonii, T. cingulatum, T. dulciolens, T. focale, T. frondosae, T. imbricatum, T. inamoenum, T. japonicum / roseoacerbum, T. matsutake, T. portentosum, T. stans, T. triste, and T. vaccinum. Among these, our analyses suggest that all except *T. stans* are represented in the PNW either as the same or a very closely related species. Additional examples will probably be found when the taxonomy of groups such as the *T. equestre*, T. saponaceum, and T. sulphureum complexes are worked out. As pointed out by Heilmann-Clausen et al. (2017), all of the widespread species are associated with widely distributed boreal tree genera such as Betula, Picea, Pinus, Populus, and Salix. So far, it appears that no species associated exclusively with lower-latitude, broad-leaved angiosperm trees, particularly Fagus and Quercus,

occurs in northern Europe, as well as in the PNW and/or Asia. Heilmann-Clausen et al. (2017) noted that T. roseoacerbum appeared to be remarkably widely distributed, with almost perfect ITS sequence matches among collections and environmental samples from Finland, Japan, Canada, and Mexico. Our analyses returned a well-supported clade comprising three well-supported subclades: European T. roseoacerbum specimens, Japanese T. japonicum specimens, and TR147 (plus an additional sample [FIG. 22A] not included in our tree), which we provisionally recognize as T. japonicum. Further study will be required before it can be determined whether the lineage should be considered a single species or not.

#### Need for well-documented field collections

Progress in furthering our taxonomic and ecological understanding of *Tricholoma* will depend to a large extent on obtaining well-documented field collections of highquality material. Ideally these will include photographs or color illustrations, a list of associated trees, and notes on ephemeral characters such as odor and taste. In some cases, ITS barcode sequences will have to be augmented with sampling of additional DNA loci to help resolve taxonomic issues and allow us to obtain a fuller understanding of the genus, *Tricholoma*, as it occurs in the PNW.

### ACKNOWLEDGMENTS

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#### APPENDIX 1. Tricholoma specimens from which ITS sequences were obtained in this study, plus type collections for which sequencing was not successful.

Sample #	Species Epithet / Name	Collector's / Herbarium #	Location / Origin
TR001	aff. bryogenum (as inamoenum cf.)	SAT-13-272-06 / WTU-F-073001	Chugach National Forest, Kenai Peninsula, Alaska (AK)
TR002	subsejunctum (as viridilutescens cf.)	SAT-13-273-05 / WTU-F-073002	Girdwood, Alaska (AK)
TR003	platyphyllum (as inamoenum)	SAT-13-313-16 / WTU-F-073003	H.J. Andrews Experimental Forest, Willamette National Forest, Lane Co., Oregon (OR)
TR004	arvernense	SAT-12-247-03 / WTU F-073004	Chugach National Forest, Kenai Peninsula, Alaska (AK)
TR005	subacutum (as virgatum)	SAT-13-313-14 / WTU-F-073005	H.J. Andrews Experimental Forest, Willamette National Forest, Lane Co., Oregon (OR)
TR007	subacutum (as virgatum)	SAT-13-274-15 / WTU-F-073006	Girdwood, Alaska (AK)
TR008	fulvum s.l. (as pessundatum group)	SAT-13-273-13 / WTU-F-073007	Girdwood, Alaska (AK)
TR009	equestre (group)	SAT-13-272-01 / WTU-F-073008	Chugach National Forest, Kenai Peninsula, Alaska (AK)
TR010	portentosum s.l.	SAT-10-309-05 / WTU-F-073009	Deception Pass State Park, Island Co., Washington (WA)
TR011	badicephalum (as robustum cf.)	ADP 131005-1 / WTU-F-073010	Olympic National Forest, Clallam Co., Washington (WA)
TR012	subacutum (as virgatum var. vinaceum)	ADP 090903-5 / WTU-F-073011	Colville National Forest, Pend Oreille Co., Washington (WA)
TR013	apium	ADP 101106-1 / WTU-F-073012	Cornet Bay area, Island Co., Washington (WA)
TR015	portentosum s.l.	ADP 031026-2 / WTU-F-073013	Colville National Forest, Pend Oreille Co., Washington (WA)
TR016	intermedium	ADP 040905-1 / WTU-F-073014	Colville National Forest, Pend Oreille Co., Washington (WA)
TR017	ammophilum (as populinum)	ADP 051013-1 / WTU-F-073015	Colville National Forest, Pend Oreille Co., Washington (WA)
TR018	davisiae	ADP 040923-1 / WTU-F-073016	Idaho Panhandle National Forests, Bonner Co., Idaho (ID)
TR019	nigrum	ADP 131005-2 / WTU-F-073017	Upper Dungeness Trail, Olympic National Forest, Clallam Co., Washington (WA)
TR020	sulphureum s.l. (as sulphureum / bufonium)	ADP 041005-1 / WTU-F-073018	Colville National Forest, Pend Oreille Co., Washington (WA)
TR021	aff. imbricatum (as imbricatum)	ADP 101023-1 / WTU-F-073019	Road FR 172 south of Slate Creek, Pend Oreille Co., Washington (WA)
TR022	focale	ADP 131008-2 / WTU-F-073020	Halliday Fen Research Natural Area, Colville National Forest, Pend Oreille Co., Washington (WA)
TR023	aurantium	ADP 100619-1 / WTU-F-073021	Road FR 325 west of Crescent Lake, Colville National Forest, Pend Oreille Co., Washington (WA)
TR024	vernaticum	ADP 140523-1 / WTU-F-073022	Road FR 175 off SR 31 N, Pend Oreille Co., Washington (WA)
TR025	badicephalum (as focale)	PK4037 / UBC-F-16235	Mount Elphinstone, British Columbia, Canada (BC)
TR025b	badicephalum (as focale)	PK4037 / UBC-F-16235	Mount Elphinstone, British Columbia, Canada (BC)
TR026	badicephalum (as robustum cf.)	PK3121 / UBC-F-17552	Manning Provincial Park, British Columbia, Canada (BC)

Habitat / Tree Ass
In deep moss, mixed forest - mostly Picea and Populus.
Picea sitchensis - Tsuga forest, with occasional Alnus and Popula
Mixed conifer forest with Pseudotsuga menziesii, Tsuga heteroph
On moss-covered soil with Picea and Tsuga.
Mixed conifer forest with Pseudotsuga menziesii, Tsuga heteroph
Picea sitchensis -Tsuga forest, with occasional Alnus and Populu
Picea sitchensis -Tsuga forest, with occasional Alnus and Populu
Mixed forest - mostly Picea and Populus.
Mixed conifer forest with <i>Pseudotsuga menziesii</i> , <i>Tsuga heteroph</i> and <i>Acer macrophyllum</i> .
Mature mixed conifer forest.
Mixed conifer forest, mostly Picea engelmannii and Abies.
Conifer forest, with <i>Pseudotsuga menziesii</i> , <i>Tsuga heterophylla</i> , <i>A</i> and <i>Acer macrophyllum</i> .
Mixed conifer forest.
Under Picea engelmannii in mixed woods.
In gravelly soil under Populus trichocarpa in mixed woods.
Conifer forest, in moss under Tsuga.
Mature mixed conifer forest with Pseudotsuga menziesii, Tsuga h
Under Pseudotsuga menziesii.
Mixed conifer forest under Pinus and Abies grandis.
Mixed forest with <i>Pseudotsuga menziesii</i> , <i>Tsuga</i> , <i>Abies grandis</i> , and <i>Betula papyrifera</i> .
With Tsuga.
In needle litter under mixed conifers - Tsuga heterophylla, Abies
Mature mixed conifer forest with <i>Pseudotsuga menziesii</i> , <i>Tsuga h</i>
Mature mixed conifer forest with Pseudotsuga menziesii, Tsuga h
Under Pseudotsuga menziesii, Tsuga heterophylla and Thuja plic

ociates	GenBank/ UNITE # (ITS)
	MW597185 /
s trichocarpa.	MW597186 /
vlla, and Thuja plicata.	MW597187 /
	MW597188 /
vlla, and Thuja plicata.	MW597189 /
trichocarpa.	MW597190 /
trichocarpa.	MW597191 /
	MW597192 /
ella, Thuja plicata, Abies grandis, Alnus rubra,	MW597193 /
	MW597194 /
	MW597195 /
bies grandis, Thuja plicata, Alnus rubra,	MW597196 /
	MW597197 /
	MW597198 /
	MW597199 /
	MW597200 /
eterophylla, and Thuja plicata.	MW597201 /
	MZ054352 /
	MW597202 /
arix occidentalis, Pinus, Thuja plicata,	MW597203 /
	MW597204 /
randis, Pinus monticola, Thuja plicata.	MW597205 /
eterophylla, and Thuja plicata.	MW597206 /
eterophylla, and Thuja plicata.	MW597207 /
ta with Rhododendron macrophyllum understory.	MW597208 /

Sample #	Species Epithet / Name	Collector's / Herbarium #	Location / Origin
TR027	badicephalum (as robustum cf.)	PK3153 / UBC-17553	Emerald Forest Trails, Whistler, British Columbia, Canada (BC)
TR028	badicephalum (as focale)	PK3154 / UBC-F-17554	Emerald Forest Trails, Whistler, British Columbia, Canada (BC)
TR029	focale (as zelleri)	PK3155 / UBC-F-17555	Emerald Forest Trails, Whistler, British Columbia, Canada (BC)
TR029b	focale (as zelleri)	PK3155 / UBC-F-17555	Emerald Forest Trails, Whistler, British Columbia, Canada (BC)
TR030b	badicephalum (as robustum cf.)	PK3171 / UBC-F-17556	Mount Elphinstone, British Columbia, Canada (BC)
TR031	focale (as robustum)	PK5305 / UBC-F-18390	Willamette National Forest, Oregon (OR)
TR031b	focale (as robustum)	PK5305 / UBC-F-18390	Willamette National Forest, Oregon (OR)
TR032	focale (as zelleri)	PK6734 / UBC-F-21190	Emerald Forest Trails, Whistler, British Columbia, Canada (BC)
TR032b	focale (as zelleri)	PK6734 / UBC-F-21190	Emerald Forest Trails, Whistler, British Columbia, Canada (BC)
TR033	dryophilum	KMS360 / SFSU	Marin Co., California (CA)
TR034	focale	KMS390 / SFSU	Sierra Co., California (CA)
TR035	batschii (as fracticum)	KMS436 / SFSU	Location unknown (Fungus Federation Fair), Santa Cruz Co., California (CA)
TR036	griseoviolaceum Holotype	KMS352 / SFSU-F-000786	Portola State Park, San Mateo Co., California (CA)
TR037	luteomaculosum	KMS292 / SFSU	Mendocino Co., California (CA)
TR039	muricatum Holotype	KMS368 / SFSU-F-000785	San Francisco State University Campus, San Francisco Co., California (CA)
TR040	mutabile Holotype	KMS424 / SFSU-F-000788	Yuba Co., California (CA)
TR041	fulvum s.l. (as nictitans)	KMS267 / SFSU	Mendocino Co., California (CA)
TR042	nigrum Holotype	CLO-1758 / SFSU-F-000790	Tillamook Co., Oregon (OR)
TR043b	vernaticum Holotype	HDT28816 / SFSU-F-000420	El Dorado National Forest, El Dorado Co., California (CA)
TR045	vernaticum	KMS378 / SFSU	Sierra Co., California (CA)
TR046	atrofibrillosum (as sejunctum cf.)	ADP 140920-2 / WTU-F-073023	Trapper Creek Trail, Idaho Panhandle National Forests, Priest Lake, Bonner Co., Idaho (ID)
TR047	portentosum s.l. (as mutabile cf.)	E. Cline 11-X-2014 / WTU-F-073024	Mt. Rainier National Park, Washington (WA)
TR048	equestre group (as sp.)	ew-11-X-2014 / WTU-F-073025	NAMA Foray Eatonville, Pierce Co., Washington (WA)
TR049	badicephalum (as focale cf.)	ADP-140927-3 / WTU-F-073026	Near mouth of Kinyon Creek, Colville National Forest, Pend Oreille Co., Washington (WA)
TR050	davisiae	ADP 141001-1 / WTU-F-073027	Road FR 638 near jct. FR 302, Idaho Panhandle National Forests, Bonner Co., Idaho (ID)
TR051	intermedium	ADP 141006-1 / WTU-F-073028	Slate Creek Trail, Colville National Forest, Pend Oreille Co., Washington (WA)
TR052	lutescens (as sulphurescens)	ADP-141006-2 / WTU-F-073029	Slate Creek Trail, Colville National Forest, Pend Oreille Co., Washington (WA)
TR053b	focale (as zelleri, Holotype)	AHS-17999 / MICH-4973	Olympic National Park, Clallam Co., Washington (WA)
TR054	<i>dulciolens</i> (as <i>Armillaria caligata</i> var. <i>occidentalis</i> , Holotype)	AHS 60431 / MICH-5578	Valley Co., Idaho (ID)
TR054b	dulciolens (as Armillaria caligata var. occidentalis, Holotype)	AHS 60431 / MICH-5578	Valley Co., Idaho (ID)

Habitat / Tree Ass
Old-growth conifer forest with Pseudotsuga menziesii, Tsuga her
Old-growth conifer forest with Pseudotsuga menziesii, Tsuga her
Old-growth conifer forest with Pseudotsuga menziesii, Tsuga her
Old-growth conifer forest with Pseudotsuga menziesii, Tsuga her
Mature mixed conifer forest with Pseudotsuga menziesii, Tsuga
Mixed conifer forest with Pseudotsuga menziesii, Tsuga heteroph
Mixed conifer forest with Pseudotsuga menziesii, Tsuga heteroph
Old-growth conifer forest with Pseudotsuga menziesii, Tsuga het
Old-growth conifer forest with Pseudotsuga menziesii, Tsuga her
With Quercus agrifolia.
Not reported.
Unknown.
With Quercus and Lithocarpus (Neolithocarpus).
Not reported.
With Pinus muricatum.
Mixed evergreen forest.
With conifers, including Pinus.
On sandy soil under Pinus contorta.
On soil under montane conifers.
Montane conifer forest with Pseudotsuga menziesii, Pinus, and A
Mature mixed conifer forest with Abies grandis, Tsuga heterophy
On soil in mixed conifer forest with Tsuga mertensiana, Abies an
Conifer forest with Alnus rubra, Populus trichocarpa, Tsuga hete
In mossy soil under Tsuga heterophylla.
In moss under mixed conifers.
With mixed conifers.
Mixed forest with Picea engelmannii, Populus.
Old-growth conifer forest with Tsuga heterophylla, Pseudotsuga
Conifer forest.
Conifer forest.

ociates	GenBank/ UNITE # (ITS)
rophylla, Abies amabilis and Thuja plicata.	MW597209 /
rophylla, Abies amabilis and Thuja plicata.	MW597210 /
rophylla, Abies amabilis and Thuja plicata.	MW597211 /
rophylla, Abies amabilis and Thuja plicata.	MW597212 /
eterophylla, and Thuja plicata.	MW597213 /
vlla, and Thuja plicata.	MW597214 /
vlla, and Thuja plicata.	MW597215 /
rophylla, Abies amabilis and Thuja plicata.	MW597216 /
rophylla, Abies amabilis and Thuja plicata.	MW597217 /
	MW597218 /
	MW597219 /
	MW597220 /
	MN809562 /
	MW597221 /
	MN809563 /
	MN809564 /
	MW597222 /
	MN809565 /
	MN809561 /
bies.	MW597223 /
la, Picea engelmannii, and Thuja plicata.	MW597224 /
abilis, and Callitropsis nootkatensis.	MW597225 /
rophylla, and Pseudotsuga menziesii.	MW597226 /
	MW597227 /
	MW597228 /
	MZ054353 /
	MW597229 /
nenziesii, and Thuja plicata.	MN809567 /
	/ UDB024113
	MN809566 /

