

Diversity and taxonomy of *Tricholoma* species from Yunnan, China, and notes on species from Europe and North America

Kai Reschke, Flavius Popa, Zhu L. Yang & Gerhard Kost

To cite this article: Kai Reschke, Flavius Popa, Zhu L. Yang & Gerhard Kost (2018): Diversity and taxonomy of *Tricholoma* species from Yunnan, China, and notes on species from Europe and North America, *Mycologia*, DOI: [10.1080/00275514.2018.1512295](https://doi.org/10.1080/00275514.2018.1512295)

To link to this article: <https://doi.org/10.1080/00275514.2018.1512295>



Published online: 01 Nov 2018.



Submit your article to this journal [↗](#)




Article views: 29



View Crossmark data [↗](#)



Diversity and taxonomy of *Tricholoma* species from Yunnan, China, and notes on species from Europe and North America

Kai Reschke ^{a,b}, Flavius Popa^{a,c}, Zhu L. Yang^d, and Gerhard Kost^a

^aDepartment for Systematic Botany and Mycology, Faculty of Biology, University of Marburg, Karl-von-Frisch-Straße 8, 35032 Marburg, Germany; ^bDepartment of Mycology, Goethe University of Frankfurt am Main, Max-von-Laue Straße 13, 60439 Frankfurt am Main, Germany; ^cDepartment for Ecosystem Monitoring, Research & Wildlife Conservation, National Park Schwarzwald, Kniebisstraße 67, 72250 Freudenstadt Kniebis, Germany; ^dKey Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences, 650201 Kunming, China

ABSTRACT

Although taxonomic knowledge on *Tricholoma* (Agaricales, Basidiomycota) is fairly comprehensive in northwest Europe, knowledge of the global diversity and distribution of *Tricholoma* spp. is still sparse. In this study, the diversity and distribution of some *Tricholoma* spp. are analyzed by morphological and molecular methods based on 70 collections from Yunnan, China, 45 from central Europe, 32 from Colorado, USA, 9 from Japan, and 3 from Ukraine. A Holarctic distribution is suggested for several species, based on collections and nuc rDNA internal transcribed spacer ITS1-5.8S-ITS2 (ITS) sequences. Six species new to science are formally described from Yunnan: five in existing sections, *Tricholoma forteflavescens*, *T. olivaceoluteolum*, *T. melleum*, *T. olivaceum*, and *T. sinoportentosum*, and one, *T. muscarioides*, in the newly described section *Muscaria* alongside several previously described species. Additional putatively new species cannot be formally described because they lack sufficient material. *Tricholoma foliicola* is recognized as a species of the genus *Gerhardtia*.

ARTICLE HISTORY

Received 7 July 2017
Accepted 13 August 2018

KEYWORDS

Agaricales; biogeography; distribution; *Gerhardtia*; Holarctic; phylogeny; Tibet; Tricholomataceae; 7 new taxa

INTRODUCTION

Tricholoma was first introduced as a tribus of the broad genus *Agaricus* (Fries 1821). Since then, it has been restricted to ectomycorrhizal fungi with central stipitate, fleshy basidiomes with sinuate lamellae, and hyaline, smooth, and inamyloid basidiospores. *Tricholoma* (Fr.) Staude is the type genus of the conserved family Tricholomataceae R. Heim ex Pouzar (McNeill et al. 2006). The genus was demonstrated to be monophyletic by Sánchez-García et al. (2014). Its exact position among other genera of the Tricholomataceae is unknown because a molecular phylogeny of the Tricholomataceae with a well-supported backbone has not yet been published.

Fries divided *Agaricus* tribus *Tricholoma* mainly based on the characters of the pileal surface, initially into four sections (Fries 1821) and then later into seven (Fries 1874). The pileal surface and the cellular structure of the pileipellis, respectively, are also the main characters for classifications proposed in more modern treatments. Bon (1984) also used the color of the pileus and the presence/absence of clamps as important characters for the definition of seven sections of *Tricholoma*, which were further divided into

subsections, series, and stirps. Singer (1986) focused on the structure of the pileipellis and the presence/absence of clamps to divide the genus into four subgenera. These were further divided into nine sections and 13 stirps, taking into account color and odor (Singer 1986). Heilmann-Clausen et al. (2017) demonstrated that pileal color, structure of the pileipellis, presence/absence of clamps, and the size and shape of the basidiospores are delimiting characters of the sections supported by molecular phylogeny.

Important modern revisions of the genus in Europe include those of Gulden (1969), Bon (1984, 1991), Riva (1988, 2003), Christensen and Noordeloos (1999), and Noordeloos and Christensen (1999). Christensen and Heilmann-Clausen (2013) and Heilmann-Clausen et al. (2017) were the first to include molecular phylogenetic information based on nuc rDNA internal transcribed spacer ITS1-5.8S-ITS2 (ITS) sequences in their comprehensive treatments. Thus, the west European species diversity of *Tricholoma* is now relatively well studied. However, knowledge about the diversity and distribution of the genus on a global scale is largely lacking.

A monograph of North American *Tricholoma* spp. was published recently (Bessette et al. 2013), whereas a

more recent study dealt with sect. *Caligata* Bon (Trudell et al. 2017). However, the taxonomy of *Tricholoma* spp. in North America is still far from resolved. The application of taxa originally described from Europe on American specimens must be reassessed for many species. The status of many species described from North America is unclear. This is especially the case for many species described by Peck at the end of the 19th and in the early years of the 20th century (e.g., Peck 1875, 1891, 1900, 1904, 1912) and those described by Murrill in the first half of the 20th century (e.g., Murrill 1913, 1938, 1942, 1945, 1949). However, further research is underway to increase the knowledge concerning the taxonomy of *Tricholoma* spp. in North America (C. Ovrebo and S. Trudell, pers. comm.).

Tricholoma includes the most expensive edible agaric mushroom, *T. matsutake* (S. Ito & S. Imai) Singer, of high economic importance in several parts of Asia. Hence, many studies have focused on sect. *Caligata*, which comprises *T. matsutake* and closely related species (e.g., Yu et al. 2006; Murata et al. 2013b; Trudell et al. 2017). Some *Tricholoma* species were described from Japan by Kawamura (1954) and Hongo (1959, 1968, 1983, 1991), who also published an overview of the genus for Japan (Hongo 1988). A checklist from China based on an extensive review of collection lists is provided by Deng et al. (2004), with some refinements by Deng and Yao (2005a). Six of the ~40 listed accepted *Tricholoma* species were described from Asia, whereas the other species were originally described from Europe. Four new species were described since then from China: *T. lavendulophyllum* F.Q. Yu (Yu et al. 2006) from Yunnan, *T. sinoacerbum* T.H. Li et al. (Hosen et al. 2016) from Guangdong, as well as *T. highlandense* Zhu L. Yang et al. and *T. sinopardinum* Zhu L. Yang et al. from Yunnan and Tibet, respectively (Yang et al. 2017).

Little is known about the presence of *Tricholoma* spp. in adjacent countries. Two species were reported from Vietnam (Kiet 1998), whereas single species were reported from Laos (Wan et al. 2012), Thailand (Sanmee et al. 2007), and Bhutan (Wan et al. 2012). Several species were reported from India (Tanti et al. 2011; Gogoi and Sarma 2012; Khaund and Joshi 2013) and Nepal (Adhikari 2000). No records of *Tricholoma* spp. were located for Burma or Bangladesh.

Northern Yunnan in southwest China is part of one of the 25 biodiversity hot spots of the world (Myers et al. 2000), the south-central China hot spot, which is centered by the Hengduan Mountains. About 15 000 seed plant species are reported from Yunnan (Yang et al. 2004), although an inventory of the fungi is still far from complete. Yang et al. (2004) reported about

7000 species of fungi for Yunnan, whereas a low estimate for fungal diversity would be at least five times the number of vascular plant species, following calculations by Hawksworth (1991, 2001).

Tricholoma is an important genus, including highly valued, economically significant mushrooms, as well as toxic species. They are present in most temperate and boreal forests of the world, where they contribute to ecosystem processes, forming ectomycorrhizae with species of Pinaceae, Fagaceae, Betulaceae, and Salicaceae. *Tricholoma* species are also specific hosts for mycoheterotrophic plants of the Ericaceae subfamily Monotropoideae (Bidartondo and Bruns 2002). Because of their preference of old and rather undisturbed forests (Christensen and Heilmann-Clausen 2013), many species genus could be used as indicators of naturalness in conservation value assessments. Despite the importance of the genus, the present state of knowledge is unsatisfactory in many respects. This study was intended to enhance knowledge on the distribution, diversity, and taxonomy of *Tricholoma* species in Yunnan and beyond.

MATERIALS AND METHODS

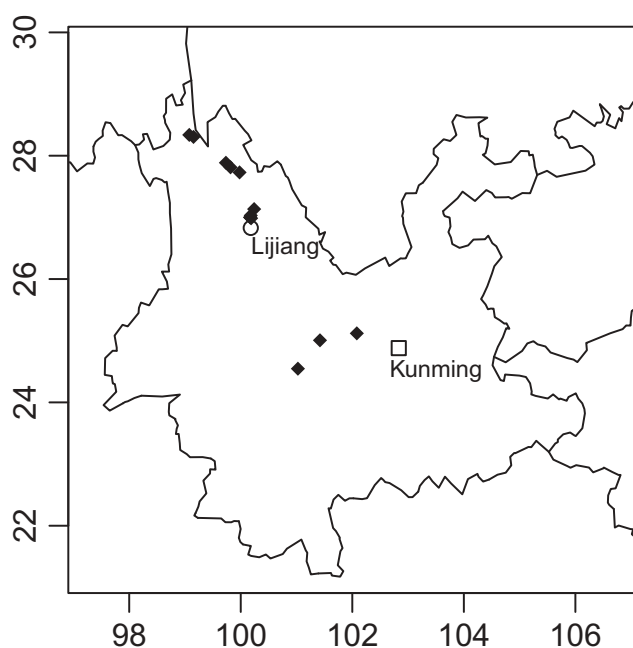
Collections and microscopy.—Basidiomes of *Tricholoma* spp. were collected in Yunnan (China) by Gerhard Kost, Flavius Popa, Karl-Heinz Rexer, and Zhu L. Yang in Jul 2006, Jul 2007, Aug 2013, and Aug 2014. Different habitats were visited, ranging from 2200 to 4700 m above sea level (a.s.l.) (TABLE 1), while a special focus was placed on mountainous regions in the northwest part of Yunnan (FIG. 1). The sample locations of most collections were recorded using a Garmin GPSmap 62 (Garmin Deutschland, Garching, Germany). Most collections were photographed, and the macroscopic characters, smell and taste, were recorded. Basidiomes were air dried at about 30 C using an electric food dehydrator and stored, thereafter, partly in the Herbarium of Cryptogams, Kunming Institute of Botany (KUN), and in the Herbarium Marburgense (MB), University of Marburg, Germany.

Many collections of *Tricholoma* spp., mainly from central Europe, were available for comparison at MB. Additional herbarium specimens were provided by the National Museum of Nature and Science, Tokyo (TNS), and the Sam Mitchel Herbarium of Fungi, Denver Botanic Gardens (DBG).

Micromorphology of the basidiomes was analyzed by bright-field microscopy, using a Zeiss Standard microscope (Carl Zeiss, Oberkochen, Germany). The sizes of basidiospores, hymenial structures, and features of the pileipellis were investigated from hand sections

Table 1. Study locations in Yunnan, China.