Sample #	Species Epithet / Name	Collector's / Herbarium #	Location / Origin
TR055	atroviolaceum Holotype	AHS-8195 / MICH 12312	Josephine Co., Oregon (OR)
TR056	aurantio-olivaceum Holotype	AHS-17666 / MICH-12313	Olympic National Park, Clallam Co., Washington (WA)
TR057	manzanitae Holotype	TJB-4084 / MICH 12322	Sonoma Co., California (CA)
TR057b	manzanitae Holotype	TJB-4084 / MICH 12322	Sonoma Co., California (CA)
TR058	subumbrinum Holotype	AHS-17671 / MICH 12330	Olympic National Park, Clallam Co., Washington (WA)
TR059	murrillianum Holotype	WAM 1044 / NY 586560	Newport, Lincoln Co., Oregon (OR)
TR059b	murrillianum Holotype	WAM 1044 / NY 586560	Newport, Lincoln Co., Oregon (OR)
TR062	dryophilum Holotype	JM27 / NY 774992	Stanford University, Santa Clara Co., California (CA)
TR063	platyphyllum Holotype	WAM419 / NY 775009	Near Seattle, King Co., Washington (WA)
TR064	subcinereiforme Holotype	WAM901 / NY 775031	Corvallis, Benton Co., Oregon (OR)
TR065	californicum Holotype	JM125 / NY 775048	Jasper Ridge, near Stanford University, Santa Clara Co., California (CA)
TR066	pinicola Holotype	WAM730 / NY 775056	Tacoma, Pierce Co., Washington (WA)
TR067	farinaceum Holotype	WAM644 / NY 775058	Near Seattle, King Co., Washington (WA)
TR069	aff. pardinum (as pardinum)	SAT-01-292-13 / WTU-F-000504	Olympic National Park, Clallam Co., Washington (WA)
TR070	nigrum	SAT-00-314-38 / WTU-F-000660	Olympic National Park, Clallam Co., Washington (WA)
TR071	vaccinum	SAT-00-264-25 / WTU-F-000661	Olympic National Park, Clallam Co., Washington (WA)
TR072	subacutum (as virgatum)	SAT-00-298-26 / WTU-F-000662	Olympic National Park, Clallam Co., Washington (WA)
TR073	subacutum (as virgatum)	SAT-00-263-26 / WTU-F-000665	Olympic National Park, Clallam Co., Washington (WA)
TR074	atrofibrillosum (as sejunctum cf.)	SAT-09-254-08 / WTU-F-010258	Mitkof Island, Alaska (AK)
TR075	murrillianum	SAT-09-304-01 / WTU-F-010474	Camp Magruder, Tillamook Co., Oregon (OR)
TR076	marquettense	PBM2052 / WTU-F-012690	Olympic National Forest, Grays Harbor Co., Washington (WA)
TR077	platyphyllum	PBM814 / WTU-F-012695	Mason Co., Washington (WA)
TR078	platyphyllum	PBM2013 / WTU-F-012704	Mt. Rainier National Park, Pierce Co., Washington (WA)
TR079	equestre group (as flavovirens)	SAT-03-308-05 / WTU-F-012824	Camp Westwind, Lincoln Co., Oregon (OR)
TR080	aff. imbricatum (as imbricatum)	SAT-03-308-03 / WTU-F-012825	Camp Westwind, Lincoln Co., Oregon (OR)
TR081	megalophaeum (as sp. NS "big dark")	SAT-00-297-38a / WTU-F-047868	Olympic National Park, Jefferson Co., Washington (WA)
TR084	aff. bryogenum (as sulphureum)	SAT-00-324-03 / WTU-F-049202	Olympic National Park, Clallam Co., Washington (WA)
TR085	murrillianum	SAT-00-283-55 / WTU-F-049207	Olympic National Park, Clallam Co., Washington (WA)
TR087	platyphyllum (as inamoenum)	SAT-00-283-16 / WTU-F-049228	Olympic National Park, Clallam Co., Washington (WA)
TR088	focale	SAT-13-313-18 / WTU-F-063944	H.J. Andrews Experimental Forest, Willamette National Forest, Lane Co., Oregon (OR)

Habitat / Tree Assoc
Under conifers.
Old-growth conifer forest with Tsuga heterophylla, Pseudotsuga me
On soil under Arctostaphylos manzanita, or under Arbutus menziesii and evergreen Quercus.
On soil under Arctostaphylos manzanita, or under Arbutus menziesia and evergreen Quercus.
Old-growth conifer forest with Tsuga heterophylla, Pseudotsuga met
Coastal sand dune woodland with Pinus contorta and Picea sitchens
Coastal sand dune woodland with Pinus contorta and Picea sitchens
Under live oaks (Quercus agrifolia?).
"in woods."
In mixed woods.
Under oaks (Quercus agrifolia?).
"on much decayed, coniferous wood."
"in humus in woods."
Mixed conifer forest with Pseudotsuga menziesii, Tsuga heterophyll
Mixed conifer forest with Pseudotsuga menziesii, Tsuga heterophyll
Mixed conifer forest with Pseudotsuga menziesii, Abies amabilis, ar
Mixed conifer forest with Pseudotsuga menziesii and Tsuga heteroph
Montane mixed conifer forest with Pseudotsuga menziesii and Abies
Picea sitchensis -Tsuga forest.
Coastal sand dune woodland with Pinus contorta and Picea sitchens
Old-growth conifer forest with Picea sitchensis, Tsuga heterophylla,
On soil with Pseudotsuga menziesii and Tsuga heterophylla.
On soil with Pseudotsuga menziesii, Tsuga heterophylla, and Abies g
Coastal sand dune woodland with Pinus contorta and Picea sitchens
Coastal sand dune woodland with Pinus contorta and Picea sitchens
Old-growth conifer forest with Picea sitchensis, Tsuga heterophylla,
Mixed conifer forest with Pseudotsuga menziesii, Tsuga heterophyll
Mixed conifer forest with Pseudotsuga menziesii, Tsuga heterophyll
Mixed conifer forest with Pseudotsuga menziesii, Tsuga heterophyll
Mixed conifer forest with Pseudotsuga menziesii, Tsuga heterophyll

sociates	GenBank/ UNITE # (ITS)
	MN809568 /
menziesii, and Thuja plicata.	MN809569 /
iesii, Pseudotsuga menziesii,	MW597230 /
iesii, Pseudotsuga menziesii,	MN809570 /
menziesii, and Thuja plicata.	MN809571 /
iensis.	LT220179 / UDB024112
nensis.	MN809572 /
	Sequencing unsuccessful.
hylla, and Thuja plicata.	OM506546 /
hylla, and Thuja plicata.	MW597231 /
s, and A. lasiocarpa.	MW597232 /
rophylla.	MW597233 /
bies lasiocarpa.	MZ054354 /
	OM506547 /
nensis.	MW597234 /
vlla, Pseudotsuga menziesii, and Thuja plicata.	MZ054355 /
	OM506548 /
ies grandis.	OM506549 /
nensis.	MW597235 /
iensis.	MW597236 /
ella, and Pseudotsuga menziesii.	MW597237 /
hylla, and Thuja plicata.	MW597238 /
hylla, and Thuja plicata.	MW597239 /
hylla, and Thuja plicata.	MW597240 /
hylla, and Thuja plicata.	MW597241 /

Sample #	Species Epithet / Name	Collector's / Herbarium #	Location / Origin	
TR089	atrofibrillosum (as sejunctum cf.)	SAT-11-244-03 / WTU-F-065669	Chugach National Forest, near Cordova, Alaska (AK)	
TR090	moseri	SAT-11-154-01 / WTU-F-065670	Mt. Baker-Snoqualmie National Forest, Kittitas Co., Washington (WA)	
TR091	vaccinum	SAT-11-235-10 / WTU-F-065673	Girdwood, Alaska (AK)	
TR091b	vaccinum	SAT-11-235-10 / WTU-F-065673	Girdwood, Alaska (AK)	
TR093	lutescens (as sulphurescens)	SAT-11-241-08 / WTU-F-065768	Chugach National Forest, Kenai Peninsula, Alaska (AK)	
TR093b	lutescens (as sulphurescens)	SAT-11-241-08 / WTU-F-065768	Chugach National Forest, Kenai Peninsula, Alaska (AK)	
TR095	vernaticum	SAT-11-133-03 / WTU-F-065848	Deschutes National Forest, Jefferson Co., Oregon (OR)	
TR096	ammophilum (as populinum)	SAT-10-241-07 / WTU-F-065863	Girdwood, Alaska (AK)	
TR097	lutescens (as sulphurescens)	SAT-11-217-10 / WTU-F-065905	Chena Lakes Recreation Area, near Fairbanks, Alaska (AK)	
TR099	badicephalum (as focale)	SAT-10-236-14 / WTU-F-066121	Chugach National Forest, Kenai Peninsula, Alaska (AK)	
TR100	sp. "turpescens"	NS-22-IV-2014 / UC-2023282	Mt. Shasta, Siskiyou Co., California (CA)	
TR101	sp. "white manzanitae" CA343	CA343 / UC-2023277	Yuba Co., California (CA)	
TR102	sp CA389	CA389 / UC-2023278	Not reported.	
TR103	aff. pardinum (as pardinum)	E.Cline 03-X-2015 / WTU-F-073035	Washington (WA)	
TR106	fulvum s.l.	ADP 151003-1 / WTU-F-073036	Heart of the Hills, Olympic National Park, Clallam Co., Washington (WA)	
TR107	argyraceum s.l. (as terreum)	ADP 150918-3 / WTU-F-073037	Slate Creek Trail, Colville National Forest, Pend Oreille Co., Washington (WA)	
TR108	aurantio-olivaceum	ADP 141028-1 / WTU-F-073038	Road FR 190 south of Hwy 31, Colville National Forest, Pend Oreille Co., Washington (WA)	
TR109	mutabile (as nigrum)	ADP 151002-1 / WTU-F-073039	Olympic National Park, Clallam Co., Washington (WA)	
TR110	mutabile	ADP 141014-1 / WTU-F-073040	Idaho Panhandle National Forests,, Bonner Co., Idaho (ID)	
TR111	aff. olivaceotinctum (as squarrulosum)	ADP 151103-1 / WTU-F-073041	Colville National Forest, Pend Oreille Co., Washington (WA)	
TR112	dulciolens (as caligatum)	CH-16-285-01 / WTU-F-073042	Mt. Baker-Snoqualmie National Forest, Pierce Co., Washington (WA)	
TR113	<i>focale</i> (as <i>focale</i> group)	SAT-16-237-22 / WTU-F-073043	Chugach National Forest, Kenai Peninsula, Alaska (AK)	
TR114	subannulatum (as dryophilum)	SAT-16-318-01 / WTU-F-073044	Ashland, Jackson Co., Oregon (OR)	
TR115	badicephalum (as focale group)	SAT-16-238-15 / WTU-F-073045	Chugach National Forest, Kenai Peninsula, Alaska (AK)	
TR116	badicephalum (as focale group)	SAT-16-237-23 / WTU-F-073046	Chugach National Forest, Kenai Peninsula, Alaska (AK)	
TR117	moseri	SAT-13-151-03 / WTU-F-073047	Valley Co., Idaho (ID)	
TR118	atrofibrillosum Holotype (as sejunctum cf.)	SAT-16-244-15 / WTU-F-073048	Girdwood, Alaska (AK)	
TR119	apium	SAT-16-319-05 / WTU-F-073049	Honeyman State Park, Lane Co., Oregon (OR)	
TR120b	vaccinum	SAT-10-309-01 / WTU-F-073050	Deception Pass State Park, Island Co., Washington (WA)	

Habitat / Tree Asso
Picea sitchensis - Tsuga forest.
Mixed conifer forest with Pinus ponderosa, Pseudotsuga menziesi
Picea sitchensis -Tsuga forest, with occasional Alnus and Populus
Picea sitchensis -Tsuga forest, with occasional Alnus and Populus
Mixed forest - mostly <i>Picea glauca/sitchensis</i> , <i>Tsuga</i> , <i>Populus treat trichocarpa</i> and occasional <i>Alnus</i> .
Mixed forest - mostly <i>Picea glauca/sitchensis</i> , <i>Tsuga</i> , <i>Populus treat trichocarpa</i> and occasional <i>Alnus</i> .
Montane mixed conifer forest with Pinus ponderosa, Pseudotsuga
Picea sitchensis -Tsuga forest, with occasional Alnus and Populus
Picea glauca - Betula papyrifera forest.
Mixed forest - mostly <i>Picea glauca/sitchensis</i> , <i>Populus tremuloide trichocarpa</i> and occasional <i>Alnus</i> .
Pinus ponderosa, P. lambertiana, and Abies concolor.
Not reported.
Mixed forest with Neolithocarpus densiflorus.
Not reported.
Mixed forest with Pseudotsuga menziesii, Tsuga heterophylla, Abi
Mixed conifer forest with Abies, Thuja plicata, Picea engelmannin
Mixed forest with Pseudotsuga menziesii, Abies grandis, Tsuga he
Old-growth mixed conifer forest with <i>Pseudotsuga menziesii</i> , <i>Tsug</i> and <i>Thuja plicata</i> .
Under Tsuga.
Mixed conifer forest.
Mixed conifer forest with Pseudotsuga menziesii, Tsuga heterophy
Mixed forest - mostly <i>Picea glauca/sitchensis</i> , <i>Populus tremuloida</i> <i>trichocarpa</i> and occasional <i>Alnus</i> .
Under Quercus garryana.
Mixed forest - mostly <i>Picea glauca/sitchensis</i> , <i>Tsuga</i> , and <i>Betula p</i> and occasional <i>Alnus</i> .
Mixed forest - mostly <i>Picea glauca/sitchensis</i> , <i>Populus tremuloide trichocarpa</i> and occasional <i>Alnus</i> .
Mixed conifer forest with <i>Pinus ponderosa</i> , <i>Pseudotsuga menziest</i> and <i>Abies grandis</i> .
Picea sitchensis -Tsuga forest, with occasional Alnus and Populus
On sandy soil with Pseudotsuga menziesii, Tsuga heterophylla, Pi
Mixed conifer forest with <i>Pseudotsuga menziesii</i> , <i>Tsuga heterophy</i> and <i>Acer macrophyllum</i> .

sociates	GenBank/ UNITE # (ITS)
	MW597242 /
esii, Larix occidentalis, and Abies grandis.	MW597243 /
lus trichocarpa.	MZ054356 /
us trichocarpa.	MW597244 /
tremuloides, and Betula papyrifera, with Populus	MW597245 /
tremuloides, and Betula papyrifera, with Populus	MW597246 /
ga menziesii, and Abies concolor.	MW597247 /
lus trichocarpa.	MW597248 /
	MW597249 /
ides, and Betula papyrifera, with Populus	MW597250 /
	MW597251 /
	MW597252 /
	MW597253 /
	MW597254 /
Abies grandis, Alnus rubra.	MW597255 /
nii, Larix occidentalis, and Tsuga.	MW597256 /
heterophylla, Pinus, and Thuja plicata.	MW597257 /
suga heterophylla, Picea sitchensis,	MW597258 /
	MW597259 /
	MW597260 /
ohylla, Abies grandis, and Thuja plicata.	MW597261 /
ides, and Betula papyrifera, with Populus	MW597262 /
	MW597263 /
la papyrifera, with Populus trichocarpa	MW597264 /
ides, and Betula papyrifera, with Populus	MW597265 /
esii, Larix occidentalis, Populus tremuloides,	MW597266 /
lus trichocarpa.	MW597267 /
Picea sitchensis, Pinus contorta, and Alnus rubra.	MW597268 /
phylla, Thuja plicata, Abies grandis, Alnus rubra,	MW597269 /

Sample #	Species Epithet / Name	Collector's / Herbarium #	Location / Origin	
TR121	argyraceum s.l. (as sp. "Stanford gray")	SAT-17-040-02 / WTU-F-073051	Nojoqui County Park, Santa Barbara Co., California (CA)	
TR122	vaccinum (as sp.)	SAT-16-238-16 / WTU-F-073052	Chugach National Forest, Kenai Peninsula, Alaska (AK)	
TR123	saponaceum s.l. (as saponaceum)	SAT-16-237-20 / WTU-F-073053	Chugach National Forest, Kenai Peninsula, Alaska (AK)	
TR124	equestre group	SAT-15-217-05 / WTU-F-073054	Coconino National Forest, north of Flagstaff, Arizona (AZ)	
TR125	dryophilum Epitype	SAT-17-041-02 / WTU-F-073055	Near San Marcos Pass, Santa Barbara Co., California (CA)	
TR126b	atroviolaceum (as sp.)	ADP 071006-2 / WTU-F-073056	Idaho Panhandle National Forests, Priest Lake, Bonner Co., Idaho (ID)	
TR127	moseri	ADP 160430-3 / WTU-F-073057	Colville National Forest, Pend Oreille Co., Washington (WA)	
TR128	vaccinum	ADP 161011-1 / WTU-F-073058	Colville National Forest, Pend Oreille Co., Washington (WA)	
TR129	subannulatum (as pessundatum group)	04MWB111008 / WTU-F-073059	Klickitat Co., Washington (WA)	
TR130	saponaceum s.l. (as saponaceum)	ADP 130521-2 / WTU-F-073060	Colville National Forest, Pend Oreille Co., Washington (WA)	
TR131b	atroviolaceum	ADP 121018-1 / WTU-F-073061	Colville National Forest, Pend Oreille Co., Washington (WA)	
TR132	atroviolaceum	ADP 081006-1 / WTU-F-073062	Idaho Panhandle National Forests, Priest Lake, Bonner Co.,Idaho (ID)	
TR133	<i>aurantio-olivaceum</i> (as <i>aurantio-olivaceum</i> cf.)	ADP 161109-2 / WTU-F-073063	Colville National Forest, Pend Oreille Co., Washington (WA)	
TR135	fulvum s.l. (as pessundatum group)	SAT-17-300-01 / WTU-F-073064	Oregon Dunes National Recreation Area, Oregon (OR)	
TR137	equestre group (as arvernense cf.)	SAT-06-291-02 / WTU-F-073065	Gifford Pinchot National Forest, Washington (WA)	
TR138	dulciolens (as caligatum group)	NS-3162 / WTU-F-073066	Chugach National Forest near Sterling, Kenai Peninsula, Alaska (AK)	
TR139	fulvum s.l.	SAT-14-239-11 / WTU-F-073067	Chugach National Forest, Kenai Peninsula, Alaska (AK)	
TR140	inamoenum (as inamoenum group)	SAT-14-238-15 / WTU-F-073068	Chugach National Forest, Kenai Peninsula, Alaska (AK)	
TR143	nigrum (as nigrum cf.)	SAT-15-289-11 / WTU-F-073070	Southwestern Olympic Peninsula, Washington (WA)	
TR144	aff. pardinum (as pardinum)	SAT-13-314-01 / WTU-F-073071	H.J. Andrews Experimental Forest, Willamette National Forest, Lane Co., Oregon (OR)	
TR145	fulvum s.l. (as pessundatum group)	SAT-08-242-10 / WTU-F-073072	Chugach National Forest, near Cordova, Alaska (AK)	
TR146	smithii	SAT-18-234-15 / WTU-F-073073	Cibola National Forest, New Mexico (NM)	
TR147	japonicum (as sp. NS3319)	NS-3319 / WTU-F-073074	Near Tonga Ridge Trailhead, Skykomish, King Co., Washington (WA)	
TR148	aff. hemisulphureum (as sp. "coaltar")	SAT-15-229-06 / WTU-F-073075	Cibola National Forest, New Mexico (NM)	
TR149	argyraceum s.l. (as sp. "Stanford gray")	NS-3518 / WTU-F-073076	Stanford University, Santa Clara Co., California (CA)	
TR150	lutescens (as sulphurescens)	SAT-14-238-14 / WTU-F-073077	Chugach National Forest, Kenai Peninsula, Alaska (AK)	
TR151	<i>lutescens</i> Holotype (as <i>sulphurescens</i> )	SAT-14-239-16 / WTU-F-073078	Chugach National Forest, Kenai Peninsula, Alaska (AK)	

Habitat / Tree Ass
With Quercus agrifolia.
Mixed forest - mostly <i>Picea glauca/sitchensis</i> , <i>Tsuga</i> , and <i>Betula</i> and occasional <i>Alnus</i> .
Mixed forest - mostly <i>Picea glauca/sitchensis</i> , <i>Populus tremuloid trichocarpa</i> and occasional <i>Alnus</i> .
Mixed forest with <i>Populus tremuloides</i> , <i>Pinus ponderosa</i> , <i>Pinus</i> and <i>Pseudotsuga menziesii</i> .
With Quercus agrifolia.
Mixed conifers.
Mixed conifer forest with Pinus contorta, Abies grandis, Pinus n
Mixed conifer forest, mostly Tsuga.
With Quercus garryana.
With Tsuga, Abies, and Pinus.
Mixed conifer forest with Picea engelmannii, Abies grandis, Tsu
With Tsuga.
Mixed forest with Pseudotsuga menziesii, Abies grandis, Tsuga
Coastal sand dune woodland with Pinus contorta and Picea sitch
Mixed conifer forest with Pseudotsuga menziesii and Tsuga heter
In moss, under Picea.
Mixed forest - mostly <i>Picea glauca/sitchensis</i> , <i>Populus tremuloid</i> <i>trichocarpa</i> and occasional <i>Alnus</i> .
In mixed forest with Picea, Betula, Populus tremuloides, and shr
Mixed conifer forest with Pseudotsuga menziesii, Tsuga heteroph
Mixed conifer forest with <i>Pseudotsuga menziesii</i> , <i>Tsuga heteropi</i> grandis/concolor, Acer macrophyllum, and Alnus rubra.
Picea sitchensis -Tsuga forest.
With Picea engelmannii, Populus tremuloides, Abies concolor, a
Mixed conifer forest with Tsuga menziesii, T. heterophylla, and A
With Picea engelmannii, Populus tremuloides, Abies concolor, a
With Quercus agrifolia.
In mixed forest with Picea, Betula, Populus tremuloides, and shr
Mixed forest - mostly <i>Picea glauca/sitchensis</i> , <i>Tsuga</i> , <i>Populus tr trichocarpa</i> and occasional <i>Alnus</i> .

ociates	GenBank/ UNITE # (ITS)
	MW597270 /
papyrifera, with Populus trichocarpa	MW597271 /
es, and Betula papyrifera, with Populus	MW597272 /
trobiformis, Abies concolor, Picea engelmannii,	MW597273 /
	MW597274 /
	MW597275 /
onticola, and Pseudotsuga menziesii.	MW597276 /
	MW597277 /
	MW597278 /
	MW597279 /
a heterophylla, and Thuja plicata.	MW597280 /
	MW597281 /
eterophylla, Pinus, and Thuja plicata.	MW597282 /
ensis.	MW597283 /
pphylla.	MW597284 /
	MW597285 /
es, and Betula papyrifera, with Populus	MW597286 /
b Alnus.	MW597287 /
vlla, and Thuja plicata.	MW597288 /
vlla, and Thuja plicata, plus occasional Abies	MW597289 /
	MW597290 /
d Pseudotsuga menziesii.	MW597291 /
bies amabilis.	MW597292 /
d Pseudotsuga menziesii.	MW597293 /
	MW597294 /
b Alnus.	MW597295 /
muloides, and Betula papyrifera, with Populus	MW597296 /

TR152 v			
	vaccinum	SAT-13-275-05 / WTU-F-073079	Along Seward Highway about 10 miles west of Girdwood, Alaska (AK)
TR153 v	venenatoides (as venenatum)	RH18-1009 / Diamond Lake Ranger District, Umpqua National Forest, Douglas Co., Oregon (0	
TR154 n	megalophaeum (as sp. NS "big dark")	NS-18-XI-2016 / WTU-F-073080	Spruce Grove, Davison Rd., Redwood National Park, Humboldt Co., California (CA)
TR156 v	venenatum Holotype	/ CUP-A-022573	Near Detroit, Michigan (MI)
TR157 n	moseri Holotype	M-8521 / F-C0002152F	D.F.: Paseo de Cortés, Mexico (MEX)
TR158 4	Amillaria badicephala Holotype	/ NY 00657605, 00657606	Newport, Lincoln Co., Oregon (OR)
TR159 s	sp.	SAT-19-299-08 / WTU-F-073081	From display, Mt. Pisgah Arboretum Mushroom Festival, Springfield, Lane Co., Oregon (OR)
<sup>a</sup> Sequence <200 bp in length so not eligible for submission to GenBank.			

#### **APPENDIX 2.** Details of materials and methods.

**DNA** extraction and ITS sequencing (UW, Tacoma).—The genomic DNA was initially extracted from dried basidiome tissue using the cetyltrimethylammonium bromide (CTAB) protocol described by Gardes and Bruns (1993) with the following modifications: the volume of CTAB lysis buffer was reduced from 300  $\mu$ L to 100  $\mu$ L, autoclaved plastic micropestles were used (Sigma, St. Louis, Missouri, USA), and the DNA extract was re-suspended in TE (10 mM Tris, 1 mM ethylenediaminetetraacetic acid (EDTA), pH 8.0). Extracted DNA samples were stored at -40 C for future analysis.

To obtain ITS sequences from these samples, we utilized various approaches depending on the condition of the sample. For samples less than 5 yr old, we used the primers ITS-1 (forward sequence: TCCGTAGGTGAACCTGCGG) and ITS-4 (reverse sequence: TCCTCCGCTTATTGATATGC) (White et al. 1990). For samples more than 5 yr old, the ITS was sequenced in two portions to minimize the impact of DNA degradation due to age. This made it possible to obtain partial sequence data in some cases when

the entire template region was no longer intact. The first half was amplified using primers ITS-1 (forward) and 5.8S (reverse sequence: CGCTGCGTTCTTCATCG), while the latter half was amplified using primers 5.8SR (forward sequence: TCGATGAAGAACGCAGCG) and ITS-4 (reverse), using primer sequences from https://sites.duke.edu/vilgalyslab/rdna primers for fungi/.

PCR was performed in a total volume of 25 μL, containing a 1:1000 dilution of the DNA extract, 200 µM each of dATP, dTTP, dCTP, dGTP, 200 nM of each primer, 2.5 mM MgCl<sub>2</sub>, 0.05 unit µL-1 of GoTaq<sup>®</sup> DNA Polymerase (ProMega), and Green GoTaq® Reaction Buffer (ProMega). Each run of PCR included a positive control and a sterile water negative control. PCR was carried out using an Eppendorf Flexlid Mastercycler<sup>®</sup> Nexus Gradient Thermal Cycler. Reaction conditions were as follows: an initial 2 min at 95 C, 40 1-min cycles at 95 C, 1 min at 55 C, 2 min at 72 C, followed by a final extension of 5 min at 72 C. Success of the PCR was measured via gel electrophoresis, using 1% agarose gels prepared with a 0.5x Sodium Bromide buffer

Habitat / Tree Ass
Picea sitchensis-Tsuga heterophylla forest with Betula, Populus t
Mixed conifer forest.
Mixed conifer forest with Picea sitchensis.
With hardwoods.
Sparse woodland with Pinus hartwegii.
Coastal sand dune woodland under Picea sitchensis.
Mixed conifer forest.

and SYBR<sup>®</sup> Safe DNA Gel Stain (Thermo Fisher Scientific).

DNA extraction and ITS sequencing (Molecular Solutions LLC).—The genomic DNA was extracted using a buffer containing Chelex resin (Di Bonito et al. 1995, Liu et al. 2015). Fungal tissue was placed in a microcentrifuge tube with 400 µL of Chelex buffer (100 mM Tris pH = 8.5, 4% Chelex 100 [Bio-Rad Laboratories, Hercules, California], and 1% Triton X-100). The tubes were heated to 95-99 C for 20 min, vortexed briefly, then frozen. After thawing, the tubes were centrifuged and the supernatant was used in PCR.

PCR was performed in 25-µL reactions with 1 µL basidiome extract, 0.4 mM each primer, 0.2mM dNTP mixture, 5 µg bovine serum albumin, and 0.5 U OneTag Hot Start DNA polymerase (New England Biolabs, Ipswich, Massachusetts) in 1X OneTaq standard buffer with 2.1 mM MgCl<sub>2</sub>. PCR conditions were 94 C for 30 s, followed by 36 cycles of 94 C for 15 s, 57 C for 30 s, and 68 C for 60 s, followed by a final extension at 68 C for 5 min.

Generally, the primers ITS1f (Gardes and Bruns 1993) and ITS4 were used. Some

ociates	GenBank/ UNITE # (ITS)
remuloides, and Alnus.	MW597297 /
	MW597298 /
	MW597299 /
	(a) /
	MW597300 /
	Sequencing unsuccessful.
	MW597301 /

specimens, particularly the older ones, were contaminated with mycotrophic fungi, leading to the generation of contaminant sequences or unreadable chromatograms. We designed a Tricholoma-specific forward primer, tri1 (CATTATTGAATAAGCTTGGTTRGGTT), that targeted the 5' end of the Tricholoma ITS1 region. The primer tri1, used with ITS4, proved to be helpful in retrieving sequences from specimens where the universal primers failed. Seventeen of the sequences generated in this study were from tri1 amplicons.

For each ITS fragment, the forward and reverse sequences were inspected and assembled using Sequencher 5 (Gene Codes, Ann Arbor, Michigan). All sequences were deposited in GenBank.

Phylogenetic analysis.—Sequences were aligned using MAFFT 7 (Katoh and Toh 2008; http://mafft.cbrc.jp/alignment/server/) using the Q-INS-i strategy and edited and manually adjusted in AliView 1.11 (Larsson 2014). Regions of the dataset with ambiguous alignments were excluded.

The aligned sequence set was analyzed using two methods: (i) maximum likelihood analyses (ML) using RAxML 8.2.9 (Stamatakis 2014), with GTRCAT

approximation across different gene partitions, and executing 1000 rapid bootstrap replicates; (ii) Bayesian inference (BI) analyses using MrBayes 3.2.6, implementing the GTR + GAMMA + I model (Ronquist et al. 2012). Two independent runs were executed. The default number of chains (four) and heating parameters were used. To ensure convergence of the two independent runs, we examined the standard deviation of split frequencies and potential scale reduction factors (PSRFs) for all model parameters following recommendations in the MrBayes user manual. Posterior probabilities were calculated after burning the first 25% of the posterior sample and ensuring that this threshold met the convergence factors described above.

Initially we ran the analysis for 25 million generations sampling trees every 2500 steps.

**APPENDIX 3.** ITS sequences obtained from GenBank and other sources and included in the phylogenetic analyses.

Epithet or Name	Label	Collector's/Herbarium #	Location/Origin
acerbum	LT000005	JV99-638 / C-F-41483	Denmark (DNK)
acerbum	LT000134	MC00-204 / C-F-96223	Slovenia (SVN)
aestuans	LT000006	JV02-540 / C-F-40955	Denmark (DNK)
aestuans	LT000007	MC94-008 / C-F-59265	Denmark (DNK)
aestuans Neotype	LT000153	MC97-072 / C-F-58885 CFT-0401	Sweden (SWE)
albobrunneum	LT000077	MC99-060 / C-F-96268	France (FRA)
albobrunneum	UDB001218	JV04-471 /	Sweden (SWE)
album	KU058506	TFB13753 / TENN-F-065130	Belgium (BEL)
album	LT000008	MC95-159 / C-F-96254	Denmark (DNK)
album	LT000135	MC01-201 / C-F-96234	Slovenia (SVN)
album	MC08109	MC08-109 /	Denmark (DNK)
ammophilum (as populinum)	KC146366	ATCC 64509 / DAVFP 23587	British Columbia, CAN (BC)
ammophilum (as populinum)	SAT-16-237-12	SAT-16-237-12 / WTU-F-073083	Chugach National Forest, Kenai Peninsula, Alaska (AK)
apium	LT000009	JV00-215 / C-F-41884	Denmark (DNK)
apium	LT000118	MC98-034 / C-F-59207	Norway (NOR)
apium	LT000154	JHC95-049 / C-F-35189	Sweden (SWE)
argyraceum (as scalpturatum)	LT000004	JHC93-243 / C-F-96206	Denmark (DNK)
argyraceum	LT000010	JHC95-112 / C-F-35092	Denmark (DNK)
argyraceum	LT000011	JHC96-244 / C-F-96212	Denmark (DNK)
argyraceum	LT000127	MC03-251 / C-F-96245	Slovakia (SVK)
argyraceum	LT000155	JHC97-092 / C-F-96213	Sweden (SWE)
argyraceum	LT000156	JHC97-174 / C-F-96215	Sweden (SWE)
argyraceum Epitype	LT000198	MEN94-91 / L0374886	Netherlands (NLD)
argyraceum aff. (as intermedium var. macrosporum)	AF377202	KMS397 / SFSU	Sierra Co., California, USA (CA)

Are We Using the Right Names?