Location	Habitat	ECM trees	Latitude (°N)	Longitude (°E)	Altitude a.s.l.	Dates
Ailao Shan	<i>Quercus</i> -dominated broad-leaved forest	<i>Quercus</i> spp., <i>Lithocarpus</i> spp.	24.54627	101.025	2500 m	19, 20, 21 Jul 2006, 15 Jul 2007
Near Lijiang	Coniferous forest	<i>Pinus</i> spp., <i>Picea</i> spp.	NA	NA	2500 m	27 Jul 2006
Zishi Mountain	<i>Pinus</i> -dominated forest with old <i>Quercus</i> and <i>Cunninghamia</i> spp.	<i>Pinus</i> spp., <i>Quercus</i> spp., <i>Cunninghamia</i> spp.	25.00682	101.42023	2500 m	12 Jul 2007
Near Lijiang	planted <i>Pinus</i> forest	<i>Pinus</i> spp.	NA	NA	2500 m	28 Jul 2006
Near Kunming	Mixed forest with <i>Pinus yunnanensis</i> , <i>Cunninghamia lanceolata</i> and broadleaf trees species	<i>Pinus yunnanensis</i> , <i>Cunninghamia lanceolata</i>	25.11936	102.08103	2200 m	10 Aug 2013
Yulong Xue Shan, lower part of the mountain	<i>Pinus yunnanensis</i> forest	<i>Pinus yunnanensis</i>	27.0315	100.17972	2700 m	13 Aug 2013
Yulong Xue Shan, middle part of the mountain	<i>Pinus armandii</i> -dominated mixed forest	<i>Pinus armandii</i> , <i>Pinus yunnanensis</i>	26.98603	100.18589	2900 m	19 Aug 2013, 15, 16 Aug 2014
Yulong Xue Shan, higher part of the mountain	<i>Quercus aquifolioides</i> intermixed with <i>Pinus yunnanensis</i>	<i>Quercus aquifolioides</i> , <i>Pinus yunnanensis</i>	27.00056	100.16903	3200 – 3500 m	15, 20 Aug 2013, 11 Aug 2014
Yulong Xue Shan, high part of the mountain	<i>Quercus aquifolioides</i>	<i>Quercus aquifolioides</i>	27.00056	100.16903	3700 m	12 Aug 2014
Near Yulong Xue Shan	<i>Picea</i> forest intermixed with <i>Pinus</i> spp.	<i>Picea</i> spp., <i>Pinus</i> spp.	27.13442	100.23975	3300 m	21 Aug 2013, 17 Aug 2014
Near Shangri-La	<i>Picea</i> forest with some <i>Quercus aquifolioides</i> intermixed	<i>Picea</i> spp., <i>Quercus aquifolioides</i>	27.72931	99.97875	3700 m	21 Aug 2014
Shangri-La, Baimang Snow Mountain, lower location	<i>Picea</i> forest intermixed with <i>Quercus aquifolioides</i>	<i>Picea</i> spp., <i>Quercus aquifolioides</i>	28.30467	99.15283	3800 m	27 Aug 2014
Shangri-La, Baimang Snow Mountain, higher location	<i>Pinus densata</i> forest	<i>Pinus densata</i>	28.33742	99.07706	4700 m	26 Aug 2014
Shangri-La, location 1	<i>Pinus densata</i> forest	<i>Pinus densata</i>	27.81206	99.81664	3400 m	25 Aug 2014
Shangri-La, location 2	<i>Pinus densata</i> and <i>Quercus aquifolioides</i> mixed forest	<i>Pinus densata</i> , <i>Quercus aquifolioides</i>	27.88572	99.73372	3450 m	23 Aug 2014

**Figure 1.** Study locations in Yunnan, China.

mounted in tap water or 5% KOH. At least 20 basidiospores were measured for each collection of the newly described species. All measurements were taken using a 100×/1.25 oil objective. In a few cases, preparations were stained using Phloxine B to enable the analysis of fine hyaline structures.

DNA extraction, polymerase chain reaction, and sequencing.—Pieces of dry basidiomes of weighing 10–30 mg, taken from 114 collections of *Tricholoma* spp., were prepared in 1.5-mL microcentrifuge tubes along with steel beads of different sizes. The samples were sent to the Biodiversity and Climate Research Center (BiK-F) in Frankfurt, Germany, for ITS sequencing within the Integrative Fungal Research (IFR) project.

DNA from 89 collections was extracted and processed at the University of Marburg. Tissues, sampled as described above, were ground in a mixer mill (MM200; Retsch, Haan, Germany). DNA was extracted from the resulting powder using the innuPREP Plant DNA Kit (Analytik Jena, Jena, Germany) following the instruction manual. The ITS was amplified in a peqSTAR 96 HPL Gradient (PEQLAB Biotechnologie, Erlangen, Germany) using the Phire Hot Start II DNA plant kit (Thermo Scientific, xx, Germany). The primers ITS1F (Gardes and Bruns 1993) and ITS4 (White et al. 1990) were used with the following polymerase chain reaction (PCR) conditions: denaturation at 98 C for 5 min followed by 30 cycles of 98 C for 5 s, 52 C for 5 s, and 72 C for 20 s, with a final elongation step at 72 C for 5 min.

For some collections, the primer pair ITS1F and ITS4 yielded poor results. For these, the primers

ITS1F and ITS2 as well as ITS3 (White et al. 1990) and ITS4 were used along with the polymerase MolPol (Projodis Medical, Butzbach, Germany). PCR conditions were as follows: denaturation at 95 C for 5 min followed by 25 cycles of 95 C for 30 s, 55 C for 30 s, and 72 C for 30 s, with a final elongation step at 72 C for 10 min.

Success of amplification was checked by gel electrophoresis using a 1% (*w/v*) agarose gel at 200 V and 90 mA for 30 min. Successfully amplified products were purified using the MSB Spin PCRapace kit (Invitek, Berlin, Germany) and sent to LGC Genomics, Berlin, Germany, for forward and reverse sequencing.

Molecular cloning.—Seven collections presented double bands in the sequence chromatograms, even after repeated extractions. These were subjected to molecular cloning to reveal the putative ITS heterogeneity. Cloning was performed using the CloneJET PCR Cloning Kit (Thermo Scientific) according to the manufacturer's instructions. PCR products of these samples were inserted into the suicide vector pjet1.2 and transformed into *E. coli* Top10 cells. *E. coli* cells were made competent using the CaCl₂ method (Mandel and Higa 1970) including an initial heat shock of 42 C for 60 s. The transformed cells were plated on Luria-Bertani broth (LB)-ampicillin agar plates. After 24 h of proliferation, six colonies were picked per agar plate and transferred separately into 5 mL fluid LB-ampicillin. After another 24 h of proliferation, 1.5 mL of culture for each clone was used for destroyer lysis plasmid preparation (Sambrook 2012). Restriction of the plasmids was carried out using Bgl II (Thermo Scientific). Restrictions were visualized by electrophoresis on a 1% (*w/v*) agarose gel. Two clones of each collection were selected for plasmid purification using the ZR Plasmid Miniprep Classic kit (Zymo Research, Freiburg, Germany). The resulting samples were sent to LGC Genomics for sequencing.

Phylogenetic analyses.—DNA sequences were edited using CodonCode Aligner 5.1.5 (<http://www.codoncode.com>). BLAST searches were conducted on UNITE and GenBank. Only sequences of suitable quality were used for molecular phylogenetic analyses, along with sequences downloaded from GenBank and UNITE (TABLE 2). Generally, sequences were aligned with MAFFT (Kato and Standley 2013) using default settings. The alignments were modified using the Gblocks online 0.91b (Castresana 2000; Talavera and Castresana 2007), allowing all options for a less

stringent selection. The ends of the resulting alignments were trimmed in MEGA6 (Tamura et al. 2013). The trimmed alignments were used for phylogenetic analyses. These alignments are available on TreeBASE (study no. S21134).

Neighbor joining (NJ) trees were built using MEGA6. The model test implemented in MEGA6 showed that the Tamura 3-parameter + G model was the most suitable analysis method in all runs. A bootstrap analysis (Felsenstein 1985) with 1000 repetitions was included to test branch topology.

Maximum likelihood (ML) trees were built using RAxML-HPC2 on XSEDE (8.2.4) (Stamatakis 2014) via the CIPRES Science Gateway (Miller et al. 2010). The GTRCAT model was used along with a bootstrap analysis (Felsenstein 1985) with 1000 repetitions.

Bayesian inference (BI) Markov chain Monte Carlo (MCMC) analyses were conducted using MrBayes on XSEDE (3.2.6) (Huelsenbeck and Ronquist 2001; Ronquist et al. 2012) via the CIPRES Science Gateway (Miller et al. 2010). Two runs of 10 million generations were set with four chains each. Sampling frequency was set to 1000 while other parameters were at default settings, including a burn-in fraction of 25%. The resulting tree files of both runs were checked using Tracer 1.5 (Rambaut et al. 2018) to ensure the burn-in of the initial phase. Consensus trees were constructed based on the 50% majority rule.

Resulting phylogenetic trees were visualized and edited using TreeGraph 2 (Stöver and Müller 2010). Clades were regarded as supported with values of BI posterior probability (PP) of at least 95, ML bootstrap value of at least 70%, and a NJ bootstrap value of at least 0.7.

RESULTS

Diversity of *Tricholoma* spp. in China.—A total of 70 collections of *Tricholoma* spp. were made during the field trips in Yunnan. These could be assigned to 22 species. The following 12 *Tricholoma* species, which were already reported from China (Deng et al. 2004; Deng and Yao 2005a), were confirmed to occur in Yunnan, China: *T. albobrunneum* (Pers.) P. Kumm., *T. aurantiipes* Hongo, *T. bonii* Basso & Candusso, *T. cingulatum* (Almfelt) Jacobasch, *T. equestre* (L.) P. Kumm., *T. imbricatum* (Fr.) P. Kumm., *T. pessundatum* (Fr.) Quél., *T. populinum* J.E. Lange, *T. saponaceum* (Fr.) P. Kumm., *T. terreum* (Schaeff.) P. Kumm., *T. triste* (Scop.) Quél., and *T. vaccinum* (Schaeff.) P. Kumm. *Tricholoma bonii* and *T. triste* were also reported recently from China based on GenBank sequences (Heilmann-Clausen et al. 2017).

Table 2. Sequenced specimens and databank sequences.

Species	Origin	Voucher	Database no.	Comments	Reference
<i>Pseudotracheloma metapodium</i>	Germany	MB-002938			This study
<i>Tricholoma acerbum</i>	Germany	MB-002943			This study
<i>Tricholoma aestuans</i>	Denmark		LT000007		Heilmann-Clausen et al. 2017
<i>Tricholoma aestuans</i>	Sweden		LT000153	Type	Heilmann-Clausen et al. 2017
<i>Tricholoma albobrunneum</i>	France		LT000077		Heilmann-Clausen et al. 2017
<i>Tricholoma albobrunneum</i>	USA, Oregon		AF458436	As <i>T. ustale</i>	Horton unpubl.
<i>Tricholoma albobrunneum</i>	China, Yunnan	MB-003002			This study
<i>Tricholoma albobrunneum</i>	China, Yunnan	MB-003003			This study
<i>Tricholoma albobrunneum</i>	China, Yunnan	MB-003004			This study
<i>Tricholoma albobrunneum</i>	China, Yunnan	MB-003006			This study
<i>Tricholoma albobrunneum</i>	China, Yunnan	MB-003007			This study
<i>Tricholoma albobrunneum</i>	China, Yunnan	MB-301912			This study
<i>Tricholoma albobrunneum</i>	China, Yunnan	MB-305048			This study
<i>Tricholoma albobrunneum</i>	China, Yunnan	MB-305554			This study
<i>Tricholoma albobrunneum</i>	China, Yunnan	MB-305558			This study
<i>Tricholoma albobrunneum</i>	China, Yunnan	MB-305567			This study
<i>Tricholoma album</i>	Germany	MB-002925			This study
<i>Tricholoma apium</i>	Denmark		LT000009		Heilmann-Clausen et al. 2017
<i>Tricholoma argenteum</i>	USA, Colorado	DBG21760			This study
<i>Tricholoma argenteum</i>	USA, Colorado	DBG23372			This study
<i>Tricholoma argenteum</i>	USA, Colorado	DBG23525			This study
<i>Tricholoma argenteum</i>	USA, Colorado	DBG27774			This study
<i>Tricholoma argyraceum</i>	Slovakia		LT000127		Heilmann-Clausen et al. 2017
<i>Tricholoma argyraceum</i>	Sweden		LT000156		Heilmann-Clausen et al. 2017
<i>Tricholoma arvernense</i>	USA, Colorado	DBG18239			This study
<i>Tricholoma arvernense</i>	Austria	MB-002876			This study
<i>Tricholoma atrodiscum</i>	Canada, Quebec		KJ705254		Berube et al. unpubl.
<i>Tricholoma atosquamosum</i>	USA, Colorado	DBG24009			This study
<i>Tricholoma atosquamosum</i>	USA, Colorado	DBG27983			This study
<i>Tricholoma atroviolaceum</i>	USA, Washington		AY750166		Cline 2004
<i>Tricholoma aurantipes</i>	China, Yunnan	MB-003000			This study
<i>Tricholoma aurantium</i>	Germany	MB-102121			This study
<i>Tricholoma auratum</i>	Japan		AB289659		Kikuchi et al. 2007
<i>Tricholoma auratum</i>	Japan		AB289660		Kikuchi et al. 2007
<i>Tricholoma bakamatsutake</i>	Japan		AF204807		Kikuchi et al. 2000
<i>Tricholoma basirubens</i>	Sweden		UDB016070	UNITE	Ruotsalainen and Vauras unpubl.
<i>Tricholoma batschii</i>	Germany	MB-003027			This study
<i>Tricholoma bonii</i>	Italy		LT000101	Type	Heilmann-Clausen et al. 2017
<i>Tricholoma bonii</i>	China, Yunnan	MB-003005			This study
<i>Tricholoma bonii</i>	China, Yunnan	MB-301516			This study
<i>Tricholoma bonii</i>	China, Yunnan	MB-305154			This study
<i>Tricholoma boreosulphurescens</i>	Finland		LT000199		Heilmann-Clausen et al. 2017
<i>Tricholoma borgsjoeense</i>	Norway		LT222030		Heilmann-Clausen et al. 2017
<i>Tricholoma boudieri</i>	Denmark		LT000014		Heilmann-Clausen et al. 2017
<i>Tricholoma boudieri</i>	Slovenia		LT000136	Type	Heilmann-Clausen et al. 2017
<i>Tricholoma boudieri</i>	Austria	MB-002507			This study
<i>Tricholoma boudieri</i>	China, Yunnan	MB-305280			This study
<i>Tricholoma bresadolanium</i>	Sweden		LT000162		Heilmann-Clausen et al. 2017
<i>Tricholoma bryogenum</i>	Sweden		LT000163		Heilmann-Clausen et al. 2017
<i>Tricholoma caligatum</i>	France		LT000079		Heilmann-Clausen et al. 2017
<i>Tricholoma cingulatum</i>	Canada, Quebec		KJ705244		Berube et al. unpubl.
<i>Tricholoma cingulatum</i>	Denmark		LT000015	Type	Heilmann-Clausen et al. 2017
<i>Tricholoma cingulatum</i>	China, Yunnan	MB-302066			this study
<i>Tricholoma colossus</i>	Germany	MB-002363			this study
<i>Tricholoma columbetta</i>	Canada, Quebec		KJ705261		Berube et al. unpubl.
<i>Tricholoma columbetta</i>	Denmark		LT000017	Type	Heilmann-Clausen et al. 2017
<i>Tricholoma columbetta</i>	USA, North Carolina		KJ417319	As <i>T. subsplendens</i>	Sánchez-García et al. 2014
<i>Tricholoma davisiae</i>	Canada, Quebec		KJ705249		Berube et al. unpubl.
<i>Tricholoma davisiae</i>	Canada, Quebec		KJ705248		Berube et al. unpubl.
<i>Tricholoma dulciolens</i>	Sweden		AB738883	Type	Murata et al. 2013a
<i>Tricholoma elegans</i>	New Zealand		KJ417316		Sánchez-García et al. 2014
<i>Tricholoma elegans</i>	New Zealand		JX178630	As <i>T. viridiolivaceum</i>	Teasdale et al. 2013
<i>Tricholoma equestre</i>	Denmark		LT000020		Heilmann-Clausen et al. 2017
<i>Tricholoma equestre</i>	Denmark		LT000018		Heilmann-Clausen et al. 2017
<i>Tricholoma equestre</i>	USA, Colorado	DBG18376			This study
<i>Tricholoma equestre</i>	USA, Colorado	DBG23922			This study
<i>Tricholoma equestre</i>	China, Yunnan	MB-301506			This study
<i>Tricholoma equestre</i>	China, Yunnan	MB-305549			This study
<i>Tricholoma equestre</i>	China, Yunnan	MB-305676			This study
<i>Tricholoma filamentosum</i>	Germany	MB-000950			This study
<i>Tricholoma filamentosum</i>	Germany	MB-002942			This study
<i>Tricholoma flavovirens</i>	Canada, British Columbia		HQ650740		Kranabetter et al. 2009
<i>Tricholoma flavovirens</i>	Japan		AB036895		Murata unpubl.
<i>Tricholoma flavovirens</i>	USA, New Mexico		AF349689		Bidartondo and Bruns 2001