However, the average standard deviation of split frequencies did not reach <0.01 until 15 million samples had been generated. Thus, we continued the analysis for an additional 10 million steps (so 35 million total) and set the sumt burnin to 15 000 001 after these had concluded. PRSFs were 1.000 to 1.002 for all parameters by this stage. Twentyeight thousand two trees were read after this

Habitat/Tree Associates	GenBank/UNITE # (ITS)	Source
Under Fagus and Quercus.	LT000005 / UDB001474	Heilmann-Clausen et al 2017
On calcareous soils with Quercus.	LT000134 / UDB002361	Heilmann-Clausen et al 2017
Under Picea.	LT000006 / UDB000779	Heilmann-Clausen et al 2017
Under Pinus sylvestris.	LT000007 /	Heilmann-Clausen et al 2017
Conifer forest on nutrient-poor sandy soils with Pinus and Picea.	LT000153 / UDB001434	Heilmann-Clausen et al 2017
On nutrient-poor soil with Pinus.	LT000077 / UDB001444	Heilmann-Clausen et al 2017
On nutrient-poor soil with Pinus.	/ UDB001218	Morten Christensen, unpublished.
In deciduous angiosperm forest with Quercus.	KU058506 /	Sánchez-García & Matheny 2017
Under Quercus and Corylus on clay soil.	LT000008 /	Heilmann-Clausen et al 2017
Under Quercus.	LT000135 / UDB001413	Heilmann-Clausen et al 2017
Under Quercus and Corylus on clay soil.	/	Morten Christensen, unpublished.
Populus trichocarpa rhizosphere.	KC146366 /	P. Gujjari et al, unpublished.
Mixed forest - mostly <i>Picea glauca/sitchensis</i> , <i>Populus tremuloides</i> , and <i>Betula papyrifera</i> , with <i>Populus trichocarpa</i> and occasional <i>Alnus</i> .	MW597140 /	N. Siegel & K. Mohatt, The mycota of Alaska, unpublished.
On nitrogen-poor sandy soil with Pinus mugo.	LT000009 / UDB001685	Heilmann-Clausen et al 2017
Under Pinus sylvestris.	LT000118 /	Heilmann-Clausen et al 2017
On nitrogen-poor sandy soil with Pinus.	LT000154 / UDB001467	Heilmann-Clausen et al 2017
Under Fagus sylvatica on clayish soil.	LT000004 / UDB000784	Heilmann-Clausen et al 2017
Under Betula.	LT000010 / UDB000780	Heilmann-Clausen et al 2017
Under Betula.	LT000011 / UDB000781	Heilmann-Clausen et al 2017
Under Fagus.	LT000127 / UDB001419	Heilmann-Clausen et al 2017
On nutrient-rich soil in mixed woodland.	LT000155 / UDB000782	Heilmann-Clausen et al 2017
On nutrient-rich soil in mixed woodland.	LT000156 / UDB001692	Heilmann-Clausen et al 2017
On nutrient-rich soil in mixed woodland.	LT000198 / UDB000785	Heilmann-Clausen et al 2017
Mixed conifer forest with <i>Pseudotsuga menziesii</i> , <i>Pinus</i> , and <i>Abies</i> .	AF377202 /	Bidartondo & Bruns 2002

burnin, and PPs were calculated from 21 002 total trees (75% of the trees read) from the two runs.

*Dermoloma magicum* was chosen as outgroup for the analyses based on Sánchez-García and Matheny (2017). We consider bootstrap values (BS)  $\geq$ 70% and Bayesian posterior probabilities (PP)  $\geq$ 0.95 to indicate strong support.

Epithet or Name	Label	Collector's/Herbarium #	Location/Origin
Armillaria caligata var. glaucescens	AF309522	HN2633 / DUKE 0350245	Buncombe Co., North Carolina, USA (NC)
Armillaria caligata var. glaucescens	KU058510	PBM3899 / TENN-F-067754	Transylvania Co., North Carolina, USA (NC)
arvernense	AKFF-004-14	AKFF-004-14 / Pending	Chugach National Forest, Kenai Peninsula, Alaska (AK)
arvernense	KU058507	ADP-081004-1 /	Near Tango Creek and shore of Priest Lake, Idaho, USA (ID)
arvernense	LT000078	MC98-120 / C-F-59255	France (FRA)
arvernense	LT000119	MC98-020/C-F-59200	Norway (NOR)
arvernense	LT000157	MC95-102 / C-F-59014	Sweden (SWE)
arvernense	MF034215	/ MB-002876	Austria (AUT)
arvernense	MF034264	/ DBG-18239	Mary Jane Ski Lift , Grand Co., Colorado (CO)
arvernense (as psammopus)	JQ888219	DG-30 /	Scotland, United Kingdom (GBR)
arvernense (as sejunctum)	FJ845448	SMI291 /	British Columbia, CAN (BC)
atrodiscum cf.	KU058508	MSG132 / TENN-F-070702	Great Smoky Mountains National Park, North Carolina, USA (NC)
atrofibrillosum (as sejunctum)	AF349691	KMS285 / SFSU-F-034071	California, USA (CA)
atrofibrillosum (as subsejunctum)	NS1908	NS1908 / Pending	Girdwood, Alaska (AK)
atrosquamosum	LT000120	/ O-F-64018	Norway (NOR)
atrosquamosum	MF034275	/ DBG-24009	Fraser Experimental Forest, Arapaho National Forest, Grand Co., Colorado (CO)
atrosquamosum	MF034279	/ DBG-27983	Fraser Experimental Forest, Arapaho National Forest, Grand Co., Colorado (CO)
atroviolaceum	AY750166	C44 EC253 / WTU-F-056406	Washington, USA (WA)
atroviolaceum	KU058509	MSG167 / TENN-F-070701	Pierce Co., Washington, USA (WA)
aurantium	AF377233	HDT-54945 / SFSU-F-032915	California, USA (CA)
aurantium	DQ367919	OUC-99349 /	Southern Interior Forest Region, British Columbia, CAN (BC)
aurantium	LT000012	MC97-227 / C-F-59330	Denmark (DNK)
aurantium	LT000100	MC96-303 / C-F-59329	Italy (ITA)
auratum	HM590867	AuFr1 /	France (FRA)
auratum	HM590868	AuFr2 /	France (FRA)
auratum	HM590869	AuFr3 /	France (FRA)
badicephalum (as focale group)	NS1894	NS1894 / Pending	Hope, Kenai Peninsula, Alaska (AK)
badicephalum (as robustum)	AB078341	Not reported.	Not reported.
badicephalum (as robustum)	AB289664	TR 1 /	Nagano, Japan (JPN)
badicephalum (as robustum)	AB699668	KB1 /	Nagano, Japan (JPN)

Habitat/Tree Associates
Not reported.
Mixed Quercus forest under Q. prinus.
Mixed forest - mostly <i>Picea glauca/sitchensis</i> , <i>Populus tremuloides</i> , and <i>Betula papyrifera</i> , with <i>Populus trichocarpa</i> and occasional <i>Alnus</i> .
Scattered under Tsuga heterophylla.
Unknown; specimen acquired at an exhibition.
On nutrient-poor soil with Pinus.
On sandy soil with Pinus sylvestris.
Montane forest with Fagus, Picea abies, and Abies alba.
Montane forest with Picea engelmannii and Abies lasiocarpa.
Pinus sylvestris plantation forest.
Southern boreal forest on relatively nutrient-poor soils with <i>Pinus</i> , <i>Abies</i> , and <i>Picea</i> .
Montane forest with Picea, Abies, and Betula.
Not reported.
Picea sitchensis-Tsuga forest with heavy moss groundcover
On calcareous soil in mixed woodland.
Montane forest with Picea engelmannii and Abies lasiocarpa.
Montane forest with Pinus contorta, Pseudotsuga menziesii, Picea engelmannii, and Populus tremuloides.
Harvested area in foothill conifer forest dominated by <i>Pseudotsuga menziesii</i> .
Mixed conifer forest with <i>Abies procera</i> , <i>Pseudotsuga menziesii</i> , and <i>Tsuga</i> .
Not reported.
Mature montane forest with <i>Pseudotsuga menziesii</i> and <i>Betula papyrifera</i> .
On calcareous soil under Fagus.
Under Quercus ilex and Q. cerris.
Sand dunes under Pinus pinaster.
Sand dunes under Pinus pinaster.
Sand dunes under Pinus pinaster.
Mixed forest with Betula, Picea, Tsuga, and Populus.
Not reported.
Not reported.
Pinus densiflora forest.

	GenBank/UNITE # (ITS)	Source
	AF309522 /	Chapela & Garbelotto 2004
	KU058510 /	Sánchez-García & Matheny 2017
ı	OM506539 /	N. Siegel & K. Mohatt, The mycota of Alaska, unpublished.
	KU058507 /	This study.
	LT000078 / UDB001438	Heilmann-Clausen et al 2017
	LT000119 / UDB002362	Heilmann-Clausen et al 2017
	LT000157 /	Heilmann-Clausen et al 2017
	MF034215 /	Reschke et al 2018
	MF034264 /	Reschke et al 2018
	JQ888219 / UDB001669	Pickles et al 2012
	FJ845448 /	Kranabetter et al 2009
	KU058508 /	Sánchez-García & Matheny 2017
	AF349691 /	Bidartondo & Bruns 2001
	OM506545 /	N. Siegel & K. Mohatt, The mycota of Alaska, unpublished.
	LT000120 /	Heilmann-Clausen et al 2017
	MF034275 /	Reschke et al 2018
	MF034279 /	Reschke et al 2018
	AY750166 /	Cline et al 2005.
esii,	KU058509 /	Sánchez-García & Matheny 2017
	AF377233 /	Bidartondo & Bruns 2002
	DQ367919 /	Durall et al 2006
	LT000012 / UDB001471	Heilmann-Clausen et al 2017
	LT000100 / UDB001470	Heilmann-Clausen et al 2017
	HM590867 /	Moukha et al 2013
	HM590868 /	Moukha et al 2013
	HM590869 /	Moukha et al 2013
	OM506544 /	N. Siegel & K. Mohatt, The mycota of Alaska, unpublished.
	AB078341 /	H. Murata, unpublished.
	AB289664 /	Kikuchi et al 2007
	AB699668 /	Ota et al 2012

Epithet or Name	Label	Collector's/Herbarium #	Location/Origin
basirubens	LT000001	MC01-209 / C-F-96240	Croatia (HRV)
basirubens	LT000158	TL5303 / C-F-38408	Sweden (SWE)
batschii	LT000002	MC01-200 / C-F-96233	Croatia (HRV)
bonii	LT000013	JHC91-721 / C-F-96201	Denmark (DNK)
bonii	LT000102	MEN96-112 / L0354472	Italy (ITA)
bonii Holotype	LT000101	/ LUG-F-8450	Italy (ITA)
boreosulphurescens	LT000159	SAE95-07 / C-F-59441	Sweden (SWE)
boreosulphurescens	LT000199	IK97-1187 / H6002040	Finland (FIN)
boreosulphurescens (as sulphurescens)	JF908737	JV05-IX-04 / MCVE-17159(1)	Finland (FIN)
boreosulphurescens (as sulphurescens)	JF908738	JV05-IX-04 / MCVE-17159(2)	Finland (FIN)
boreosulphurescens Holotype	O-F-187683	/ O-F-187683	Norway (NOR)
borgsjoeënse	LT000160	JHC95-067 / C-F-96211	Sweden (SWE)
borgsjoeënse	LT000161	JHC95-307 / C-F-96219	Sweden (SWE)
boudieri	LT000014	MC95-317 / C-F-59305	Denmark (DNK)
boudieri	MC08103	MC08-103 /	Denmark (DNK)
boudieri	MS2009_61644	MS2009-61644	Denmark (DNK)
boudieri (Epitype)	LT000136	MC01-600 / C-F-90092	Slovenia (SVN)
bresadolanum	LT000103	MC96-264 / C-F-59341	Italy (ITA)
bresadolanum	LT000104	MC96-265 / C-F-59342	Italy (ITA)
bresadolanum	LT000105	/ TRgmb00652	Italy (ITA)
bresadolanum	LT000162	CL94-166 / C-F-59442	Sweden (SWE)
<i>bryogenum</i> Holotype (as <i>sulphureum</i> )	AY462034	MC97-101 / C-F-59167	Sweden (SWE)
bryogenum Holotype	LT000163	MC97-101 / C-F-59167	Sweden (SWE)
caligatum	AB699667	/ SCM-B-5116	Spain (ESP)
caligatum	AB738885	NBRC 109036 / TFM-M-R107	Italy (ITA)
caligatum	AF309520	REH7321 / NY	Costa Rica (CRI)
caligatum	KC565866	CM030 / MPU028328	Algeria (DZA)
caligatum	LT000079	РН99-519 / С-F-96274	France (FRA)
caligatum	LT000152	JV07-451 / C-F-76630	Spain (ESP)
cedrotorum	MC99049	MC99-049 /	France (FRA)
cingulatum	LT000016	MC96-170 / C-F-59068	Denmark (DNK)
cingulatum	LT000128	MC03-252 / C-F-96246	Slovakia (SVK)
cingulatum	LT000200	MEN95-210 / L-MEN95210	Netherlands (NLD)
cingulatum Neotype	LT000015	MC96-134 / C-F-59057	Denmark (DNK)
colossus	LT000137	MC01-205 / C-F-96238	Slovenia (SVN)
colossus	LT000164	MC97-047 / C-F-59154	Sweden (SWE)
columbetta	FJ596909	CLO4550 / TENN-F-60893	Great Smoky Mountains National Park, Tennessee, USA (TN)

Habitat/Tree Associates
On calcareous soil with Quercus.
On calcareous soil with Quercus and Fagus.
On calcareous soil with Pinus.
Under <i>Pinus</i> , next to road.
Not reported.
Not reported.
On calcareous soil in boreal forest with Betula.
On calcareous soil in boreal forest with Betula.
Not reported.
Not reported.
In boreal forest with Betula.
On nutrient-rich soil with Picea.
On nutrient-rich soil with Picea.
Under Fagus and Quercus on calcareous soil.
Under Fagus on calcareous soil.
Under Fagus and Quercus.
In mixed woodland on calcareous soil.
Under Quercus.
Mixed deciduous woodland.
In Mediterranean forest under Quercus.
In Mediterranean forest under Quercus.
In mixed forests with Picea.
On calcareous soil under Picea.
On sand dune soil with <i>Pinus</i> .
Pinus pinea forest.
Not reported.
Quercus suber and Pinus halepensis forest.
In Mediterranean forest with Pinus.
In Mediterranean forest with Pinus.
Under Cedrus atlanticus.
Roadside under Salix.
Under Salix.
Under Salix.
On sandy soil under Salix.
Under Pinus.
Under <i>Pinus</i> in dry forest.
Not reported.

GenBank/UNITE # (ITS)	Source
LT000001 /	Heilmann-Clausen et al 2017
LT000158 /	Heilmann-Clausen et al 2017
LT000002 / UDB001412	Heilmann-Clausen et al 2017
LT000013 / UDB000811	Heilmann-Clausen et al 2017
LT000102 / UDB000791	Heilmann-Clausen et al 2017
LT000101 / UDB000790	Heilmann-Clausen et al 2017
LT000159 / UDB001475	Heilmann-Clausen et al 2017
LT000199 /	Heilmann-Clausen et al 2017
JF908737 /	Osmundson et al 2013
JF908738 /	Osmundson et al 2013
/	Heilmann-Clausen et al 2017
LT000160 /	Heilmann-Clausen et al 2017
LT000161 / UDB000807	Heilmann-Clausen et al 2017
LT000014 / UDB001428	Heilmann-Clausen et al 2017
/	Morten Christensen, unpublished.
/	Morten Christensen, unpublished.
LT000136 /	Heilmann-Clausen et al 2017
LT000103 / UDB000549	Heilmann-Clausen et al 2017
LT000104 / UDB000550	Heilmann-Clausen et al 2017
LT000105 /	Heilmann-Clausen et al 2017
LT000162 / UDB000792	Heilmann-Clausen et al 2017
AY462034 /	Comandini et al 2004
LT000163 /	Heilmann-Clausen et al 2017
AB699667 /	Murata et al 2013
AB738885 /	Murata et al 2013
AF309520 /	Chapela & Garbelotto 2004
KC565866 /	Benazza-Bouregba et al 2016
LT000079 / UDB000793	Heilmann-Clausen et al 2017
LT000152 /	Heilmann-Clausen et al 2017
/	Morten Christensen, unpublished.
LT000016 / UDB000544	Heilmann-Clausen et al 2017
LT000128 / UDB001420	Heilmann-Clausen et al 2017
LT000200 /	Heilmann-Clausen et al 2017
LT000015 / UDB000543	Heilmann-Clausen et al 2017
LT000137 / UDB001417	Heilmann-Clausen et al 2017
LT000164 / UDB001433	Heilmann-Clausen et al 2017
FJ596909 /	Hughes et al 2009

Epithet or Name	Label	Collector's/Herbarium #	Location/Origin
columbetta	MC07011	MC07-011 /	Poland (POL)
columbetta	MG773829	RAS212 / TENN-F-071792	Great Smoky Mountains National Park, North Carolina, USA (NC)
columbetta (as subresplendens)	KJ417319	SAT-10-279-01 / TENN-F-065679	Great Smoky Mountains National Park, North Carolina, USA (NC)
columbetta Neotype	LT000017	MC95-181 / C-F-58898	Denmark (DNK)
davisiae	KJ705248	/ 2346-QFB-25632	Quebec, CAN (QC)
davisiae	KJ705249	4689-HRL 1256	Amos, Quebec, CAN (QC)
davisiae cf.	KU058511	TFB13409 / TENN-F-061672	Great Smoky Mountains National Park, Tennessee, USA (TN)
Dermoloma magicum	KU058495	GG220904 / TENN-F-063736	Wales, United Kingdom (GBR)
Dermoloma sp.	KU058494	ECV4208 / TENN-F-065324	Great Smoky Mountains National Park, Tennessee, USA (TN)
Dermoloma sp.	KU058497	/ SAV4102	Slovakia (SVK)
dryophilum	AF377239	KMS362 / SFSU-F-032952	Marin Co., California, USA (CA)
dulciolens	JF908732	/ MCVE-14633	Italy (ITA)
dulciolens (as caligatum)	AF309523	HDT48319 / SFSU	Yuba Co., California, USA (CA)
dulciolens (as caligatum)	AF527373	/ DAVFP 26219	British Columbia, CAN (BC)
dulciolens Holotype	AB738883	/ H-7002022	Sweden (SWE)
elegans	KJ417316	PBM3142 / TENN-F-063711	New Zealand (NZL)
equestre	HM590870	EqFr1 /	France (FRA)
equestre	HM590871	EqFr2 /	France (FRA)
equestre	HM590872	EqFr3 /	France (FRA)
equestre	HM590873	EqFrPa /	France (FRA)
equestre	LT000018	MC94-027 / C-F-58886	Denmark (DNK)
equestre	LT000020	MC96-155 /	Denmark (DNK)
equestre cf.	LT000019	MC95-187 / C-F-96256	Denmark (DNK)
equestre group (as flavovirens group)	AKFF-078-14	AKFF-078-14 / Pending	Chugach National Forest, Kenai Peninsula, Alaska (AK)
equestre group (as flavovirens group)	AKFF-087-14	AKFF-087-14 / Pending	Chugach National Forest, Kenai Peninsula, Alaska (AK)
equestre group (as flavovirens)	AB036895	613 / NBRC 33142	Japan (JPN)
equestre group (as flavovirens)	AF349689	HDT-54614 / SFSU	New Mexico, USA (NM)
equestre group (as flavovirens)	AF458452	trh546 /	Oregon Dunes National Recreation Area, Oregon, USA (OR)
equestre group (as flavovirens)	AF458456	trh652 /	Oregon Dunes National Recreation Area, Oregon, USA (OR)
equestre group (as flavovirens)	DQ822834	KGP52 /	Marin Co., California, USA (CA)
equestre group (as flavovirens)	EU186292	AP19 /	Portugal (PRT)
equestre group (as flavovirens)	EU186304	FIPo4 (AP33) /	Portugal (PRT)
equestre group (as flavovirens)	EU186309	AP39 /	Portugal (PRT)

Habitat/Tree Associates
In rich forest of Quercus and Picea.
Under Tsuga canadensis and Betula.
Mixed woods with Quercus, Tsuga, etc.
Under Quercus.
Not reported.
Under Pinus banksiana.
Under Tsuga and Quercus.
Not reported.
Mixed woods - Tsuga, Quercus, Fagus, Pinus, etc.
Not reported.
With Quercus agrifolia.
Not reported.
Not reported.
Not reported.
Picea and Vaccinium myrtillus forest.
Under Nothofagus.
Hill forest under Pinus sylvestris.
Hill forest under Abies alba and Quercus pubescens.
Hill forest under conifers.
Not reported.
Under Pinus, Picea, and Tsuga.
On sandy soil under Pinus sylvestris and P. mugo.
On sandy soil under Pinus.
Mixed forest - mostly Picea glauca/sitchensis, Populus tremuloides, and Betula papyrifera, with Populus trichocarpa and occasional Alnus.
Mixed forest - mostly <i>Picea glauca/sitchensis</i> , <i>Populus tremuloides</i> , and <i>Betula papyrifera</i> , with <i>Populus trichocarpa</i> and occasional <i>Alnus</i> .
Pinus densiflora forest.
Not reported.
Coastal sand dune woodland with <i>Pinus contorta</i> and <i>Picea sitchensis</i> .
Coastal sand dune woodland with <i>Pinus contorta</i> and <i>Picea sitchensis</i> .
With Pinus muricata.
Not reported.
With conifers.
Not reported.

	GenBank/UNITE # (ITS)	Source
	/	Morten Christensen, unpublished.
	MG773829 /	This study.
	KJ417319 /	Sánchez-García et al 2014
	LT000017 / UDB001468	Heilmann-Clausen et al 2017
	KJ705248 /	Bérubé et al unpublished: The Quebec Mushroom Project
	KJ705249 /	Bérubé et al unpublished: The Quebec Mushroom Project
	KU058511 /	Sánchez-García & Matheny 2017
	KU058495 /	Sánchez-García & Matheny 2017
	KU058494 /	Sánchez-García & Matheny 2017
	KU058497 /	Sánchez-García & Matheny 2017
	AF377239 /	Bidartondo & Bruns 2002
	JF908732 /	Osmundson et al 2013
	AF309523 /	Chapela & Garbelotto 2004
	AF527373 /	Lim et al 2003
	AB738883 /	Murata et al 2013
	KJ417316 /	Sánchez-García et al 2014
	HM590870 /	Moukha et al 2013
	HM590871 /	Moukha et al 2013
	HM590872 /	Moukha et al 2013
	HM590873 /	Moukha et al, unpublished.
	LT000018 / UDB001508	Heilmann-Clausen et al 2017
	LT000020 / UDB001469	Heilmann-Clausen et al 2017
	LT000019 /	Heilmann-Clausen et al 2017
·	OM506540 /	N. Siegel & K. Mohatt, The mycota of Alaska, unpublished.
a	OM506542 /	N. Siegel & K. Mohatt, The mycota of Alaska, unpublished.
	AB036895 /	Murata et al 2013
	AF349689 /	Bidartondo & Bruns 2001
	AF458452 /	Thomas R. Horton, unpublished.
	AF458456 /	Thomas R. Horton, unpublished.
	DQ822834 /	Peay et al 2007
	EU186292 /	A. Portugal et al, unpublished.
	EU186304 /	Moukha et al 2013
	EU186309 /	A. Portugal et al, unpublished.

Epithet or Name	Label	Collector's/Herbarium #	Location/Origin
equestre group (as flavovirens)	EU186310	AP40 /	Portugal (PRT)
equestre group (as flavovirens)	KU058513	TFB13553 / TENN-F-062900	Sweden (SWE)
equestre var. pallidifolia	HM590874	EqFrW /	France (FRA)
equestre var. populinum	HM590875	EqFrPop /	France (FRA)
eucalypticum	KU058512	PBM3154 / TENN-F-066413	New South Wales, Australia (AUS)
eucalypticum	MC00248	MC00-248 /	Spain (ESP)
felschii	KU058527	MSG160 / TENN-F-070700	Cherokee National Forest, Tennessee, USA (TN)
felschii	MH704857	CLO-4562 /	Great Smoky Mountains National Park, Tennessee, USA (TN)
felschii	MH704862	CLO-5177 /	Ozark-St. Francis National Forest, Arkansas, USA (AR)
felschii Holotype	MH704855	AGF21 /	Costa Rica (CRI)
filamentosum	LT000129	MC03-242 / C-F-96243	Slovakia (SVK)
filamentosum	LT000138	JHC01-202 / C-F-96191	Slovenia (SVN)
filamentosum	LT000139	MC00-218 / C-F-96226	Slovenia (SVN)
filamentosum	LT000165	/ C-F-35924	Sweden (SWE)
filamentosum (as pardinum)	EF493302	UP177 /	Munich, Germany (DEU)
filamentosum (as pardinum)	JF908730	/ MCVE-14072	Italy (ITA)
filamentosum aff. (as sp. RAS373)	MT197008	RAS373 / TENN-F-074697	William Hastie Natural Area, Tennessee, USA (TN)
focale	AF241521	CBS 575.96	Not reported (Korea?)
focale	AF462639	trh597 /	Oregon Dunes National Recreation Area, Oregon, USA (OR)
focale	FJ845447	SMI260 /	British Columbia, CAN (BC)
focale	KJ705238	4502 /	Quebec, CAN (QC)
focale	LT000021	JV99-603 / C-F-41444	Denmark (DNK)
focale	LT000022	MC98-600 / C-F-96260	Denmark (DNK)
<i>focale</i> (as <i>focale</i> group)	NS1831	NS1831 / Pending	Chugach National Forest, Kenai Peninsula, Alaska (AK)
focale Neotype	LT000166	JV97-239 / C-F-27500 CFT-0398	Sweden (SWE)
forteflavescens Holotype	MF034207	/ KUN-HKAS-93511	China (CHN)
fracticum	AF377238	KMS436 / SFSU	California, USA (CA)
frondosae	JHC08045	JHC08-045 /	Denmark (DNK)
frondosae	LT000023	MC96-235 / C-F-59084	Denmark (DNK)
frondosae	LT000075	MC98-086 / C-F-59243	France (FRA)
frondosae	LT000140	MC00-225 / C-F-96227	Slovenia (SVN)
frondosae	LT000167	MC95-130 / C-F-59031	Sweden (SWE)
frondosae	LT000168	MC97-151 / C-F-59188	Sweden (SWE)
frondosae	LT000169	MC97-158 / C-F-59395	Sweden (SWE)

Habitat/Tree Associates
Not reported.
Under Populus and Betula.
Hill forest under Quercus pubescens.
Hill forest under Betula pendula and Populus sp.
Under Eucalyptus.
Under Eucalyptus in plantation on sandy soil.
On soil with Betula, Quercus, and Rhododendron.
Not reported.
Not reported.
Under Fagus sylvatica.
Under deciduous angiosperm trees.
Under Fagus sylvatica.
On calcareous soil under Fagus.
Mixed forest.
Not reported.
On ground in hardwood forest under Quercus, Fagus.
Not reported.
Coastal sand dune woodland with <i>Pinus contorta</i> and <i>Picea sitchensis</i> .
Southern boreal forest on relatively nutrient-poor soils with <i>Pinus</i> , <i>Abies</i> , and <i>Picea</i> .
Not reported.
On nutrient-poor sandy soil with Pinus.
On nutrient-poor sandy soil with Pinus.
Mixed forest - mostly <i>Picea glauca/sitchensis</i> , <i>Populus tremuloides</i> , and <i>Betula papyrifera</i> , with <i>Populus trichocarpa</i> and occasional <i>Alnus</i> .
On nutrient-poor sandy soil with Pinus.
With Quercus.
Not reported.
On clay soil under Populus.
Under Populus tremula.
In mixed forest with <i>Abies</i> , <i>Picea</i> , and deciduous angiosperm trees.
On nutrient-rich soil with Populus and Picea.
Under Picea, Pinus, and Populus.
On nutrient-rich soil with Populus and Picea.
On nutrient-rich soil under Populus tremula.

	GenBank/UNITE # (ITS)	Source
	EU186310 /	A. Portugal et al, unpublished.
	KU058513 /	Sánchez-García & Matheny 2017
	HM590874 /	Moukha et al 2013
	HM590875 /	Moukha et al 2013
	KU058512 /	Sánchez-García & Matheny 2017
	/	Morten Christensen, unpublished.
	KU058527 /	Sánchez-García & Matheny 2017
	MH704857 /	Ovrebo et al 2019
	MH704862 /	Ovrebo et al 2019
	MH704855 /	Ovrebo et al 2019
	LT000129 / UDB000803	Heilmann-Clausen et al 2017
	LT000138 / UDB000804	Heilmann-Clausen et al 2017
	LT000139 /	Heilmann-Clausen et al 2017
	LT000165 / UDB001506	Heilmann-Clausen et al 2017
	EF493302 /	Nygren et al 2008
	JF908730 /	Osmundson et al 2013
	MT197008 /	This study.
	AF241521 /	S.J. Suh & J.G. Kim, unpublished.
	AF462639 /	Thomas R. Horton, unpublished.
	FJ845447 /	Kranabetter et al 2009
	KJ705238 /	Bérubé et al unpublished: The Quebec Mushroom Project
	LT000021 / UDB001500	Heilmann-Clausen et al 2017
	LT000022 / UDB002364	Heilmann-Clausen et al 2017
<i>pa</i>	OM506543 /	N. Siegel & K. Mohatt, The mycota of Alaska, unpublished.
	LT000166 / UDB001501	Heilmann-Clausen et al 2017
	MF034207 /	Reschke et al 2018
	AF377238 /	Bidartondo & Bruns 2002
	/	Morten Christensen, unpublished.
	LT000023 / UDB001509	Heilmann-Clausen et al 2017
	LT000075 / UDB001504	Heilmann-Clausen et al 2017
	LT000140 /	Heilmann-Clausen et al 2017
	LT000167 /	Heilmann-Clausen et al 2017
	LT000168 /	Heilmann-Clausen et al 2017
	LT000169 / UDB002363	Heilmann-Clausen et al 2017

Epithet or Name	Label	Collector's/Herbarium #	Location/Origin
frondosae	TF98111	TF98-111 /	Denmark (DNK)
fucatum	LT000121	MC98-023 / C-F-59201	Norway (NOR)
fucatum Neotype	LT000170	MC97-149 / C-F-58980 CFT-0403	Sweden (SWE)
fulvum	KU058514	BPL304 / TENN-F-068348	Great Smoky Mountains National Park, Tennessee, USA (TN)
fulvum	KY744154	PBM3988 / TENN-F-068436	Mt. Mitchell State Park, North Carolina, USA (NC)
fulvum	KY777366	PBM3970 / TENN-F-068956	Great Smoky Mountains National Park, Tennessee, USA (TN)
fulvum	LT000080	MC98-078 / C-F-96259	France (FRA)
fulvum	LT000130	JHC03-019 / C-F-96193	Slovakia (SVK)
fulvum	LT000171	JHC04-251 / C-F-96195	Sweden (SWE)
fulvum aff.	KU058505	TFB14052 / TENN-F-065997	Macon Co., North Carolina, USA (NC)
fulvum s.l. (as muricatum)	AF458438	trh610 /	Not reported (probably Oregon)
fulvum s.l. (as pessundatum group)	SAT-16-244-03	SAT-16-244-03 / WTU-F-073082	Girdwood, Alaska (AK)
fulvum s.l. (as pessundatum)	FJ845446	SMI303 /	British Columbia, CAN (BC)
fulvum s.l. (as transmutans)	KJ705236	4499 /	Quebec, CAN (QC)
griseoviolaceum aff. (as saponaceum cf.)	HQ604757	BD 39 / UBC-F-09755	CAN (BC?)
guldeniae	KU058515	MSG131 / TENN-F-070705	Great Smoky Mountains National Park, North Carolina, USA (NC)
guldeniae	LT000070	JuV16997 / TUR-JuV16997	Finland (FIN)
guldeniae	LT000122	MC95-103 / C-F-96251	Norway (NOR)
hemisulphureum	LT000065	JV08-364 / C-F-96217	Estonia (EST)
highlandense Holotype	KY488549	HKAS-70192	China (CHN)
ilkkae	AB738881	/ SCM B-4205	Spain (ESP)
ilkkae	LT000172	MC98-602 / C-F-96261	Sweden (SWE)
ilkkae Holotype	LT222029	S-F513823 / UPS-F-513823	Sweden (SWE)
imbricatum	JV04469	JV04-469 /	Denmark (DNK)
imbricatum Neotype	LT000024	MC94-046 / C-F-59268 CFT-0394	Denmark (DNK)
<i>imbricatum</i> aff.	AF377242	KMS296 / SFSU-F-033251	California, USA (CA)
imbricatum aff. (as intermedium)	AF319434	KMS593 / SFSU-F-033249	California, USA (CA)
inamoenum	JN021105	/ TRTC156828	Algonquin Provincial Park, Ontario, CAN (ON)
inamoenum	LT000174	MC95-115 / C-F-59020	Sweden (SWE)
inamoenum (as platyphyllum)	FJ845445	SMI309 /	British Columbia, CAN (BC)
inamoenum Neotype	LT000173	JHC95-042 / C-F-35182 CFT-0399	Sweden (SWE)
inocybeoides	LT000025	MC03-229 / C-F-96242	Denmark (DNK)
inocybeoides	LT000026	MC95-152 / C-F-59272	Denmark (DNK)
inocybeoides	LT000027	MC96-172 / C-F-59094	Denmark (DNK)