(Continued)

Table 2. (Continued).

Species	Origin	Voucher	Database no.	Comments	Reference
<i>Tricholoma flavovirens</i>	USA, Oregon		AF458449		Horton unpubl.
<i>Tricholoma flavovirens</i>	USA, Oregon		AF458452		Horton unpubl.
<i>Tricholoma focale</i>	Canada, British Columbia		FJ845447		Kranabetter et al. 2009
<i>Tricholoma focale</i>	Sweden		LT000166	Type	Heilmann-Clausen et al. 2017
<i>Tricholoma forteflavescens</i>	China, Yunnan	KUN-HKAS 93511		Type	This study
<i>Tricholoma forteflavescens</i>	China, Yunnan	MB-301985			This study
<i>Tricholoma forteflavescens</i>	China, Yunnan	MB-302010			This study
<i>Tricholoma forteflavescens</i>	China, Yunnan	MB-305034			This study
<i>Tricholoma frondosae</i>	Denmark		LT000023		Heilmann-Clausen et al. 2017
<i>Tricholoma frondosae</i>	Sweden		LT000167		Heilmann-Clausen et al. 2017
<i>Tricholoma frondosae</i>	Sweden		LT000168		Heilmann-Clausen et al. 2017
<i>Tricholoma frondosae</i>	Sweden		LT000169		Heilmann-Clausen et al. 2017
<i>Tricholoma frondosae</i>	USA, Colorado	DBG23967			This study
<i>Tricholoma frondosae</i>	China, Yunnan	MB-301979			This study
<i>Tricholoma frondosae</i>	China, Yunnan	MB-301993			This study
<i>Tricholoma frondosae</i>	China, Yunnan	MB-302008			This study
<i>Tricholoma fucatum</i>	Austria	MB-001318			This study
<i>Tricholoma fucatum</i>	Austria	MB-102537			This study
<i>Tricholoma fulvocastaneum</i>	Japan		AB737847		Yamada et al. unpubl.
<i>Tricholoma fulvum</i>	Austria	MB-000915			This study
<i>Tricholoma fulvum</i>	Austria	MB-001087			This study
<i>Tricholoma fulvum</i>	Austria	MB-002891			This study
<i>Tricholoma fulvum</i>	Germany	MB-002926			This study
<i>Tricholoma fulvum</i>	Germany	MB-002927			This study
<i>Tricholoma fulvum</i>	Austria	MB-002994			This study
<i>Tricholoma fulvum</i>	Germany	MB-102678			This study
<i>Tricholoma fulvum</i>	Austria	MB-002711			This study
<i>Tricholoma fulvum</i>	Germany	MB-102827			This study
<i>Tricholoma fumosoluteum</i>	Canada, Quebec		KJ705245		Berube et al. unpubl.
<i>Tricholoma guldeniae</i>	Austria	MB-001409			This study
<i>Tricholoma guldeniae</i>	Austria	MB-002257			This study
<i>Tricholoma guldeniae</i>	Austria	MB-002258			This study
<i>Tricholoma guldeniae</i>	Austria	MB-002988			This study
<i>Tricholoma huronense</i>	USA		AF377229		Bidartondo and Bruns 2002
<i>Tricholoma ilkkæ</i>	Sweden		LT222029	Type	Heilmann-Clausen et al. 2017
<i>Tricholoma imbricatum</i>	Denmark		LT000024	Type	Heilmann-Clausen et al. 2017
<i>Tricholoma imbricatum</i>	USA, Colorado	DBG18278			This study
<i>Tricholoma imbricatum</i>	USA, Colorado	DBG18375			This study
<i>Tricholoma imbricatum</i>	USA, Colorado	DBG23986			This study
<i>Tricholoma imbricatum</i>	USA, Colorado	DBG24049			This study
<i>Tricholoma imbricatum</i>	Austria	MB-102330			This study
<i>Tricholoma imbricatum</i>	China, Yunnan	MB-301505			This study
<i>Tricholoma inamoenum</i>	Canada, British Columbia		FJ845445	As <i>T. platyphyllum</i>	Kranabetter et al. 2009
<i>Tricholoma inamoenum</i>	USA, Colorado	DBG25240			This study
<i>Tricholoma inamoenum</i>	Austria	MB-002139			This study
<i>Tricholoma inamoenum</i>	Austria	MB-102773			This study
<i>Tricholoma inocybeoides</i>	Germany	MB-003215			This study
<i>Tricholoma intermedium</i>	Canada, British Columbia		DQ097867		Durall et al. unpubl.
<i>Tricholoma japonicum</i>	Japan		AB036900		Murata unpubl.
<i>Tricholoma japonicum</i>	Japan		AF204810		Kikuchi et al. 2000
<i>Tricholoma joachimii</i>	Sweden		LT000177		Heilmann-Clausen et al. 2017
<i>Tricholoma josserandii</i>	France		LT000081		Heilmann-Clausen et al. 2017
<i>Tricholoma lascivum</i>	Ukraine	MB-303096			This study
<i>Tricholoma leucophyllum</i>	Canada, British Columbia		EU597086		Jones et al. 2008
<i>Tricholoma leucophyllum</i>	Canada, Ontario		JN021108		Dentinger et al. 2010
<i>Tricholoma luridum</i>	Austria	MB-002901			This study
<i>Tricholoma luteomaculosum</i>	Canada, British Columbia		HM240543		Berbee and Lim unpubl.
<i>Tricholoma luteomaculosum</i>	USA, Oregon		AF458448		Horton unpubl.
<i>Tricholoma magnivelare</i>	New Hampshire		KF010157		Frank and Arora unpubl.
<i>Tricholoma matsutake</i>	Sweden		LT000178		Heilmann-Clausen et al. 2017
<i>Tricholoma melleum</i>	China, Yunnan	KUN-HKAS 93514		Type	This study
<i>Tricholoma melleum</i>	China, Yunnan	MB-305015			This study
<i>Tricholoma muscarioides</i>	China, Yunnan	KUN-HKAS 93512		Type	This study
<i>Tricholoma muscarioides</i>	China, Yunnan	MB-002997			This study
<i>Tricholoma muscarioides</i>	China, Yunnan	MB-003001			This study
<i>Tricholoma muscarium</i>	Japan	TNS-F-39016			This study

(Continued)

Table 2. (Continued).

Species	Origin	Voucher	Database no.	Comments	Reference
<i>Tricholoma mutabile</i>	USA, California		AF349703		Bidartondo and Bruns 2001
<i>Tricholoma mutabile</i>	USA, Oregon		AF458444		Horton unpubl.
<i>Tricholoma myomyces</i>	USA, Tennessee		JN389292		Yu et al. unpubl.
<i>Tricholoma olivaceoluteolum</i>	China, Yunnan	KUN-HKAS 93510		Type	This study
<i>Tricholoma olivaceoluteolum</i>	China, Yunnan	MB-002998			This study
<i>Tricholoma olivaceoluteolum</i>	China, Yunnan	MB-002999			This study
<i>Tricholoma olivaceotinctum</i>	Sweden		LT000182	Type	Heilmann-Clausen et al. 2017
<i>Tricholoma olivaceum</i>	China, Yunnan	KUN-HKAS 93513		Type	This study
<i>Tricholoma olivaceum</i>	China, Yunnan	MB-002991			This study
<i>Tricholoma olivaceum</i>	China, Yunnan	MB-301918			This study
<i>Tricholoma orirubens</i>	Slovakia		LT000132		Heilmann-Clausen et al. 2017
<i>Tricholoma palustre</i>	Canada, Quebec		KJ705252	As <i>T. aestuans</i>	Berube et al. unpubl.
<i>Tricholoma palustre</i>	USA, Massachusetts		DQ494699		Matheny et al. 2006
<i>Tricholoma pardinum</i>	USA, Colorado	DBG25191			This study
<i>Tricholoma pessundatum</i>	Denmark		LT000032	Type	Heilmann-Clausen et al. 2017
<i>Tricholoma pessundatum</i>	China, Yunnan	MB-305071			This study
<i>Tricholoma populinum</i>	Canada		KC146366	Strain ATCC 64509	Gujjari et al. unpubl.
<i>Tricholoma populinum</i>	Slovenia		LT000143		Heilmann-Clausen et al. 2017
<i>Tricholoma populinum</i>	China, Yunnan	MB-301648			This study
<i>Tricholoma portentosum</i>	USA, Colorado	DBG18411			This study
<i>Tricholoma portentosum</i>	USA, Colorado	DBG21652			This study
<i>Tricholoma portentosum</i>	Germany	MB-102645			This study
<i>Tricholoma portentosum</i>	Germany	MB-102689			This study
<i>Tricholoma psammopus</i>	Slovenia		LT000145		Heilmann-Clausen et al. 2017
<i>Tricholoma psammopus</i>	UK, Scotland		JQ888219		Pickles et al. 2012
<i>Tricholoma rapipes</i>	Denmark		LT000037		Heilmann-Clausen et al. 2017
<i>Tricholoma rapipes</i>	France		LT000085	Type	Heilmann-Clausen et al. 2017
<i>Tricholoma roseoacervum</i>	Finland		LT000073		Heilmann-Clausen et al. 2017
<i>Tricholoma saponaceum</i>	Canada, British Columbia		KP406580		Kranabetter et al. unpubl.
<i>Tricholoma saponaceum</i>	Canada, British Columbia		FJ845442		Kranabetter et al. 2009
<i>Tricholoma saponaceum</i>	France		LT000087		Heilmann-Clausen et al. 2017
<i>Tricholoma saponaceum</i>	France		LT000086		Heilmann-Clausen et al. 2017
<i>Tricholoma saponaceum</i>	USA, Colorado	DBG18233			This study
<i>Tricholoma saponaceum</i>	USA, Colorado	DBG18234			This study
<i>Tricholoma saponaceum</i>	USA, Colorado	DBG19256			This study
<i>Tricholoma saponaceum</i>	USA, Colorado	DBG20517			This study
<i>Tricholoma saponaceum</i>	USA, Colorado	DBG21393			This study
<i>Tricholoma saponaceum</i>	USA, Colorado	DBG23531			This study
<i>Tricholoma saponaceum</i>	USA, Colorado	DBG23667			This study
<i>Tricholoma saponaceum</i>	USA, Colorado	DBG23751			This study
<i>Tricholoma saponaceum</i>	Austria	MB-002682			This study
<i>Tricholoma saponaceum</i>	China, Yunnan	MB-301995			This study
<i>Tricholoma saponaceum</i>	China, Yunnan	MB-302089			This study
<i>Tricholoma saponaceum</i>	Ukraine	MB-303042			This study
<i>Tricholoma saponaceum</i>	China, Yunnan	MB-305741			This study
<i>Tricholoma saponaceum</i> var. <i>squamosum</i>	Germany	MB-002941			This study
<i>Tricholoma saponaceum</i> var. <i>squamosum</i>	China, Yunnan	MB-305282			This study
<i>Tricholoma scalpturatum</i>	Sweden		AF377201	Type	Bidartondo and Bruns 2002
<i>Tricholoma sciodes</i>	Germany	MB-002928			this study
<i>Tricholoma sejunctum</i>	Italy		LT000110		Heilmann-Clausen et al. 2017
<i>Tricholoma sinoportentosum</i>	China, Tibet	KUN-HKAS 46084		Type	This study
<i>Tricholoma sinoportentosum</i>	China, Tibet	KUN-HKAS 58002			This study
<i>Tricholoma sinoportentosum</i>	China, Yunnan	MB-302015			This study
<i>Tricholoma sinoportentosum</i>	China, Yunnan	MB-302067			This study
<i>Tricholoma sinoportentosum</i>	China, Yunnan	MB-302071			This study
<i>Tricholoma sinoportentosum</i>	China, Yunnan	MB-302073			This study
<i>Tricholoma sinoportentosum</i>	China, Yunnan	MB-302074			This study
<i>Tricholoma sinoportentosum</i>	China, Yunnan	MB-305284			This study
<i>Tricholoma</i> sp.	China, Yunnan	MB-301976			This study
<i>Tricholoma</i> sp.	China, Yunnan	MB-305716			This study
<i>Tricholoma</i> spec.	Canada, Quebec		KJ705247	As <i>T. quercetorum</i>	Berube et al. unpubl.
<i>Tricholoma</i> spec.	Canada, Quebec		KJ705246	As <i>T. quercetorum</i>	Berube et al. unpubl.
<i>Tricholoma squarrulosum</i>	Croatia		LT000003		Heilmann-Clausen et al. 2017
<i>Tricholoma stans</i>	Canada, Quebec		KJ705239		Berube et al. unpubl.
<i>Tricholoma stans</i>	Sweden		LT000189	Type	Heilmann-Clausen et al. 2017
<i>Tricholoma stiparophyllum</i>	Sweden		LT000190		Heilmann-Clausen et al. 2017

(Continued)

Table 2. (Continued).

Species	Origin	Voucher	Database no.	Comments	Reference
<i>Tricholoma stiparophyllum</i>	Germany	MB-003025			This study
<i>Tricholoma subluteum</i>	Canada, Quebec		KJ705257		Berube et al. unpubl.
<i>Tricholoma subluteum</i>	Canada, Quebec		KJ705255		Berube et al. unpubl.
<i>Tricholoma sudum</i>	Denmark		LT000051	Type	Heilmann-Clausen et al. 2017
<i>Tricholoma sudum</i>	Denmark		LT000050		Heilmann-Clausen et al. 2017
<i>Tricholoma sulphurescens</i>	Germany	MB-102501			This study
<i>Tricholoma sulphureum</i>	Germany	MB-002930			This study
<i>Tricholoma terreum</i>	Denmark		LT000057		Heilmann-Clausen et al. 2017
<i>Tricholoma terreum</i>	France		LT000092		Heilmann-Clausen et al. 2017
<i>Tricholoma terreum</i>	Norway		LT222021		Heilmann-Clausen et al. 2017
<i>Tricholoma terreum</i>	USA		JN389295		Yu et al. unpubl.
<i>Tricholoma terreum</i>	China, Yunnan	MB-304903			This study
<i>Tricholoma terreum</i>	China, Yunnan	MB-305046			This study
<i>Tricholoma transmutedans</i>	Canada, Quebec		KJ705236		Berube et al. unpubl.
<i>Tricholoma triste</i>	Sweden		LT000194		Heilmann-Clausen et al. 2017
<i>Tricholoma triste</i>	USA, Colorado	DBG22631			This study
<i>Tricholoma triste</i>	China, Yunnan	MB-301532			This study
<i>Tricholoma triste</i>	China, Yunnan	MB-305297			This study
<i>Tricholoma umbonatum</i>	Italy		LT000114		Heilmann-Clausen et al. 2017
<i>Tricholoma ustale</i>	Germany	MB-002924			This study
<i>Tricholoma ustale</i>	Ukraine	MB-303111			This study
<i>Tricholoma ustalooides</i>	Portugal		LT000126		Heilmann-Clausen et al. 2017
<i>Tricholoma ustalooides</i>	Germany	MB-002929			this study
<i>Tricholoma vaccinum</i>	Sweden		LT000195		Heilmann-Clausen et al. 2017
<i>Tricholoma vaccinum</i>	USA, Colorado	DBG23466			This study
<i>Tricholoma vaccinum</i>	China, Yunnan	MB-302070			This study
<i>Tricholoma venenatum</i>	USA		AF377230		Bidartondo and Bruns 2002
<i>Tricholoma vernaticum</i>	USA		AF377203		Bidartondo and Bruns 2002
<i>Tricholoma virgatum</i>	Germany	MB-102690			This study
<i>Tricholoma viridiolivaceum</i>	New Zealand		JX178633	As <i>T. elegans</i>	Teasdale et al. 2013
<i>Tricholoma viridiolivaceum</i>	New Zealand		LT000117		Heilmann-Clausen et al. 2017
<i>Tricholoma viridilutescens</i>	Canada, Ontario		JN021102	As <i>T. aff. sejunctum</i>	Dentinger et al. 2010
<i>Tricholoma viridilutescens</i>	Japan		AB848695	As <i>T. spec.</i>	Miyamoto et al. 2014
<i>Tricholoma viridilutescens</i>	Austria	MB-002842			This study
Uncultured ectomycorrhiza	Mexico		FJ197008	Of <i>Quercus</i>	Morris et al. 2009
Uncultured mycorrhizal fungus	China, Yunnan		JQ396486	Monotropoid mycorrhiza	Shen unpubl.

Two species are recorded here for the first time: *T. boudieri* (Barla) Sacc. and *T. frondosae* Kalamees & Shchukin. Six species were recognized as new to science and are described below. Two collections (MB-301976 in sect. *Genuina*, MB-305716 in sect. *Tricholoma*) probably represent new species (FIG. 2), but the material was insufficient for detailed descriptions. Four lineages, two in the *T. equestre* complex (MB-301506 together with MB-305549, as well as MB-305676; FIG. 5) and two in sect. *Rigida* (MB-305741, as well as MB-305282 together with MB-302089; FIG. 7), potentially represent further undescribed species from Yunnan.

Distribution patterns.—Newly generated sequences and data deposited in GenBank indicated the occurrence of *T. albobrunneum*, *T. cingulatum*, *T. triste*, *T. vaccinum*, and *T. viridilutescens* M.M. Moser in Europe, Asia, and North America (see FIGS. 3, 4, and 6). *Tricholoma imbricatum* sequences were generated from specimens of Europe, Asia, and North

America, but the monophyletic status of the species was not clearly supported by phylogenetic analyses, wherein the sequences of American collections formed a well-supported separate clade (FIG. 3). Likewise, sequences assigned to *T. populinum* were separated into a highly supported European and a well-supported Yunnan/North America clade (FIG. 3). Although *T. bonii* is present in Yunnan, two sequences of specimens from North America, labeled *T. myomyces* and *T. terreum*, formed a highly supported, closely related clade to *T. bonii*.

Several collections from northern Austria were identified as *T. guldeniae* Mort. Chr. This species was originally described from boreal Fennoscandia (Christensen and Heilmann-Clausen 2009) and was previously believed to be restricted to northern Europe (Christensen and Heilmann-Clausen 2013).

Phylogenetic analyses.—In total, 133 ITS sequences were generated. Sixty ITS sequences were obtained

This study

AUS = Austria
 COL = Colorado, USA
 GER = Germany
 TIB = Tibet, China
 UKR = Ukraine
 YUN = Yunnan, China

GenBank sequences

BC = British Columbia
 DK = Denmark
 FI = Finland
 FR = France
 HR = Croatia
 JP = Japan
 MX = Mexico
 NO = Norway
 NZ = New Zealand
 SE = Sweden
 SK = Slovakia
 US = USA

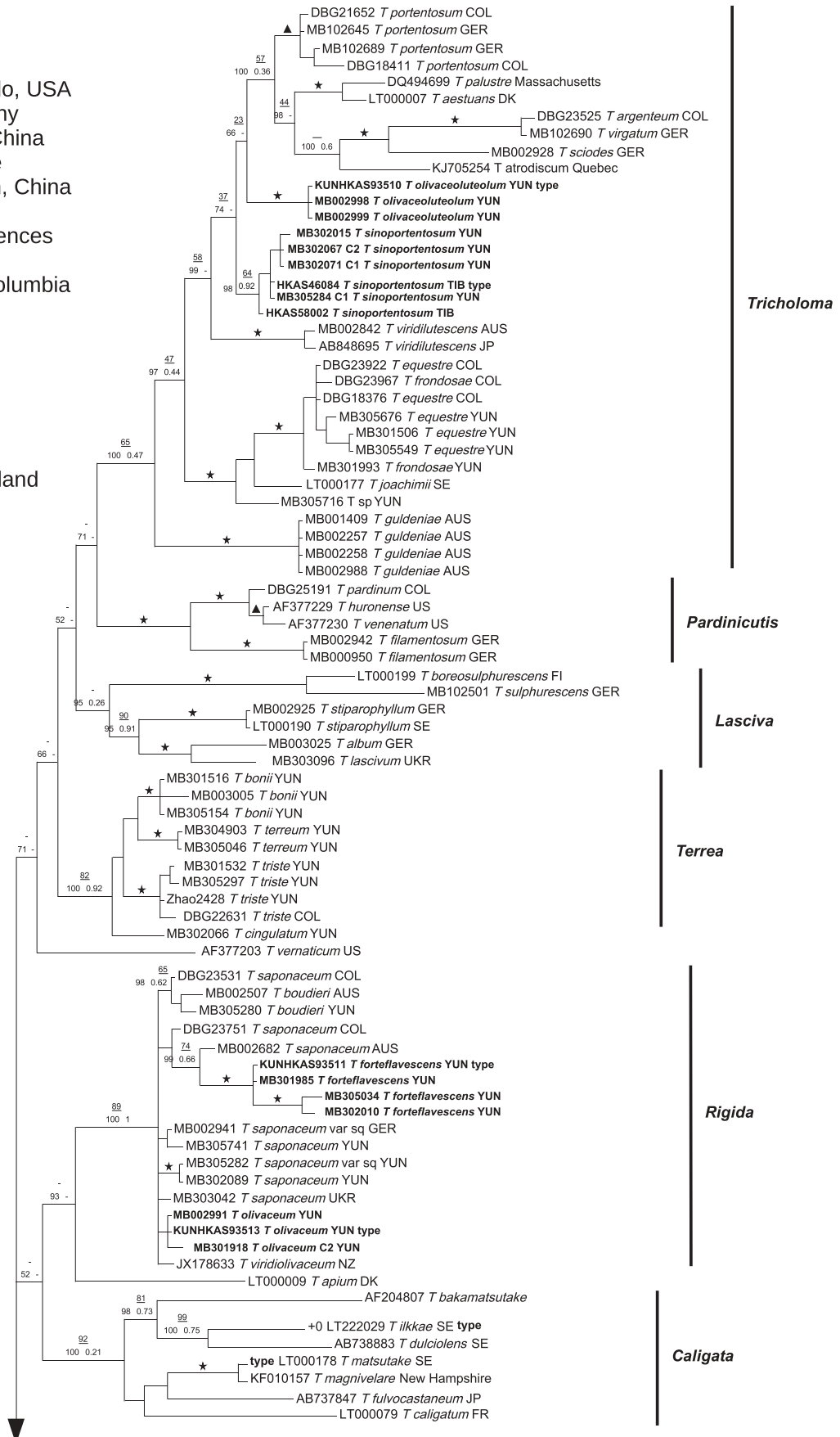


Figure 2. Bayesian MCMC tree of *Tricholoma* based on nuc rDNA internal transcribed spacer sequences (ITS1-5.8S-ITS2 = ITS). Rooted to *Pseudotracholoma metapodium*. Species new to science are indicated in bold. Support values above the branches: left side = % BI posterior probability (PP); right side = NJ bootstrap value in absolute numbers; underlined on the top = % ML bootstrap value. A star denotes PP = 100 and bootstrap values at least 0.9 and 90, respectively. A triangle denotes PP at least 95 and bootstrap values at least 0.8 and 80, respectively. Not all intra-section support values are shown.