Hakitat/Trac Associator	ConBonk/UNITE # (ITS)	Source
nabitat/ free Associates	Gendank/UNITE # (115)	Source
On nutrient-rich soil with <i>Populus</i> and <i>Picea</i> .	/	Morten Christensen, unpublished.
Under Picea.	LT000121 /	Heilmann-Clausen et al 2017
On calcareous soil under <i>Picea</i> .	LT000170 /	Heilmann-Clausen et al 2017
On soil near <i>Isuga canadensis</i> in mixed forest with <i>Betula</i> , <i>Fagus</i> , and <i>Rhododendron</i> .	KU058514 /	Sánchez-García & Matheny 2017
Montane forest under Abies.	KY744154 /	This study.
On soil and hardwood leaf litter in mixed forest of <i>Quercus</i> , <i>Pinus rigida</i> , <i>Betula</i> , and <i>Tsuga canadensis</i> .	KY777366 /	This study.
Mixed woods with Betula, Abies, and Picea.	LT000080 / UDB002365	Heilmann-Clausen et al 2017
Under Betula.	LT000130 / UDB001695	Heilmann-Clausen et al 2017
Mixed forest with Betula and Picea.	LT000171 / UDB001700	Heilmann-Clausen et al 2017
Not reported.	KU058505 /	Sánchez-García & Matheny 2017
Not reported.	AF458438 /	Thomas R. Horton, unpublished.
Picea sitchensis - Tsuga forest with heavy moss groundcover	MW597179 /	N. Siegel & K. Mohatt, The mycota of Alaska, unpublished.
Southern boreal forest on medium to relatively nutrient-rich soils with <i>Pinus</i> , <i>Abies</i> , and <i>Picea</i> .	FJ845446 /	Kranabetter et al 2009
Not reported.	KJ705236 /	Bérubé et al unpublished: The Quebec Mushroom Project
Not reported.	HQ604757 /	M. Berbee et al, unpublished.
Montane forest with Picea, Abies, and Betula.	KU058515 /	Sánchez-García & Matheny 2017
In moist Picea forest.	LT000070 / UDB001701	Heilmann-Clausen et al 2017
In moist Picea forest.	LT000122 /	Heilmann-Clausen et al 2017
In alvar with <i>Helianthemum</i> .	LT000065 /	Heilmann-Clausen et al 2017
Highland forest dominated by Pinus yunnanensis.	KY488549 /	Yang et al 2017
Abies alba forest.	AB738881 /	Murata et al 2013
Mixed conifer forest with Pinus and Picea.	LT000172 /	Heilmann-Clausen et al 2017
Conifer forest with Pinus sylvestris and scattered Picea.	LT222029 /	Heilmann-Clausen et al 2017
Roadside under Pinus.	/	Morten Christensen, unpublished.
Under Prunus and Pinus sylvestris.	LT000024 / UDB001421	Heilmann-Clausen et al 2017
Not reported.	AF377242 /	Bidartondo & Bruns 2002
Not reported.	AF319434 /	K.M. Shanks, unpublished.
Not reported.	JN021105 /	Dentinger et al 2011
In deep moss with Picea.	LT000174 / UDB001424	Heilmann-Clausen et al 2017
Southern boreal forest on medium to relatively nutrient-rich soils with <i>Pinus</i> , <i>Abies</i> , and <i>Picea</i> .	FJ845445 /	Kranabetter et al 2009
In deep moss with Picea.	LT000173 / UDB001688	Heilmann-Clausen et al 2017
On nutrient-rich soil with Betula.	LT000025 / UDB000783	Heilmann-Clausen et al 2017
On nutrient-rich soil with Betula.	LT000026 / UDB000537	Heilmann-Clausen et al 2017
Roadside with Populus canescens.	LT000027 / UDB000538	Heilmann-Clausen et al 2017

Epithet or Name	Label	Collector's/Herbarium #	Location/Origin
inocybeoides	LT000175	JHC95-072 / C-F-35211	Sweden (SWE)
inocybeoides	LT000176	MC97-060 / C-F-59159	Sweden (SWE)
japonicum	AB036900	MR27 /	Japan (JPN)
japonicum	AF204810	Тј 3 /	Japan (JPN)
joachimii	HM590876	JoFr / HM590876	France (FRA)
joachimii	LT000106	/ TRgmb00060	Italy (ITA)
joachimii	LT000177	MC98-603 / C-F-96262	Sweden (SWE)
josserandii	LT000081	MC99-053 / C-F-96266	France (FRA)
josserandii	LT000082	MC99-056 / C-F-96267	France (FRA)
lascivum	AF241513	/ CBS 100136	Switzerland (CHE)
lascivum	AF377206	MC99-197 / C-F-59446	Denmark (DNK)
lascivum	EU186281	AP61 / K(M) 125042	Not reported (Portugal?)
lascivum	LT000028	MC00-519 / C-F-96230	Denmark (DNK)
lascivum	LT000029	MC99-197 / C-F-59446	Denmark (DNK)
lascivum	LT000131	JHC03-020 / C-F-96194	Slovakia (SVK)
leucophyllum	EU597086	UBCOGTR0475s	British Columbia, CAN (BC)
luridum	MC13XXX	MC13-XXX /	Austria (AUT)
luridum	MF034217	/ MB-002901	Austria (AUT)
luridum	TF98119	TF98-119 /	France (FRA)
luteomaculosum	KU058516	CLO-4632 / TENN-F-061807	Great Smoky Mountains National Park, Tennessee, USA (TN)
luteomaculosum	MH704858	CLO-4623 /	Tennessee, USA (TN)
luteomaculosum aff.	AF458446	trh-914 /	Oregon, USA (OR)
luteomaculosum aff.	AF458447	trh-1033 /	Oregon, USA (OR)
luteomaculosum aff.	AF458448	trh-1187 /	Oregon, USA (OR)
luteomaculosum aff.	HM240543	/ UBC-F-19693	Capilano River Regional Park, North Vancouver, British Columbia, CAN (BC)
magnivelare	AF309539	ICh-AF309539	New England, USA
magnivelare	KJ705262	/ 2150-QFB-25947	Quebec, CAN (QC)
magnivelare Holotype	LT220177	/ NYS f2421	New York, USA (NY)
marquettense	MH704861	CLO-4912 /	Alabama, USA (AL)
matsutake	AF202772	Tm A-5 /	Japan (JPN)
matsutake	AF204806	Tm 33 /	Japan (JPN)
matsutake	AF204868	Tm 1 /	Japan (JPN)
matsutake	AY391712	TM25112.2 /	China (CHN)
matsutake	EU051918	Not reported	Not reported (China?)
matsutake	LT000071	JuV23362F / TUR-JuV23362F	Finland (FIN)
matsutake	LT000178	MC03-600 / C-F-96247	Sweden (SWE)

Habitat/Tree Associates	GenBank/UNITE # (ITS)	Source
On nutrient-rich soil with Betula and Populus.	LT000175 / UDB000796	Heilmann-Clausen et al 2017
In park under Betula.	LT000176 / UDB000539	Heilmann-Clausen et al 2017
Not reported.	AB036900 /	Reschke et al 2018
Not reported.	AF204810 /	Kikuchi et al 2000
Hill forest under Quercus pubescens.	HM590876 /	Moukha et al 2013
In dry Pinus forest on sandy soil.	LT000106 /	Heilmann-Clausen et al 2017
In dry Pinus forest on sandy soil.	LT000177 /	Heilmann-Clausen et al 2017
Under Cedrus and Pinus.	LT000081 / UDB000797	Heilmann-Clausen et al 2017
Under Cedrus and Pinus.	LT000082 / UDB000798	Heilmann-Clausen et al 2017
Not reported.	AF241513 /	S.J. Suh & J.G. Kim, unpublished.
Under Fagus.	AF377206 /	Bidartondo & Bruns 2002
Not reported.	EU186281 /	A. Portugal et al, unpublished.
On mull soil with Fagus.	LT000028 / UDB000005	Heilmann-Clausen et al 2017
Under Fagus.	LT000029 /	Heilmann-Clausen et al 2017
On mull soil with Fagus.	LT000131 / UDB001696	Heilmann-Clausen et al 2017
Not reported.	EU597086 /	Jones et al 2008
Mixed Fagus and Abies forest on calcareous bedrock.	/	Morten Christensen, unpublished.
Montane Fagus-Picea-Abies forest.	MF034217 /	Reschke et al 2018
Unknown; specimen acquired at an exhibition.	/	Morten Christensen, unpublished.
Scattered under Quercus, Tsuga, and Pinus strobus.	KU058516 /	Sánchez-García & Matheny 2017
Not reported.	MH704858 /	Ovrebo et al 2019
Not reported.	AF458446 /	Ovrebo et al 2019
Not reported.	AF458447 /	Ovrebo et al 2019
Not reported.	AF458448 /	Thomas R. Horton, unpublished.
Caespitose on very rotten log covered with soil. Western redcedar ( <i>Thuja plicata</i> ) and western Hemlock ( <i>Tsuga heterophylla</i> ) nearby.	HM240543 /	Reschke et al 2018
Not reported.	AF309539 /	Chapela & Garbelotto 2004
Not reported.	KJ705262 /	Bérubé et al unpublished: The Quebec Mushroom Project
Not reported.	LT220177 / UDB024110	Trudell et al 2017
Not reported.	MH704861 /	Ovrebo et al 2019
Not reported.	AF202772 /	Kikuchi et al 2000
Not reported.	AF204806 /	Kikuchi et al 2000
Not reported.	AF204868 /	Kikuchi et al 2000
Not reported.	AY391712 /	T. Sha et al, unpublished.
Not reported.	EU051918 /	H-M Tang et al, unpublished.
On nutrient-poor sandy soil with Pinus sylvestris.	LT000071 /	Heilmann-Clausen et al 2017
On nutrient-poor sandy soil with Pinus sylvestris.	LT000178 /	Heilmann-Clausen et al 2017

Epithet or Name	Label	Collector's/Herbarium #	Location/Origin
melleum Holotype	MF034210	/ KUN-HKAS-93514	China (CHN)
moseri	AF377211	KMS447 / SFSU	California, USA (CA)
murrillianum Epitype	KY660032	SAT-16-319-01 / WTU-F-068823	Oregon Dunes National Recreation Area, Oregon, USA (OR)
murrillianum (as magnivelare)	AB712395	CA1 / TFM M-L903	Canada (CAN)
murrillianum (as magnivelare)	AF309541	DED5372 / SFSU	Washington, USA (WA)
murrillianum (as magnivelare)	AF527369	/ DAVFP 26221	British Columbia, CAN (BC)
murrillianum (as magnivelare)	KF010164	JLF2815 /	Mendocino Co., California, USA (CA)
murrillianum Holotype	LT220179	WA Murrill 1044 / NY586560	Newport, Lincoln Co., Oregon (OR)
muscarioides Holotype	MF034208	/ KUN-HKAS-93512	China (CHN)
mutabile	AF349703	KMS428 / SFSU	Yuba Co., California, USA (CA)
mutabile	AF458444	trh-916 /	Oregon Dunes National Recreation Area, Oregon, USA (OR)
mutabile	AF458445	trh-1184 /	Oregon Dunes National Recreation Area, Oregon, USA (OR)
<i>mutabile</i> aff.	MH704860	CLO-4711 /	Texas, USA (TX)
olivaceoluteolum Holotype	MF034206	/ KUN-HKAS-93510	China (CHN)
olivaceoluteolum aff. (as sejunctum)	EU819447	JMP0091 /	Wisconsin, USA (WI)
olivaceotinctum	LT000179	JHC95-070 / C-F-35209	Sweden (SWE)
olivaceotinctum	LT000180	KJ1993 / S-KJ1993	Sweden (SWE)
olivaceotinctum	LT000181	MC95-135 / C-F-59036	Sweden (SWE)
olivaceotinctum	LT000182	MC97-103 / C-F-59168	Sweden (SWE)
olivaceotinctum	LT000183	OP1981 / UPS-OP1981	Sweden (SWE)
olivaceum Holotype	MF034209	/ KUN-HKAS-93513	China (CHN)
orirubens	LT000030	JHC93-261 / C-F-96208	Denmark (DNK)
orirubens	LT000031	MC97-258 / C-F-59427	Denmark (DNK)
orirubens	LT000107	MC96-301 / C-F-59365	Italy (ITA)
orirubens	LT000132	MC03-243 / C-F-96244	Slovakia (SVK)
orirubens	LT000141	JHC01-200 / C-F-96189	Slovenia (SVN)
orirubens	LT000202	MC98-214 / C-F-59315	England (GBR)
palustre	DQ494699	PBM2494 (AFTOL-ID 497) /	Massachusetts, USA (MA)
pardinum	AF377228	KMS197 / SFSU-F-033715	Salt Point State Park, Sonoma Co., California, USA (CA)
pardinum	DQ367921	/ OUC99350	British Columbia, CAN (BC)
pardinum	JF899575	/ DAVFP 28035	Western Canada (CAN)
pardinum	JV931023	JV93-1023 /	Switzerland (CHE)
pardinum	LT000142	JHC01-201 / C-F-96190	Slovenia (SVN)
pardinum	MF955178	/ UBC-F-32191	Whistler, British Columbia, CAN (BC)
pardinum	MG719952	PBM828 / WTU-F-012756	Yakima Co., Washington, USA (WA)

Habitat/Tree Associates
Mixed forest with Quercus.
Not reported.
Mixed woodland with abundant shore pine ( <i>Pinus contorta</i> var. <i>bolanderi</i> ) on dune sand.
Not reported.
Not reported.
Not reported.
Not reported.
Mixed woodland with abundant shore pine ( <i>Pinus contorta</i> var. <i>bolanderi</i> ) on dune sand.
Broad-leaved forests with Quercus and Lithocarpus spp.
Not reported.
Coastal sand dune woodland with <i>Pinus contorta</i> and <i>Picea sitchensis</i> .
Coastal sand dune woodland with <i>Pinus contorta</i> and <i>Picea sitchensis</i> .
Not reported.
Broad-leaved forests with Quercus and Lithocarpus spp.
Castanea-dominated forest.
Under Picea.
In Pinus forests or mixed forests with Pinus.
On base-rich soil with Fagus sylvaticus.
Under Fagus and Quercus.
Under Quercus ilex, Q. cerris, and Cupressus sempervirens.
Under Fagus sylvatica.
Under Fagus.
Under Fagus on calcareous soil.
Not reported.
Mixed forest with (among others) <i>Pseudotsuga menziesii</i> and <i>Notholithocarpus densiflorus</i> .
Not reported.
With Tsuga heterophylla.
Mixed Fagus and Abies forest on calcareous bedrock.
In mixed forest on calcareous soil.
Montane mixed conifer forest.
Under Abies, Thuja, Populus, Picea, Larix.