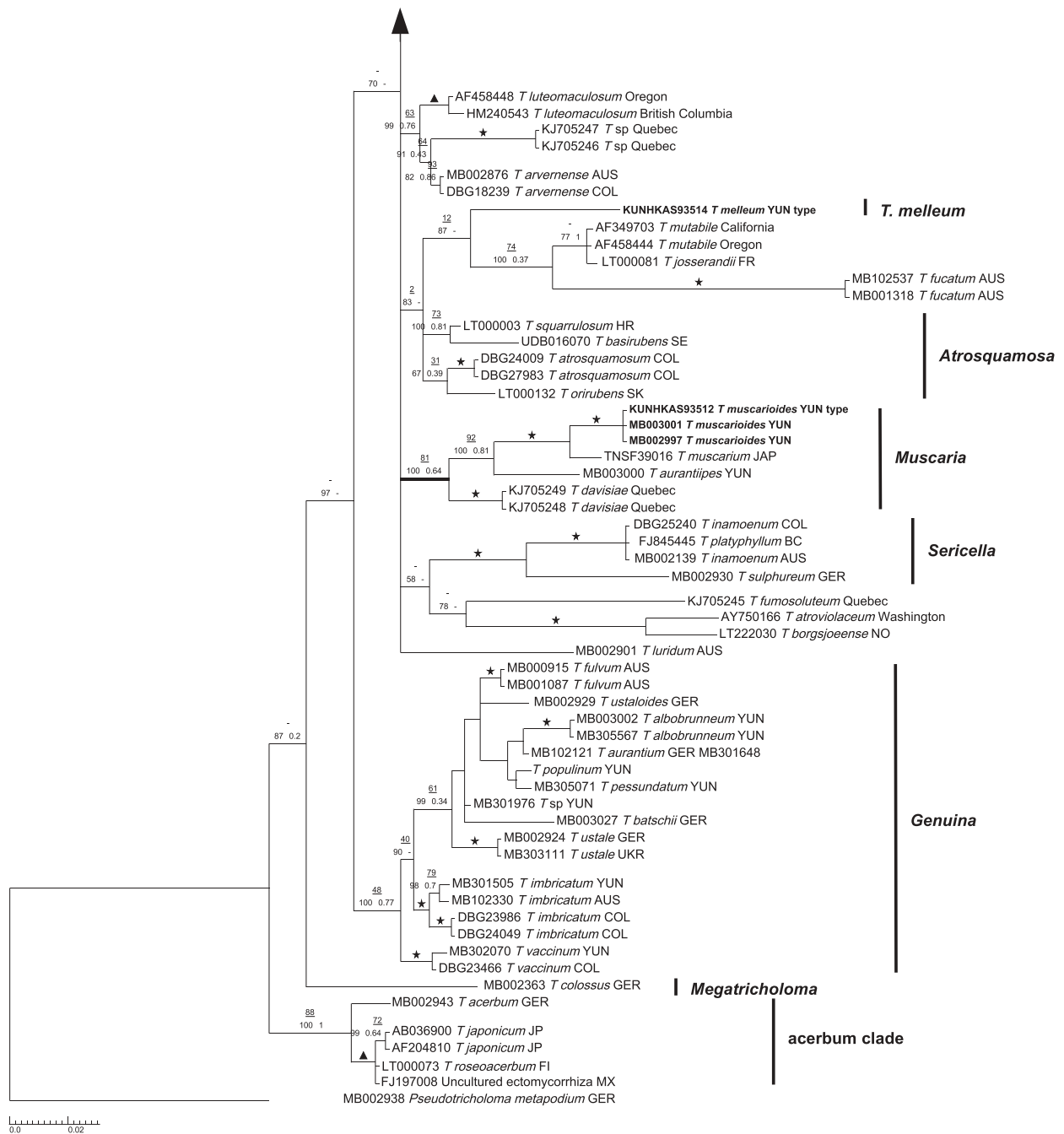


Figure 2. (Continued)

from collections from Yunnan, including two clones from each of four collections. Further, 42 ITS sequences were obtained from collections from central Europe, 27 ITS sequences from collections from Colorado, 3 ITS sequences from collections from Ukraine, and 1 ITS sequence from a collection of Japan. These ITS sequences were used in addition to 108 ITS sequences downloaded from GenBank and 1 ITS sequence from UNITE (TABLE 2).

The major clades resulting from our molecular phylogenetic analyses (FIG. 2) were similar to those presented by Christensen and Heilmann-Clausen (2013). Only sect. *Atrosquamosa* sensu Christensen & Heilmann-Clausen 2013 was split into two clades, located at a trichotomy with a unsupported clade of the new species *T. melleum*, *T. josserandii* Bon, and *T. fucatum* (Fr.) P. Kumm. Section *Lasciva* Bon was only poorly supported in the BI analysis and

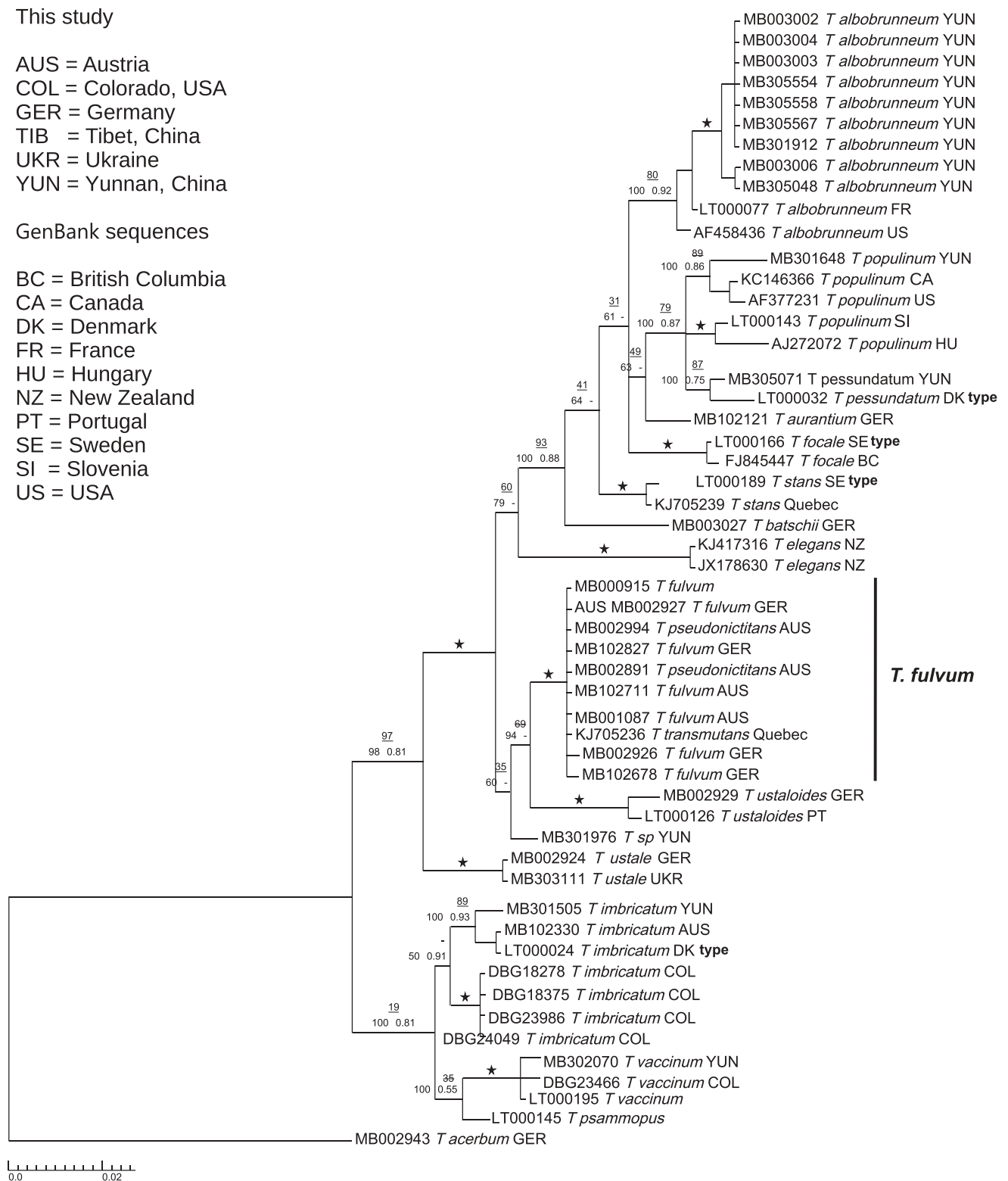


Figure 3. BI MCMC tree of sect. *Genuina* based on ITS. Rooted to *T. acerbum*. Support values above the branches: left side = % BI posterior probability (PP); right side = NJ bootstrap value in absolute numbers; underlined on the top = % ML bootstrap value. A star denotes PP = 100 and bootstrap values at least 0.9 and 90, respectively. Not all intra-species support values are shown.

unsupported in the ML and NJ analyses. This section was also inconsistently supported in preliminary analyses. A clade comprising *T. acerbum* (Bull.) Quél., *T.*

japonicum, and *T. colossus* (Fr.) Quél., as proposed by Heilmann-Clausen et al. (2017), could not be confirmed.

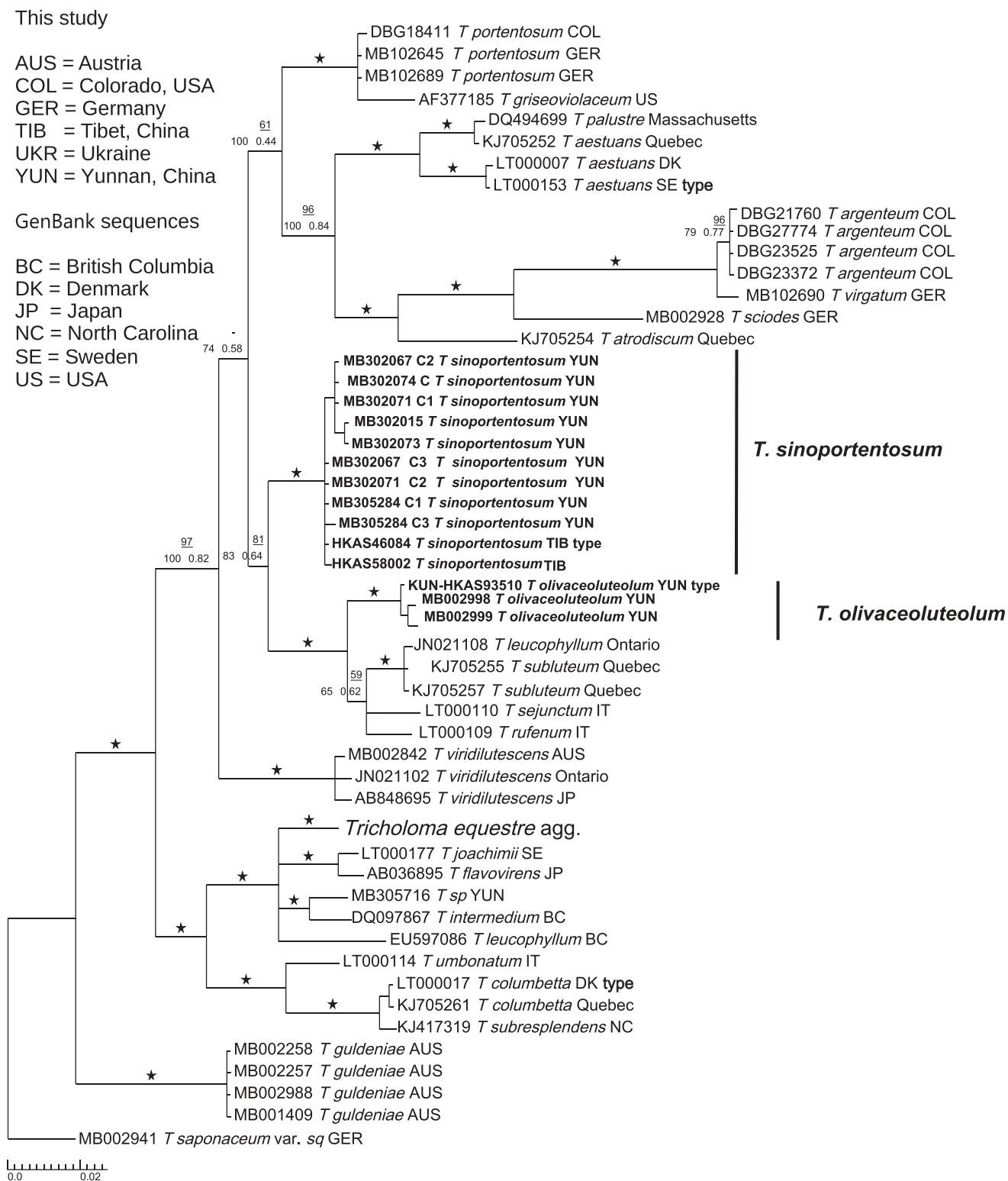


Figure 4. BI MCMC tree of sect. *Tricholoma* based on ITS. Rooted to *T. saponaceum*. Species new to science are indicated in bold. Support values above the branches: left side = % BI posterior probability (PP); right side = NJ bootstrap value in absolute numbers; underlined on the top = % ML bootstrap value. A star denotes PP = 100 and bootstrap values at least 0.9 and 90, respectively. Not all intra-species support values are shown. Twenty sequences of the *T. equestre* complex included in the analyses are not shown in the tree.

A clade comprising *T. aurantiipes*, *T. davisiae* Peck, *T. muscarium* Kawam. ex Hongo, and the new species

T. muscarioides (FIG. 2) was recognized as a new section, formally described below as sect. *Muscaria*.

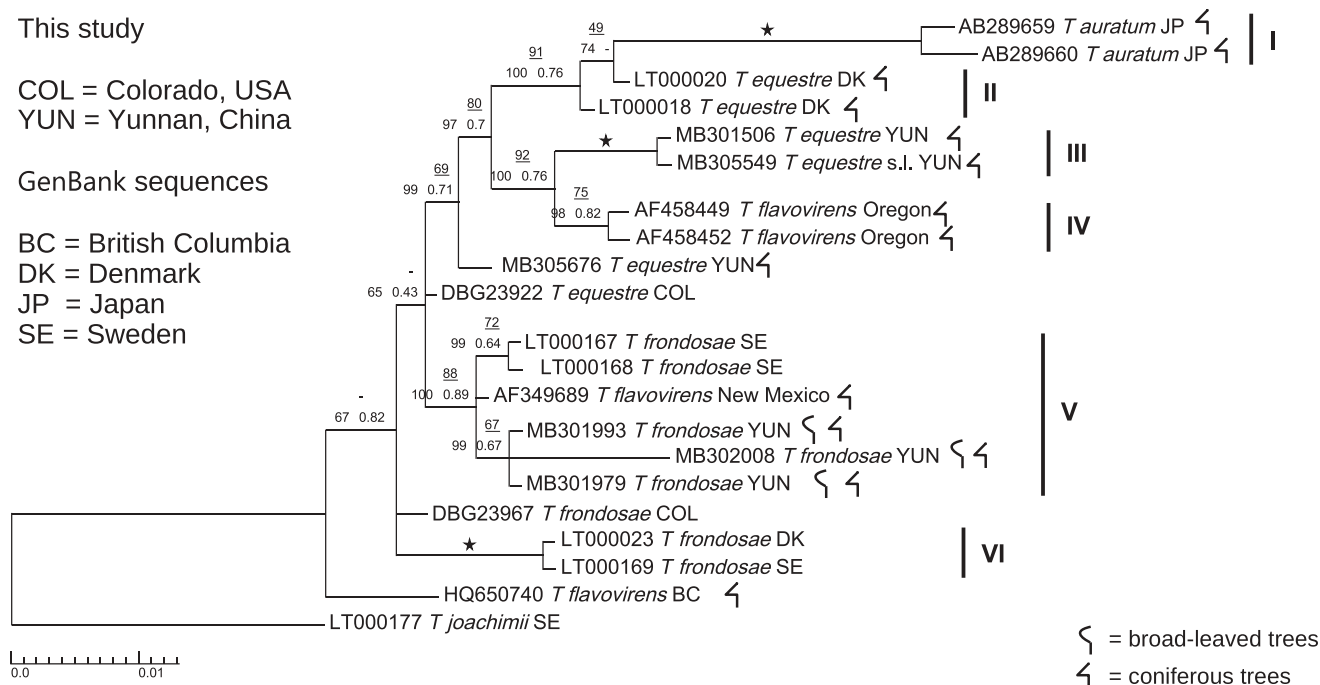


Figure 5. BI MCMC tree of the *T. equestre* complex based on ITS. Rooted to *T. joachimii*. Support values above the branches: left side = % BI posterior probability (PP); right side = NJ bootstrap value in absolute numbers; underlined on the top = % ML bootstrap value. A star denotes PP = 100 and bootstrap values at least 0.9 and 90, respectively.

Section *Genuina* (Fr.) Sacc. (FIG. 3). Within sect. *Genuina*, the species with a dry pileal surface, *T. imbricatum*, *T. psammopus* (Kalchbr.) Quél., and *T. vaccinum*, formed a clade that was unsupported by the ML analysis, whereas the species with a viscid pileal surface formed a well-supported clade. These results support some interpretations of relationships from the morphological analyses of species of sect. *Genuina* by Kost (1981). Sequences of specimens assigned to *T. imbricatum* from Colorado formed a highly supported clade that was separated from the Asian/European *T. imbricatum* clade. However, the separation was inconsistent and was only supported by NJ. *Tricholoma ustale* (Fr.) P. Kumm. had a basal position among the species with viscid pilei, whereas a highly supported subclade was formed by the other species with a viscid cap. The conspecificity of *T. pseudonictitans* Bon with *T. fulvum* (Fr.) Bigeard & H. Guill., as proposed by Christensen and Heilmann-Clausen (2013), was well supported in our data analyses. The *T. fulvum* clade included a sequence of *T. transmutans* (Peck) Sacc. from Quebec, Canada. In contrast, a collection from Yunnan (MB-301976), which is morphologically similar to *T. fulvum*, was not part of that clade.

Section *Tricholoma* (FIG. 4). In the clade representing sect. *Tricholoma*, *T. guldeniae* had a basal position in all analyses. A highly supported subclade included *T. columbetta* (Fr.) P. Kumm., *T. umbonatum* Cléménçon

& Bon, and species related to *T. joachimii* Bon & A. Riva and *T. equestre*. Within this subclade, the sequence of MB-305716 from Yunnan formed a separate lineage close to *T. intermedium* Peck. Another highly supported clade consisted of the new species *T. olivaceoluteolum*, *T. subluteum* Peck, *T. sejunctum* (Sowerby) Quél., and *T. rufenum* P. Donati. The species with bitter to acrid basidiomes, namely, *T. aestuans* (Fr.) Gillet, *T. palustre* A.H. Sm., *T. atrodiscum* Ovrebo, *T. sciodes* (Pers.) C. Martín, *T. virgatum* (Fr.) P. Kumm., and *T. argenteum* Ovrebo, formed another well-supported clade. Within this clade, the yellow species, *T. palustre* and *T. aestuans*, formed a highly supported subclade, whereas the gray species, *T. virgatum* and relatives, formed another. *Tricholoma argenteum* and *T. virgatum* were not supported as two distinct species by the BI analysis.

Tricholoma equestre complex (FIG. 5). Within the *T. equestre* complex, six clades were supported. Clade I consisted of two Japanese sequences labeled “*T. auratum*.” Clade III was very well supported and consisted of two sequences representing collections from Yunnan. Clade V consisted of six sequences from New Mexico, Sweden, and Yunnan. The corresponding specimens were mainly labeled *T. frondosae*. The three collections of Yunnan included in Clade V were collected in a mixed *Quercus/Pinus* forest, whereas the associated trees of the specimen from New Mexico were exclusively conifers (Bidartondo and Bruns 2001;

This study

COL = Colorado, USA

GER = Germany

YUN = Yunnan, China

GenBank sequences

DK = Denmark

FR = France

IT = Italy

NO = Norway

SE = Sweden

SK = Slovakia

US = USA

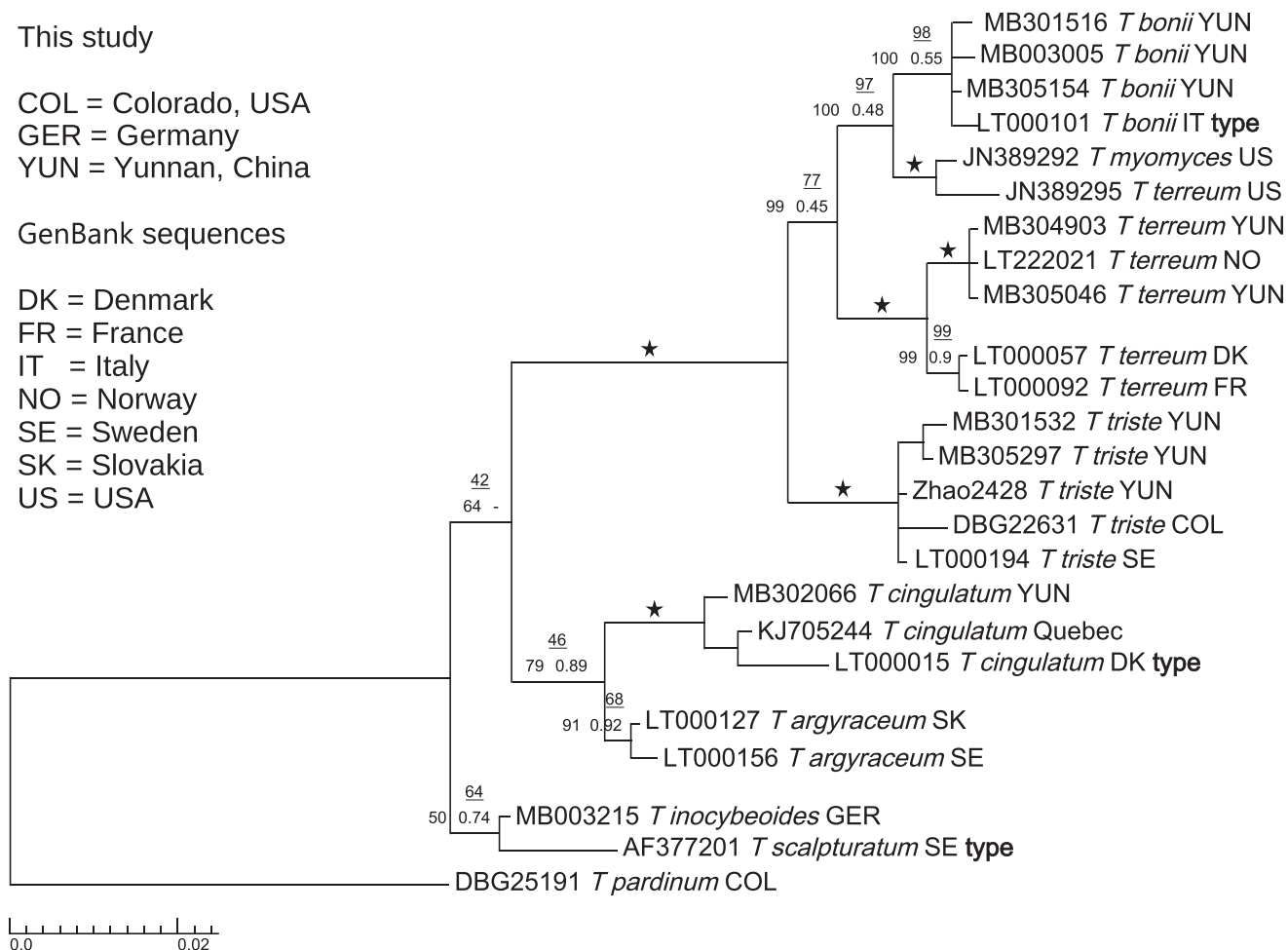


Figure 6. BI MCMC Tree of sect. *Terrea* based on ITS. Rooted to *T. pardinum*. Support values above the branches: left side = % BI posterior probability (PP); right side = NJ bootstrap value in absolute numbers; underlined on the top = % ML bootstrap value. A star denotes PP = 100 and bootstrap values at least 0.9 and 90, respectively. Not all intra-species support values are shown.

Moukha et al. 2013). Clade VI included two Scandinavian sequences, also labeled *T. frondosae*. All specimens of clades I, II, III, and IV were associated with *Pinus* spp.

Section *Terrea* Konrad & Maubl. (FIG. 6). The subclade formed by sequences of *T. terreum*, *T. bonii*, and *T. triste* was highly supported. *Tricholoma terreum* consists of two separate lineages. In addition, two sequences of specimens from North America formed a separate clade close to *T. bonii*. A subclade comprising *T. argyraceum* (Bull.) Gillet, *T. cingulatum*, *T. inocybeoides* A. Pearson, and *T. sculpturatum* (Fr.) Quél. was unsupported, with a bootstrap value of 0.45 in the NJ analysis, and was not evident in the BI and ML analyses (not shown).

Section *Rigida* (Fr.) Quél. (FIG. 7). Within sect. *Rigida*, *T. sudum* (Fr.) Quél., *T. rapipes* (Krombh.) Heilm.-Claus. & Mort. Chr., the new species *T. forteflavescens*, and *T. viridiolivaceum* G. Stev. formed highly supported clades. The clade of the new species

T. olivaceum was adequately supported by the BI and ML analyses but unsupported by the NJ analysis. Sequences of specimens identified as *T. saponaceum* were placed in four supported clades. Clade I consisted of North American specimens and the clade including *T. boudieri*. The clade formed by sequences attributed to *T. boudieri* Barla was unsupported by the ML and NJ analyses. Clade II was close to *T. rapipes*. It consisted of specimens from France and Germany. Clade III consisted of a single collection from Ukraine. Its separate position also was consistent in preliminary analyses. Clade IV was a very well supported clade of two sequences derived from collections from Yunnan. Three clades included a sequence of a collection regarded as *T. saponaceum* var. *squamosum* (Cooke) Rea because of the distinctly scaly stipes.

A clade of six sequences of North American specimens was not supported. It also included the sequence of MB-002682 from Austria in the NJ analysis.