GenBank/UNITE # (ITS)	Source
MF034210 /	Reschke et al 2018
AF377211 /	Bidartondo & Bruns 2002
KY660032 /	Trudell et al 2017
AB712395 /	Ota et al 2012
AF309541 /	Chapela & Garbelotto 2004
AF527369 /	Lim et al 2003
KF010164 /	J.L. Frank, unpublished.
LT220179 / UDB024112	Trudell et al 2017
MF034208 /	Reschke et al 2018
AF349703 /	Bidartondo & Bruns 2001
AF458444 /	Ovrebo et al 2019
AF458445 /	Ovrebo et al 2019
MH704860 /	Ovrebo et al 2019
MF034206 /	Reschke et al 2018
EU819447 /	Palmer et al 2008
LT000179 / UDB000526	Heilmann-Clausen et al 2017
LT000180 / UDB000799	Heilmann-Clausen et al 2017
LT000181 / UDB000527	Heilmann-Clausen et al 2017
LT000182 / UDB000525	Heilmann-Clausen et al 2017
LT000183 / UDB000800	Heilmann-Clausen et al 2017
MF034209 /	Reschke et al 2018
LT000030 / UDB000523	Heilmann-Clausen et al 2017
LT000031 / UDB000521	Heilmann-Clausen et al 2017
LT000107 / UDB000522	Heilmann-Clausen et al 2017
LT000132 / UDB000801	Heilmann-Clausen et al 2017
LT000141 / UDB000524	Heilmann-Clausen et al 2017
LT000202 / UDB000520	Heilmann-Clausen et al 2017
DQ494699 /	Matheny et al 2006 (as aestuans).
AF377228 /	Bidartondo & Bruns 2002
DQ367921 /	Durall et al 2006
JF899575 /	S.H.A. Guichon, unpublished.
/	Morten Christensen, unpublished.
LT000142 / UDB000802	Heilmann-Clausen et al 2017
MF955178 /	M. Berbee et al, unpublished.
MG719952 /	Ovrebo & Hughes 2018

Epithet or Name	Label	Collector's/Herbarium #	Location/Origin
pardinum aff. (as huronense)	AF377229	KMS248 / SFSU-F-033187	California, USA (CA)
pessundatum Epitype	LT000032	JV04-482 / C-F-43780 CFT-0400	Denmark (DNK)
platyphyllum (as inamoenum)	AF377246	KMS249 / SFSU-F-033184	Patrick's Point State Park, Humboldt Co., California, USA (CA)
populinum	EF493259	UP603 /	Uppsala, Sweden (SWE)
populinum	JV08398	JV08-398 / C-F-76788	Estonia (EST)
populinum	LT000143	MC00-236 / C-F-96229	Slovenia (SVN)
populinum cf.	EU819446	JMP0090 /	Wisconsin, USA (WI)
portentosum	AF349686	KMS304 / SFSU-F-033823	California, USA (CA)
portentosum	EU186273	AP50 / K(M) 121539	Not reported.
portentosum	LT000033	JHC92-277 / C-F-96202	Denmark (DNK)
portentosum	LT000034	MC94-082 / C-F-58959	Denmark (DNK)
portentosum	LT000083	MC98-116 / C-F-59262	France (FRA)
portentosum	LT000144	MC00-206 / C-F-96224	Slovenia (SVN)
portentosum	LT000184	JHC04-431 / C-F-96197	Sweden (SWE)
portentosum Neotype	LT000035	MC96-156 / C-F-59053 CFT-0404	Denmark (DNK)
portentosum s.l. (as sp.)	AF349688	Ork2058 /	Sweden (SWE)
psammopus	LT000036	MC98-048 / C-F-59212	Denmark (DNK)
psammopus	LT000084	MC99-089 / C-F-96273	France (FRA)
psammopus	LT000108	MC96-345 / C-F-59324	Italy (ITA)
psammopus	LT000145	MC04-600 / C-F-96248	Slovenia (SVN)
quercetorum	LT000125	MC99-044 / C-F-96263	Portugal (PRT)
rapipes	LT000037	MC03-228 / C-F-96241	Denmark (DNK)
rapipes Epitype	LT000085	MC98-106 / C-F-59258 CFT-0406	France (FRA)
roseoacerbum	LT000072	IK88-1120 / H6002032	Finland (FIN)
roseoacerbum	LT000073	IK92-2945 / H6002034	Finland (FIN)
rufenum	LT000109	MC96-376 / C-F-59393	Italy (ITA)
saponaceum	DQ494700	PBM2514 (AFTOL 672) /	Massachusetts, USA (MA)
saponaceum	KU058517	TFB12328 / TENN-F-060376	Great Smoky Mountains National Park, Tennessee, USA (TN)
saponaceum	LT000038	/ C-F-23337	Denmark (DNK)
saponaceum	LT000039	JHC95-165 / C-F-35147	Denmark (DNK)
saponaceum	LT000040	JHC97-237 / C-F-96216	Denmark (DNK)
saponaceum	LT000041	JV87-682 / C-F-96218	Denmark (DNK)
saponaceum	LT000086	MC98-059 / C-F-59217	France (FRA)
saponaceum	LT000087	TF98-098 / C-F-96276	France (FRA)
saponaceum	LT000123	JHC00-049 / C-F-96188	Norway (NOR)
saponaceum	LT000133	JHC03-015 / C-F-96192	Slovakia (SVK)
saponaceum	LT000185	JHC04-429 / C-F-96196	Sweden (SWE)

Habitat/Tree Associates
Not reported.
On nutrient-poor sandy soil with Pinus.
Coastal conifer forest including Picea.
Mixed forest.
Under Populus tremula.
On nutrient-rich soil under Populus.
Castanea-dominated forest with <i>Populus</i> present in low abundance.
Not reported.
Not reported.
Under Tilia on clayish soil.
Under Pinus.
Unknown; specimen acquired at an exhibition.
Under Fagus sylvatica.
Under Fagus on rich soil.
Under Pinus sylvestris and P. mugo on sandy soil.
Not reported.
Under Larix on clayish soil.
Under Pinus.
Under Cupressus sempervirens.
Under Larix.
Under Quercus suber.
Under Fagus on calcareous soil.
Under Abies and Picea.
Under Pinus.
Under Pinus.
In Mediterranean woodland with Pinus and Quercus.
Not reported.
Under <i>Pinus rigida</i> , <i>P. strobus</i> , <i>P. pungens</i> , and <i>Tsuga</i> , plus occasional <i>Quercus</i> and <i>Carya</i> .
Under Tilia on clayish soil.
Under Fagus sylvatica.
On rich soil under Fagus.
Under Fagus sylvatica.
Under Fagus on non-calcareous soil.
Not reported.
Under Betula and Corylus on rich soil.
Under Fagus.
Under Fagus and Quercus on poor soil.

GenBank/UNITE # (ITS)	Source
AF377229 /	Bidartondo & Bruns 2002
LT000032 / UDB001502	Heilmann-Clausen et al 2017
AF377246 /	Bidartondo & Bruns 2001
EF493259 /	Nygren et al 2008
/	Morten Christensen, unpublished.
LT000143 / UDB001410	Heilmann-Clausen et al 2017
EU819446 /	Palmer et al 2008
AF349686 /	Bidartondo & Bruns 2001
EU186273 /	A. Portugal et al, unpublished.
LT000033 / UDB001686	Heilmann-Clausen et al 2017
LT000034 /	Heilmann-Clausen et al 2017
LT000083 /	Heilmann-Clausen et al 2017
LT000144 / UDB001409	Heilmann-Clausen et al 2017
LT000184 / UDB001698	Heilmann-Clausen et al 2017
LT000035 / UDB001429	Heilmann-Clausen et al 2017
AF349688 /	Bidartondo & Bruns 2001
LT000036 / UDB001472	Heilmann-Clausen et al 2017
LT000084 / UDB001503	Heilmann-Clausen et al 2017
LT000108 /	Heilmann-Clausen et al 2017
LT000145 /	Heilmann-Clausen et al 2017
LT000125 / UDB000795	Heilmann-Clausen et al 2017
LT000037 / UDB001418	Heilmann-Clausen et al 2017
LT000085 / UDB001439	Heilmann-Clausen et al 2017
LT000072 /	Heilmann-Clausen et al 2017
LT000073 /	Heilmann-Clausen et al 2017
LT000109 / UDB001432	Heilmann-Clausen et al 2017
DQ494700 /	Matheny et al 2006
KU058517 /	Sánchez-García & Matheny 2017
LT000038 / UDB001499	Heilmann-Clausen et al 2017
LT000039 / UDB001505	Heilmann-Clausen et al 2017
LT000040 / UDB001689	Heilmann-Clausen et al 2017
LT000041/ UDB001507	Heilmann-Clausen et al 2017
LT000086 /	Heilmann-Clausen et al 2017
LT000087 / UDB001498	Heilmann-Clausen et al 2017
LT000123 / UDB001693	Heilmann-Clausen et al 2017
LT000133 / UDB001694	Heilmann-Clausen et al 2017
LT000185 / UDB001697	Heilmann-Clausen et al 2017

Epithet or Name	Label	Collector's/Herbarium #	Location/Origin
saponaceum	LT000186	JHC04-439 / C-F-96198	Sweden (SWE)
saponaceum	MF034200	/ DBG-23531	Roosevelt National Forest, Boulder Co.,Colorado, USA (CO)
saponaceum	MF034202	/ DBG-23751	Roosevelt National Forest, Boulder Co.,Colorado, USA (CO)
saponaceum	SAT-16-237-07	SAT-16-237-07 / WTU-F-073084	Chugach National Forest, Kenai Peninsula, Alaska (AK)
saponaceum	SAT-16-237-14	SAT-16-237-14 / WTU-F-073085	Chugach National Forest, Kenai Peninsula, Alaska (AK)
saponaceum group	AKFF-082-14	AKFF-082-14 / Pending	Chugach National Forest, Kenai Peninsula, Alaska (AK)
scalpturatum	EU160590	JHC96-249 /	Denmark (DNK)
scalpturatum	LT000042	JHC93-263 / C-F-96210	Denmark (DNK)
scalpturatum	LT000043	JHC94-231 / C-F-35309	Denmark (DNK)
scalpturatum	LT000146	MC00-207 / C-F-96225	Slovenia (SVN)
scalpturatum (Neotype)	LT000187	MC95-165 / C-F-59399	Sweden (SWE)
sciodes	LT000044	MC94-007 / C-F-58902	Denmark (DNK)
sciodes	LT000045	MC95-182 / C-F-96255	Denmark (DNK)
sciodes	PAM14100601	PAM14100601	France (FRA)
sejunctum	LT000046	MC95-187 / C-F-58998	Denmark (DNK)
sejunctum	LT000110	MC96-314 / C-F-58979	Italy (ITA)
sinopardinum Holotype	KY488553	HKAS-58001	China (CHN)
sinoportentosum Holotype	MF034326	KUN-HKAS-46084	China (CHN)
smithii (as pardinum)	MF034205	/ DBG-25191	Roosevelt National Forest, Gilpin Co., Colorado, USA (CO)
smithii Holotype	MG719956	CLO-4510 /	New Mexico, USA (NM)
sp.	KJ417317	PBM3141 / TENN-F-063710	New Zealand (NZL)
sp.	KJ417318	PBM3085 / TENN-F-063664	New Zealand (NZL)
sp.	KU058525	PBM3168 / TENN-F-066438	Australia (AUS)
sp.	KU058526	PBM3170 / TENN-F-066434	Australia (AUS)
sp.	KU058528	PBM3144 / TENN-F-063713	New Zealand (NZL)
sp.	KY462348	СТ-4370 /	Argentina (ARG)
sp.	KY462372	CT-4439 /	Chile (CHL)
sp.	KY462373	CT-4441 /	Chile (CHL)
sp.	KY462382	СТ-4474 /	Chile (CHL)
sp.	KY462553	MES-1766 /	Chile (CHL)
sp.	KY462555	MES-1769 /	Chile (CHL)
sp.	KY462581	MES-1834 /	Chile (CHL)
sp.	KY462610	MES-1890 /	Argentina (ARG)
sp.	KY462692	MES-928 /	Chile (CHL)

Habitat/Tree Associates	GenBank/UNITE # (ITS)	Source
Under Fagus on rich soil.	LT000186 / UDB001699	Heilmann-Clausen et al 2017
Montane conifer forest with <i>Picea engelmannii</i> and <i>Abies concolor</i> .	MF034200 /	Reschke et al 2018
Montane conifer forest including Pseudotsuga menziesii.	MF034202 /	Reschke et al 2018
Mixed forest - mostly <i>Picea glauca/sitchensis</i> , <i>Populus tremuloides</i> , and <i>Betula papyrifera</i> , with <i>Populus trichocarpa</i> and occasional <i>Alnus</i> .	MW597135 /	N. Siegel & K. Mohatt, The mycota of Alaska, unpublished.
Mixed forest - mostly <i>Picea glauca/sitchensis</i> , <i>Populus tremuloides</i> , and <i>Betula papyrifera</i> , with <i>Populus trichocarpa</i> and occasional <i>Alnus</i> .	MW597142 /	N. Siegel & K. Mohatt, The mycota of Alaska, unpublished.
Mixed forest - mostly <i>Picea glauca/sitchensis</i> , <i>Populus tremuloides</i> , and <i>Betula papyrifera</i> , with <i>Populus trichocarpa</i> and occasional <i>Alnus</i> .	OM506541 /	N. Siegel & K. Mohatt, The mycota of Alaska, unpublished.
Under Fagus sylvatica.	EU160590 /	Jargeat et al 2010
Under Fagus sylvatica on clayish soil.	LT000042 / UDB000541	Heilmann-Clausen et al 2017
Under Fagus sylvatica.	LT000043 / UDB000542	Heilmann-Clausen et al 2017
Under Carpinus.	LT000146 /	Heilmann-Clausen et al 2017
In park under Betula.	LT000187 /	Heilmann-Clausen et al 2017
Under Fagus sylvatica.	LT000044 / UDB000547	Heilmann-Clausen et al 2017
Under Fagus sylvatica on clayish soil.	LT000045 / UDB000548	Heilmann-Clausen et al 2017
Under Fagus.	/	Morten Christensen, unpublished.
Under Fagus sylvatica on clayish soil.	LT000046 /	Heilmann-Clausen et al 2017
In decidous woodland dominated by Quercus.	LT000110 / UDB001431	Heilmann-Clausen et al 2017
Not reported.	KY488553 /	Yang et al 2017
Conifer forest with Picea and Pinus.	MF034326 /	Reschke et al 2018
Montane forest with Pinus contorta and Pseudotsuga menziesii.	MF034205 /	Reschke et al 2018
Not reported.	MG719956 /	Ovrebo & Hughes 2018
Nothofagus forest.	KJ417317 /	Sánchez-García et al 2014
Nothofagus forest.	KJ417318 /	Sánchez-García et al 2014
Under Eucalyptus.	KU058525 /	Sánchez-García & Matheny 2017
Under Eucalyptus.	KU058526 /	Sánchez-García & Matheny 2017
Nothofagus forest.	KU058528 /	Sánchez-García & Matheny 2017
Nothofagus pumilio (bosque de lenga).	KY462348 /	Truong et al 2017
Bosque Valdevieso with Nothofagus dombeyi.	KY462372 /	Truong et al 2017
Bosque Valdevieso with Nothofagus dombeyi.	KY462373 /	Truong et al 2017
Bosque Valdevieso with Nothofagus dombeyi.	KY462382 /	Truong et al 2017
Under Nothofagus pumilio (lenga)	KY462553 /	Truong et al 2017
Under Nothofagus pumilio (lenga)	KY462555 /	Truong et al 2017
Mixed Nothofagus dombeyi and N. obliqua forest.	KY462581 /	Truong et al 2017
Mixed Nothofagus dombeyi and N. pumilio forest.	KY462610 /	Truong et al 2017
Mixed forest with <i>Nothofagus dombeyi</i> , <i>N. alpina</i> , and mixed <i>Myrtaceae</i> .	KY462692 /	Truong et al 2017

Epithet or Name	Label	Collector's/Herbarium #	Location/Origin
sp.	KY462706	MES-997 /	Chile (CHL)
squarrulosum	LT000003	MC01-202 / C-F-96235	Croatia (HRV)
squarrulosum	LT000047	JHC93-224 / C-F-96205	Denmark (DNK)
squarrulosum	LT000048	JHC93-262 / C-F-96209	Denmark (DNK)
squarrulosum	LT000049	JHC95-169 / C-F-35151	Denmark (DNK)
squarrulosum	LT000088	MC98-081 / C-F-59238	France (FRA)
squarrulosum	LT000111	MC96-269 / C-F-59343	Italy (ITA)
squarrulosum	LT000147	MC01-700 / C-F-96239	Slovenia (SVN)
squarrulosum aff. (as atrosquamosum cf.)	AF349701	KMS435 / SFSU-F-032886	Santa Cruz Co., California, USA (CA)
stans	LT000124	MC98-018 / C-F-96258	Norway (NOR)
stans	LT000188	MC95-131 / C-F-59032	Sweden (SWE)
stans Epitype	LT000189	MC95-145 / C-F-59042 CFT-0396	Sweden (SWE)
stiparophyllum	LT000190	MC95-117 / C-F-96252	Sweden (SWE)
stiparophyllum (as lascivum)	AY573542	Trilas2IV /	Europe (Germany?)
subacutum (as argenteum)	KJ705253	4770-HRL 1337	Saint-Chrysostome, Quebec, CAN (QC)
subacutum (as terreum cf.)	DQ097883	OUC-99342 /	British Columbia, CAN (BC)
subacutum (as virgatum cf.)	AKFF-076-14	SAT-14-239-18 / WTU-F-073086	Chugach National Forest, Kenai Peninsula, Alaska (AK)
subacutum (as virgatum)	KU058522	MSG165 / TENN-F-070703	Pack Forest, Pierce Co., Washington, USA (WA)
subannulatum (as ustaloides)	AF377240	KMS324 / SFSU-F-034213	California, USA (CA)
subluteum	KJ705255	/ 2139-QFB-25830	Quebec, CAN (QC)
subluteum	KJ705256	3793 /	Quebec, CAN (QC)
subluteum	KU058519	MSG134 / TENN-F-070707	Great Smoky Mountains National Park, North Carolina, USA (NC)
subluteum (as leucophyllum)	JN021108	ALG-06-42 / TRTC-150955	Ontario, CAN (ON)
subsejunctum (as sejunctum aff.)	JN021102	/ TRTC156944	Algonquin Provincial Park, Ontario, CAN (ON)
subsejunctum (as sejunctum)	KU058518	MSG133 / TENN-F-070704	Great Smoky Mountains National Park, North Carolina, USA (NC)
subumbrinum	JQ711805	FFP509 /	British Columbia, CAN (BC)
sudum	LT000050	JV96-306 / C-F-96221	Denmark (DNK)
sudum Neotype	LT000051	MC98-601 / C-F-90094 CFT-0403	Denmark (DNK)
sulphurescens	JHC09050	JHC09-050 /	Sweden (SWE)
sulphurescens	LT000089	MC99-063 / C-F-96269	France (FRA)
sulphurescens	LT000112	MC96-296 / C-F-59362	Italy (ITA)
sulphurescens	MC12002	MC12-002 /	Italy (ITA)
sulphurescens	MH2013_643789	MH2013_643789 /	Denmark (DNK)
sulphurescens aff.	LT000113	TRgmb00062 / C-F-101489	Italy (ITA)