This study

AUS = Austria
COL = Colorado, USA
GER = Germany
UKR = Ukraine
YUN = Yunnan, China

GenBank sequences

BC = British Columbia
DK = Denmark
FR = France
NZ = New Zealand
SE = Sweden
SI = Slovenia

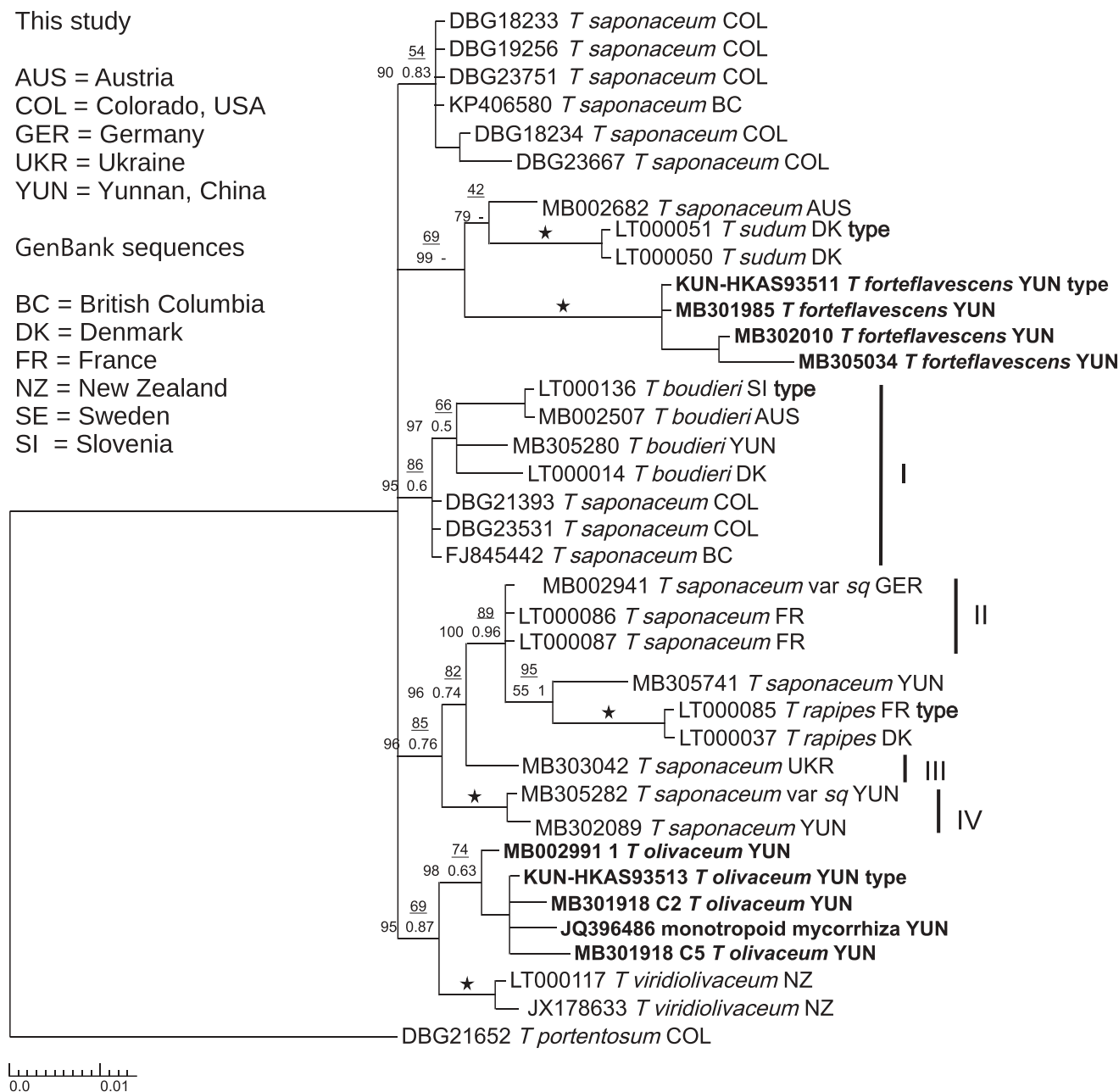


Figure 7. BI MCMC tree of sect. *Rigida* based on ITS. Rooted to *T. portentosum*. Species new to science are indicated in bold. Support values above the branches: left side = % BI posterior probability (PP); right side = NJ bootstrap value in absolute numbers; underlined on the top = % ML bootstrap value. A star denotes PP = 100 and bootstrap values at least 0.9 and 90, respectively. Not all intra-species support values are shown.

Further taxa. The following taxa could not be placed in accepted sections based on the current ITS data: *T. apium* Jul. Schäff., *T. arvernense* Bon, *T. fucatum*, *T. fumosoluteum* (Peck) Sacc., *T. josselandii*, *T. luridum* (Schaeff.) P. Kumm., *T. luteomaculosum* A.H. Sm., *T. melleum*, *T. mutabile* Shanks, and *T. vernaticum* Shanks, as well as *Tricholoma atrovioleaceum* A.H. Sm. and *T. borgsjoeense* Jacobsson & Muskos, which formed a highly supported clade (FIG. 2).

Notes on *Tricholoma foliicola*.—Two vouchers of *Tricholoma foliicola* Har. Takah. (Takahashi 2001) were analyzed. Both had minutely verrucous basidiospores. The basidiospores measured $4.5\text{--}6 \times 2\text{--}4 \mu\text{m}$ and were of rather variable shape, from oblong, ellipsoidal to amygdaloid, and also frequently dacryoid. The verrucosity was difficult to observe but became distinct after staining with Phloxine B. An ITS sequence generated had a 96% pairwise similarity to a sequence of *Gerhardtia borealis* (Fr.) Contu & Ortega.

Unfortunately, our sequence was of unsatisfactory quality and attempts to achieve reliable sequences were unsuccessful. The photographs in the original description show basidiomes with glabrous and shiny pilei. Furthermore, the pileus was described as hygrophanous. The base of the basidiomes was described as “attached to an extensive mycelial mat in the substratum,” whereas the pigmentation was reported to be “intercellular but not incrusting” (Takahashi 2001). These characters exclude classification in *Tricholoma*, because species of this genus are obligate ectomycorrhizal, lack a hygrophanous pileus, and the pigmentation is mainly encrusted and intracellular but not intercellular. However, the characters would fit quite well with *Gerhardtia*, which is consistent with the observed verrucose basidiospores. Unfortunately, the studied collections were insufficient to decide whether *T. foliicola* is conspecific with *G. borealis* or a distinct congeneric species.

Specimens examined: JAPAN. ISHIKAWA: 4 Jul 2010, TNS-F-38513. JAPAN. 12 Oct 2008, Y. Nakamura, TNS-F-44221.

TAXONOMY

Tricholoma sect. *Muscaria* K. Reschke, sect. nov.

Mycobank MB821179

Typification: *Tricholoma muscarium* Kawam. ex Hongo.

Etymology: Derived from the name of the type species of the section.

Pileus small to large, conical to convex with a pronounced rounded to acute umbo when young, later broad conical to convex, usually with pronounced umbo, yellowish, orange, olivaceous, greenish, or brownish, dry, fibrillose, often with minute scales. Stipe cylindrical to clavate, white, yellowish to orange, or a combination of these colors, often with minute scales.

Pileipellis a cutis, breaking up into small trichodermal scales. Subpellis of parenchymatoid inflated cells. Basidiospores ellipsoidal, 5–9.5 × 4–6 μm, hyaline, thin-walled, smooth, inamyloid. Cystidioid cells in hymenium present or absent. Clamps absent.

Species in the section, beside the type, are *T. aurantiipes* (Hongo 1991), *T. davisiae* (Peck 1900), and *T. muscarioides* (described below).

Notes: Species of sect. *Muscaria* are characterized by an umbonate to conical pileus with a dry, fibrillose to fine scaly surface and a distinct parenchymatoid subpellis. By their form and the often yellowish coloration, basidiomes of species of sect. *Muscaria* can be mistaken

for those of sect. *Tricholoma*. However, most species of sect. *Tricholoma* have an at least slightly viscid surface of the pileus, whereas the pileus of species in sect. *Muscaria* is dry. Species of sect. *Tricholoma* that are similar to species of sect. *Muscaria* are *T. aestuans* and *T. palustre*. These also have an umbonate to conical pileus with a dry, fibrillose and slightly scaly surface. However, in contrast to species in sect. *Muscaria*, both have an acrid to bitter taste and no distinct subpellis. *Tricholoma muscarium* and *T. davisiae* have been hypothesized to be closely related to *T. sejunctum*, *T. viridilutescens*, and closely related species (Heilmann-Clausen et al. 2017). They share yellow, greenish, and olivaceous colors and all lack clamp connections. The pilei of *T. olivaceoluteolum*, *T. sejunctum*, *T. subluteum*, and *T. viridilutescens* can also be distinctly conical, especially in young basidiomes. However, species of sect. *Muscaria* have a more pronounced umbonate pileus. All species related to *T. sejunctum* have an ixocutis with cylindrical to slightly inflated hyphae below, whereas species of sect. *Muscaria* have a cutis of parallel hyphae with a parenchymatoid subpellis. In addition, species of sect. *Muscaria* have predominantly ellipsoidal basidiospores with higher Q values on average, whereas species related to *T. sejunctum* have subglobose to broad ellipsoidal basidiospores. Species of sect. *Terrea* share characters such as a yellowing reaction and a parenchymatoid subpellis with species of sect. *Muscaria* but are generally rather monotonously blackish, grayish, brownish, or whitish. Moreover, species of sect. *Terrea* that have a distinct subpellis do not stain yellow and vice versa.

The geographical distribution of species of sect. *Muscaria* appears to be restricted to Asia and North America. Fragmentary data of two collections from China indicate a further species in Asia.

Tricholoma muscarioides K. Reschke, F. Popa, Zhu L. Yang & G. Kost, sp. nov. (FIGS. 8A, 9)

Mycobank MB821173

Typification: CHINA. YUNNAN: Ailao Shan, 24° 32.776'N, 101°01.507'E, 2500 m a.s.l., *Quercus*-dominated broad-leaved forest, 15 Jul 2007, K. Donges, G. Kost & K.-H. Rexer (holotype KUN-HKAS 93512). Isotype MB-101187.

Etymology: Named for similarity of the basidiomes of this species to those of *Tricholoma muscarium*.

Pileus 5–8 cm diam, conical to pronounced umbonate when young, later becoming convex with a distinct rounded to subacute umbo, olive-gray to olivaceous brown in the center, becoming bright yellow towards the margin, umbo sometimes whitish. Pileal surface dry, innately fibrillose, breaking up into minute scales.

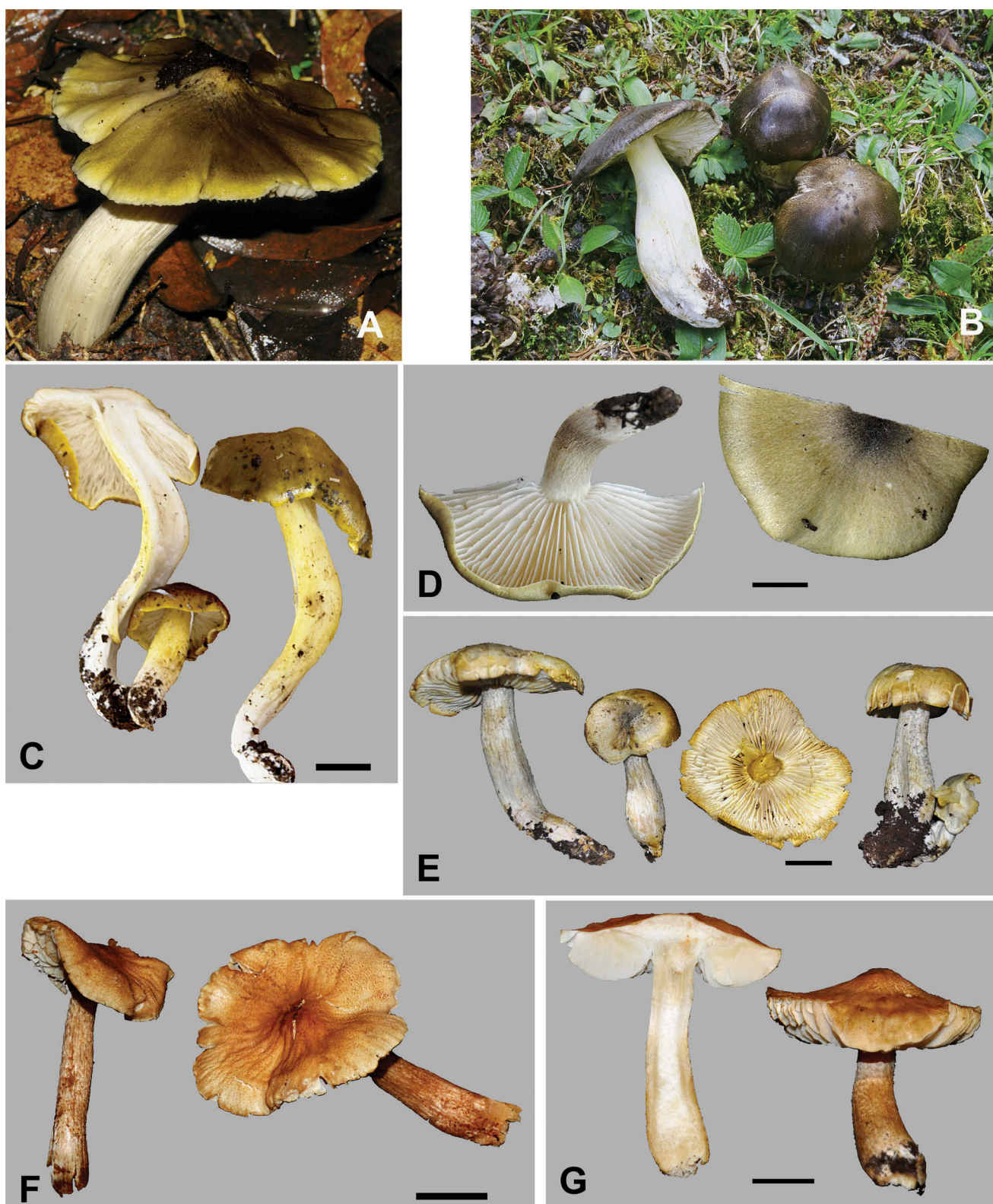


Figure 8. Photographs of basidiomes of the newly described *Tricholoma* spp. A. *T. muscarioides*, holotype (KUN-HKAS 93512), photo by G. Kost. B. *T. sinoportentosum*, holotype (KUN-HKAS 46084), photo by Z. W. Ge. C. *T. olivaceoluteolum*, holotype (KUN-HKAS 93510), photo by G. Kost. D. *T. olivaceum*, holotype (KUN-HKAS 93513), photo by F. Popa. E. *T. forteflavescens* (KUN-HKAS 93511), photo by F. Popa. F. *T. melleum*, holotype (KUN-HKAS 93514), photo by F. Popa. G. *T. melleum* (MB-305015), photo by F. Popa. Bars = 2 cm.