Habitat/Tree Associates
Under Nothofagus alpina
Under Quercus ilex.
Under Fagus sylvatica on clayish soil.
Under Fagus sylvatica on clayish soil.
Under Fagus sylvatica.
Under Picea and Abies on calcareous soil.
Under Quercus.
Under Fagus and Quercus.
Not reported.
On nutrient-poor soil with Pinus.
Under Pinus and Picea.
Under Pinus and Betula.
Under Betula.
Not reported.
Under Pinus rigida.
Not reported.
Mixed forest - mostly <i>Picea glauca/sitchensis</i> , <i>Populus tremuloides</i> , and <i>Betula papyrifera</i> , with <i>Populus trichocarpa</i> and occasional <i>Alnus</i> .
In moss in mixed conifer forest with <i>Pseudotsuga menziesii</i> and <i>Tsuga heterophylla</i> .
Not reported.
Not reported.
Not reported.
Montane forest with Picea, Abies, and Betula.
Not reported.
Not reported.
Montane forest with Picea, Abies, and Betula.
Pinus contorta forest.
On nutrient-poor sandy soil with Pinus.
On nutrient-poor sandy soil with Pinus.
Not reported.
Under Fagus and Quercus.
Under Quercus ilex.
Under Fagus on calcareous soil.
Under Fagus and Quercus on calcareous soil.
Not reported.

GenBank/UNITE # (ITS)	Source
KY462706 /	Truong et al 2017
LT000003 / UDB001414	Heilmann-Clausen et al 2017
LT000047 / UDB000532	Heilmann-Clausen et al 2017
LT000048 / UDB000530	Heilmann-Clausen et al 2017
LT000049 / UDB000786	Heilmann-Clausen et al 2017
LT000088 / UDB000529	Heilmann-Clausen et al 2017
LT000111 / UDB000531	Heilmann-Clausen et al 2017
LT000147 / UDB000528	Heilmann-Clausen et al 2017
AF349701 /	Bidartondo & Bruns 2001
LT000124 /	Heilmann-Clausen et al 2017
LT000188 / UDB001426	Heilmann-Clausen et al 2017
LT000189 / UDB001427	Heilmann-Clausen et al 2017
LT000190 /	Heilmann-Clausen et al 2017
AY573542 /	K. Krause & E. Kothe, unpublished.
KJ705253 /	Bérubé et al unpublished: The Quebec Mushroom Project
DQ097883 /	Durall et al, unpublished.
MW597129 /	N. Siegel & K. Mohatt, The mycota of Alaska, unpublished.
KU058522 /	Sánchez-García & Matheny 2017
AF377240 /	Bidartondo & Bruns 2002
KJ705255 /	Bérubé et al unpublished: The Quebec Mushroom Project
KJ705256 /	Bérubé et al unpublished: The Quebec Mushroom Project
KU058519 /	Sánchez-García & Matheny 2017
JN021108 /	Dentinger et al 2011
JN021102 /	Dentinger et al 2011
KU058518 /	Sánchez-García & Matheny 2017
JQ711805 /	Ovrebo et al 2019; Jones et al 2012
LT000050 / UDB001684	Heilmann-Clausen et al 2017
LT000051 / UDB002366	Heilmann-Clausen et al 2017
/	Morten Christensen, unpublished.
LT000089 / UDB002367	Heilmann-Clausen et al 2017
LT000112 / UDB000809	Heilmann-Clausen et al 2017
/	Morten Christensen, unpublished.
/	Morten Christensen, unpublished.
LT000113 /	Heilmann-Clausen et al 2017

Epithet or Name	Label	Collector's/Herbarium #	Location/Origin
sulphureum	AF377245	HO70098 / O	Norway (NOR)
sulphureum	AY462035	MC96-162 / C-F-59062	Denmark (DNK)
sulphureum	AY462036	MC94-023 / C-F-58914	Denmark (DNK)
sulphureum	AY462037	MC96-245 / C-F-59115	Denmark (DNK)
sulphureum	AY462038	MC95-188 / C-F-59292	Denmark (DNK)
sulphureum	AY462039	DED4539 / SFSU-F-034076	Florida, USA (FL)
sulphureum	EU819448	JMP0092 /	Wisconsin, USA (WI)
sulphureum	HQ650743	Not reported.	British Columbia, CAN (BC)
sulphureum	KM576674	LM2344 /	Romania (ROU)
sulphureum	KU058520	PBM3959 / TENN-F-068897	Great Smoky Mountains National Park, Tennessee, USA (TN)
sulphureum	LT000053	JHC07-236 / C-F-96199	Denmark (DNK)
sulphureum	LT000090	MC98-109 / C-F-59260	France (FRA)
sulphureum	LT000091	TF06-045 / C-F-96275	France (FRA)
sulphureum	LT000148	MC01-204 / C-F-96237	Slovenia (SVN)
sulphureum	LT000191	JHC08-049 / C-F-96200	Sweden (SWE)
sulphureum	LT000192	MC07-001 / C-F-101488	Sweden (SWE)
terreum	LT000057	JHC93-260 / C-F-96207	Denmark (DNK)
terreum	LT000058	JHC95-118 / C-F-35098	Denmark (DNK)
terreum	LT000059	JHC95-172 / C-F-35154	Denmark (DNK)
terreum	LT000060	TL11-317 / C-F-96277	Denmark (DNK)
terreum	LT000061	JHC93-222 / C-F-96204	Denmark (DNK)
terreum	LT000062	JV95-519 / C-F-96220	Denmark (DNK)
terreum	LT000092	MC99-071 / C-F-96271	France (FRA)
terreum	LT000093	MC99-074 / C-F-96272	France (FRA)
terreum	LT000116	MC05-200 / C-F-96249	Nepal (NPL)
terreum	LT000149	MC01-020 / C-F-96232	Slovenia (SVN)
terreum	LT000193	MC95-119 / C-F-96253	Sweden (SWE)
terreum	LT000201	MC98-209 / C-F-59313	Netherlands (NLD)
terreum Epitype	LT000098	MEN95-192 / L0374887	Germany (DEU)
tridentinum	LT000076	JV99-700 / C-F-96222	France (FRA)
triste	LT000066	JuV5271F / TUR-JuV5271F	Estonia (EST)
triste	LT000194	JHC97-169 / C-F-96214	Sweden (SWE)
triste	MF034270	/ DBG-22631	Pike National Forest, Teller Co., Colorado, USA (CO)
triste Neotype	LT000099	E3754 / L-E3754	Germany (DEU)
ulvinenii	LT000067	IK93-1613 / H6002036	Finland (FIN)
ulvinenii	LT000068	JuV13229F / TUR-JuV13229F	Finland (FIN)
ulvinenii	LT000069	JuV26740F / TUR-JuV26740F	Finland (FIN)

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Habitat/Tree Associates	GenBank/UNITE # (ITS)	Source
Not reported.	AF377245 /	Bidartondo & Bruns 2002
Under Fagus sylvaticus.	AY462035 /	Comandini et al 2004
Under Populus tremula and Quercus.	AY462036 /	Comandini et al 2004
Under Quercus.	AY462037 /	Comandini et al 2004
Under Fagus sylvaticus.	AY462038 /	Comandini et al 2004
Under Quercus and Pinus.	AY462039 /	Comandini et al 2004
Castanea-dominated forest.	EU819448 /	Palmer et al 2008
Southern boreal forest on relatively nutrient-rich soils with <i>Pinus, Abies,</i> and <i>Picea</i> .	HQ650743 /	Kranabetter et al 2009
Root of Quercus petraea.	KM576674 /	Suz et al 2014
Under Tsuga, Betula, Carya.	KU058520 /	Sánchez-García & Matheny 2017
Under Fagus on rich soil.	LT000053 /	Heilmann-Clausen et al 2017
Under Abies.	LT000090 / UDB001440	Heilmann-Clausen et al 2017
Not reported.	LT000091 /	Heilmann-Clausen et al 2017
Under Picea, Abies and Fagus.	LT000148/ UDB001416	Heilmann-Clausen et al 2017
Under Fagus on rich soil.	LT000191 /	Heilmann-Clausen et al 2017
Under Fagus sylvatica.	LT000192 /	Heilmann-Clausen et al 2017
Under Fagus and Corylus on clay soil.	LT000057 / UDB000536	Heilmann-Clausen et al 2017
Under Picea, Pinus, and Quercus.	LT000058 /	Heilmann-Clausen et al 2017
Under Pinus.	LT000059 / UDB000812	Heilmann-Clausen et al 2017
Under Abies and Picea on calcareous soil.	LT000060 / UDB000808	Heilmann-Clausen et al 2017
Under Fagus sylvatica on clayish soil.	LT000061 / UDB000534	Heilmann-Clausen et al 2017
Under Fagus sylvatica on rich soil.	LT000062 / UDB000535	Heilmann-Clausen et al 2017
Under Pinus.	LT000092 / UDB001445	Heilmann-Clausen et al 2017
Under Pinus.	LT000093 / UDB001446	Heilmann-Clausen et al 2017
Under Pinus wallichiana.	LT000116 / UDB002368	Heilmann-Clausen et al 2017
Under Pinus.	LT000149 / UDB001411	Heilmann-Clausen et al 2017
Under Populus and Pinus.	LT000193 / UDB001425	Heilmann-Clausen et al 2017
Under Pinus nigra on dune sands.	LT000201 / UDB000533	Heilmann-Clausen et al 2017
Under Pinus.	LT000098 / UDB000813	Heilmann-Clausen et al 2017
Under Cedrus and Pinus.	LT000076 / UDB000805	Heilmann-Clausen et al 2017
Not reported.	LT000066 /	Heilmann-Clausen et al 2017
Under <i>Picea</i> on rich soil.	LT000194 / UDB001691	Heilmann-Clausen et al 2017
Montane conifer forest with Salix, Populus tremuloides, Picea engelmannii, and Pinus flexilis.	MF034270 /	Reschke et al 2018
Under Pinus.	LT000099 / UDB000814	Heilmann-Clausen et al 2017
Not reported.	LT000067 /	Heilmann-Clausen et al 2017
Not reported.	LT000068 /	Heilmann-Clausen et al 2017
Not reported.	LT000069 /	Heilmann-Clausen et al 2017

Epithet or Name	Label	Collector's/Herbarium #	Location/Origin
umbonatum	JHC10055	JHC10-055 /	Denmark (DNK)
umbonatum	LT000063	MC00-A01 / C-F-96231	Denmark (DNK)
umbonatum	LT000114	TRgmb00651 / C-F-101490	Italy (ITA)
ustale	LT000064	JHC92-299 / C-F-96203	Denmark (DNK)
ustaloides	JV08135	JV08-135 /	Denmark (DNK)
ustaloides	LT000094	MC99-067 / C-F-96270	France (FRA)
ustaloides	LT000126	MC99-047 / C-F-96264	Portugal (PRT)
vaccinum	KU058521	TFB13554 / TENN-F-062901	Sweden (SWE)
vaccinum	LT000150	MC00-229 / C-F-96228	Slovenia (SVN)
vaccinum	LT000195	MC95-109 / C-F-59017	Sweden (SWE)
venenatoides (as venenatum)	AF377230	KMS396 / SFSU-F-031292	California, USA (CA)
venenatoides (as venenatum)	DQ367922	OUC99352 /	British Columbia, CAN (BC)
venenatoides (as venenatum)	MG719950	MK01140602 /	California, USA (CA)
venenatum	AY656986	Tricholoma #01 /	Coweeta Hydrologic Laboratory, Macon Co., North Carolina (NC)
vernaticum	AF377203	KMS246 / SFSU-F-034307	Not reported (probably CA)
virgatum	LT000151	MC01-203 / C-F-96236	Slovenia (SVN)
virgatum	LT000196	JHC95-063 / C-F-35203	Sweden (SWE)
virgatum Neotype	LT000197	MC97-164 / C-F-59398 CFT-0408	Sweden (SWE)
virgatum aff.	MC05201	MC05-201 /	Nepal (NPL)
viridilutescens (Type I)	LT000095	MC98-061 / C-F-59219	France (FRA)
viridilutescens (Type I)	LT000096	MC98-080 / C-F-59237	France (FRA)
viridilutescens (Type I)	LT000097	MC98-093 / C-F-59249	France (FRA)
viridilutescens (Type II)	UDB011588	VL-25.08.2009 / TU106550	Estonia (EST)
viridilutescens (Type II)	UDB011595	VL-10.09.2010 / TU106841	Estonia (EST)
viridilutescens (Type II) aff. (as sejunctum)	AB036899	NA12 /	Japan (JPN)?
viridiolivaceum	LT000117	MC96-002 / C-F-96257	New Zealand (NZL)

Habitat/Tree Associates
On calcareous soil under Fagus sylvatica.
On calcareous soil under Fagus sylvatica.
On calcareous soil under Fagus sylvatica.
On mineral-rich soil under Fagus sylvatica.
Under Fagus and Quercus near the coast.
Under Quercus and Fagus.
Under Quercus suber.
Under Populus and Betula.
On sandy nutrient-poor soil under Picea.
Roadside under Picea.
Not reported.
Not reported.
Not reported.
On root of Quercus rubra seedling in mixed mesic woodland.
Not reported.
Under Picea, Abies, and Fagus.
Under Picea.
Under Picea in moss-rich forest on calceous soil.
Under Tsuga and Abies in high montane forest.
Under Picea, Populus, Betula, and Quercus.
Under Picea, Abies and Fagus.
In mixed forest with Pinus and deciduous angiosperm trees.
Not reported.
Not reported.
Not reported.
Under Nothofagus solandri.

	GenBank/UNITE # (ITS)	Source
	/	Morten Christensen, unpublished.
	LT000063 / UDB002369	Heilmann-Clausen et al 2017
	LT000114 /	Heilmann-Clausen et al 2017
	LT000064 / UDB000551	Heilmann-Clausen et al 2017
	/	Morten Christensen, unpublished.
	LT000094 / UDB000815	Heilmann-Clausen et al 2017
	LT000126 / UDB000816	Heilmann-Clausen et al 2017
	KU058521 /	Sánchez-García & Matheny 2017
	LT000150 / UDB001511	Heilmann-Clausen et al 2017
	LT000195 / UDB001423	Heilmann-Clausen et al 2017
	AF377230 /	Bidartondo & Bruns 2002
	DQ367922 /	Durall et al 2006
	MG719950 /	Ovrebo & Hughes 2018
l.	AY656986 /	Walker et al 2005
	AF377203 /	Bidartondo & Bruns 2002
	LT000151 / UDB001415	Heilmann-Clausen et al 2017
	LT000196 / UDB000546	Heilmann-Clausen et al 2017
	LT000197 / UDB000545	Heilmann-Clausen et al 2017
	/	Morten Christensen, unpublished.
	LT000095 / UDB001436	Heilmann-Clausen et al 2017
	LT000096 / UDB001473	Heilmann-Clausen et al 2017
	LT000097 / UDB001437	Heilmann-Clausen et al 2017
	/ UDB011588	Heilmann-Clausen et al 2017
	/ UDB011595	Heilmann-Clausen et al 2017
	AB036899 /	H. Murata, unpublished.
	LT000117 /	Heilmann-Clausen et al 2017