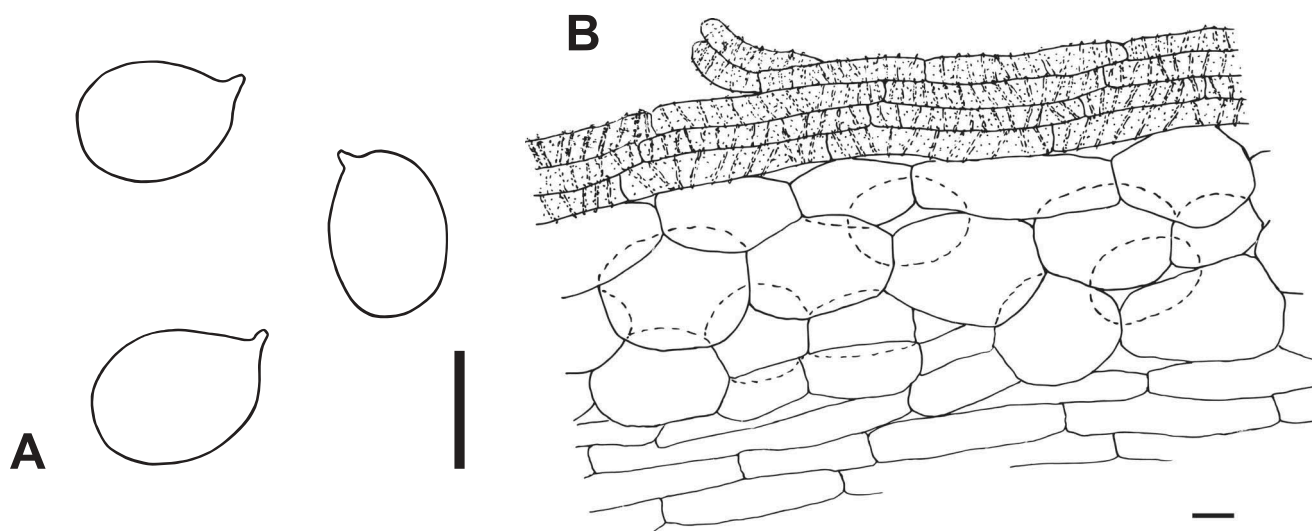


Figure 9. *Tricholoma muscarioides*, holotype (KUN-HKAS 93512). A. Spores. B. Pileipellis. Del. K. Reschke. Bars: A = 5 µm; B = 10 µm.

Lamellae sinuate, medium spaced, white to cream, with even edges. Stipe 7–15 × 1–2 cm, cylindrical, solid in young basidiomes, becoming stuffed to hollow, white, strongly fibrillose, bruising yellow after touch. Basal mycelium white. Flesh white to pale grayish. No odor noticed. Taste farinaceous and slightly bitter.

Basidiospores 6–7 × 5–5.5 µm, Q = 1.2–1.4, predominantly ellipsoidal, hyaline, thin-walled, smooth, inamyloid. Basidia 28–38 × 7–7.5 µm, clavate, hyaline, predominantly 4-spored, sterigmata up to 6 µm long. Cystidioid cells in hymenium absent. Pileipellis a cutis of cylindrical 5–6 µm wide hyphae, with encrusting and intracellular pigment, yellow to brown in KOH. Subpellis composed of nonpigmented, wide, inflated cells, 25–45 × 20–35 µm. Hyphae of stipe surface 4–7 µm wide, not distinctly pigmented. Clamps absent.

Basidiomes found scattered to gregarious, with *Quercus* spp. and *Lithocarpus* spp. in *Quercus*-dominated and *Quercus*-*Lithocarpus*-dominated broad-leaved forests at around 2500 m a.s.l. in Yunnan, China.

Additional specimens examined: CHINA. YUNNAN: Ailao Shan, 24°32'50"N, 101°1'30"E, 2500 m a.s.l., *Quercus*-*Lithocarpus*-dominated broad-leaved forest, 20 Jul 2006, G. Kost, K.-H. Rexer & Z.L. Yang (MB-002997) and 21 Jul 2006, G. Kost, K.-H. Rexer & Z.L. Yang (MB-003001). *Tricholoma muscarium*: JAPAN. KAMAKO-MURA: Iwaki, 20 Sep 1952, R. Watanabe, holotype (TNS-F-23762). JAPAN. 9 Oct 2010, T. Kudo (TNS-F-39197); ISHIKAWA: 5 Oct 2009, Y. Ikeda (TNS-F-39016).

Notes: *Tricholoma muscarioides* belongs to sect. *Muscaria*. It is characterized by a dry, distinctively umbonate pileus with bright yellow colors at the margin and olivaceous colors towards the center. It is close related and morphologically similar to *T.*

muscarium. However, *T. muscarioides* has a bright yellow pileus, becoming olive-gray towards the center, whereas *T. muscarium* is ochre with a slight olivaceous tinge, becoming brownish towards the center. The basidiospores of the *T. muscarium* specimens analyzed were on average slightly longer and narrower, 6.5–8 × 4–5.5 µm, resulting in a higher Q of 1.4–1.7. Hongo (1959) reported spore sizes of 6.5–7.5 × 4–5 µm, but did not provide Q values in his descriptions of species. He described *T. muscarium* as endemic to Honshu. Chinese reports of *T. muscarium* (Deng et al. 2004) may represent *T. muscarioides*. Coexistence of both species in the same area, however, cannot be excluded. Basidiomes of *T. davisiae* have similar colors to those of *T. muscarioides* but develop pinkish orange stains on the stipe and the lamellae edges. The basidiospores of *T. davisiae* are larger, and this species is associated with conifers. It has not yet been reported from China. *Tricholoma olivaceoluteolum* can also be quite similar in color and shape, especially in young stages. However, *T. olivaceoluteolum* has a viscid pileal surface when wet, which is evident as an ixocutis in dry specimens and has broadly ellipsoidal to subglobose basidiospores. Basidiomes of *T. sejunctum* can have similar colors, but they differ by a rather broad umbo, a viscid pileal surface, and the absence of a parenchymatoid subpellis.

Tricholoma sinoportentosum Zhu L. Yang, K. Reschke, F. Popa & G. Kost, sp. nov. (FIGS. 8B, 10)
Mycobank MB821174

Typification: CHINA. TIBET: Changdu City, Zhuge, 4200 m a.s.l., on ground under *Picea* spp., 7 Aug 2004, Z.G. We (holotype KUN-HKAS 46084).

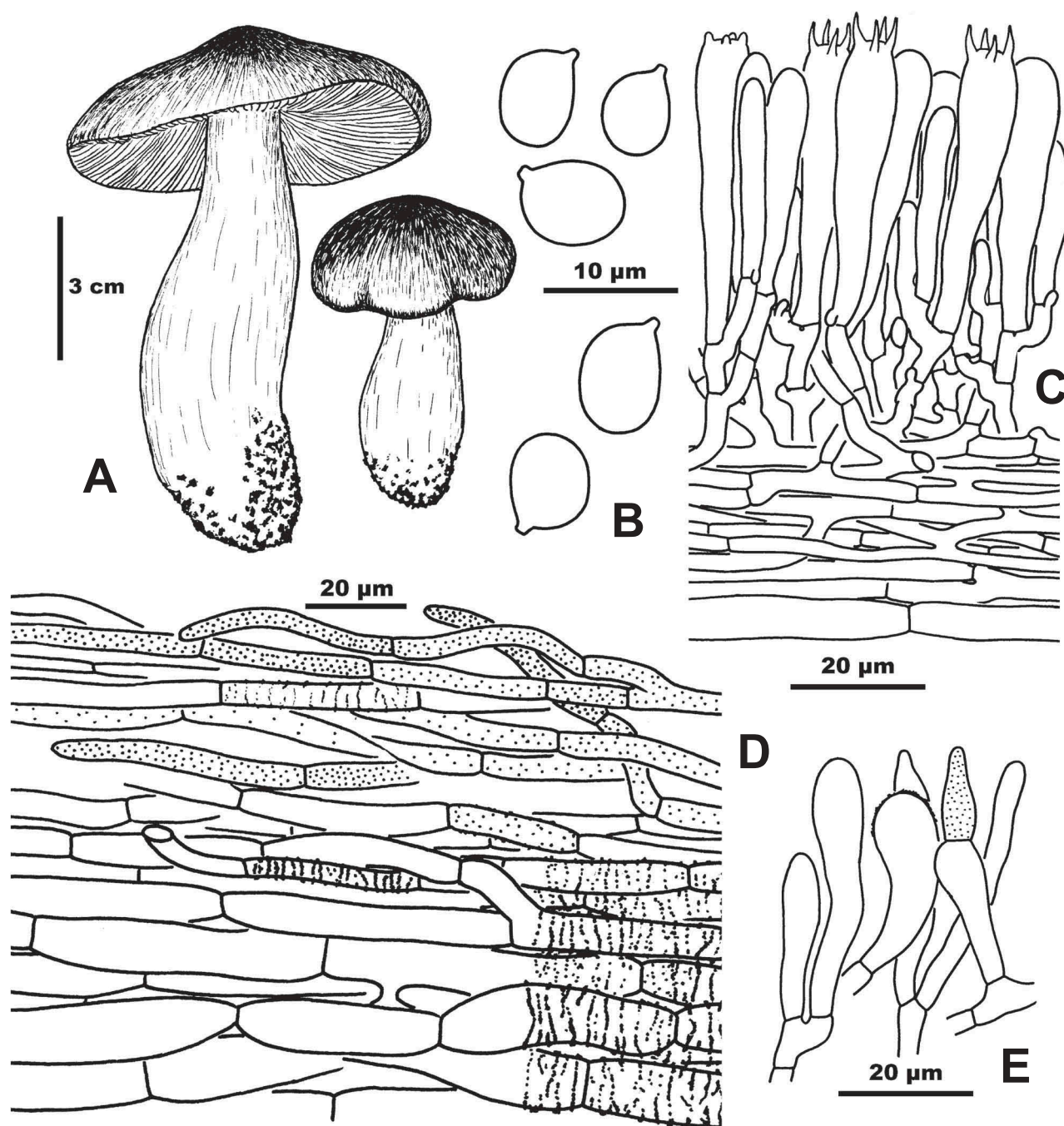


Figure 10. *Tricholoma sinoportentosum*, holotype (KUN-HKAS 46084). A. Basidiomes. B. Spores. C. Hymenial structure. D. Pileipellis. E. Young basidia and marginal cells. Del. Z. L. Yang.

Etymology: *sino* (Latin) = China, reflecting that the basidiomes were collected in China + *portentosum* for similarity of the basidiomes of this species to those *Tricholoma portentosum*.

Pileus 5–10 cm diam, hemispherical to umbonate with involute margin when young, becoming convex, usually with an umbo, dark brown to black in the center, brown to pale yellow towards the margin, pileal

surface viscid with innate radiating brown to black fibrils. Lamellae sinuate, rather crowded, white to grayish white, with even edges, becoming yellow in old or damaged basidiomes, especially near the pileus margin. Stipe 8–14 × 1–2.5 cm, cylindrical to slightly clavate, solid in young basidiomes, becoming stuffed to hollow, white fibrillose, becoming yellow with age and bruising brownish after touch. Basal mycelium white. Flesh

white to pale grayish. Odor indistinct to farinaceous. Taste mild.

Basidiospores $5.5\text{--}7 \times 5\text{--}5.5 \mu\text{m}$, $Q = 1.1\text{--}1.4$, predominantly broadly ellipsoidal, hyaline, thin-walled, smooth, inamyloid. Single basidiospores very large, up to $9 \times 8 \mu\text{m}$, especially distinct in young basidiomes. Basidia $26\text{--}34 \times 7\text{--}8 \mu\text{m}$, clavate, hyaline, predominantly 4-spored but also 1-, 2- and 3-spored, sterigmata up to $5 \mu\text{m}$ long at 4-spored basidia. Cystidioid cells on lamellar edge erratically cylindrical to clavate, some septate, sometimes with intracellular pigment, not present in all analyzed collections. Pileipellis an ixocutis formed by cylindrical $3.5\text{--}7 \mu\text{m}$ wide hyphae, pigment predominantly intracellular in the upper hyphae but strongly spirally encrusting in the bottom of the pileipellis, yellow to brownish in KOH. Hyphae of stipe surface $3.5\text{--}7 \mu\text{m}$ wide, not distinctly pigmented. Clamps frequently present at the base of basidia and in the subhymenium, but absent in other parts of the fruiting body.

Basidiomes found scattered to gregarious, with *Picea* spp. and *Pinus* spp. in coniferous forests between 3300 and 4200 m a.s.l. in Tibet and Yunnan, China.

Additional specimens examined: CHINA. TIBET: Jiangda County, Jiada, Guopi, 3900 m, on ground under *Picea* spp., 4 Aug 2009, Z.L. Yang (KUN-HKAS 58002); YUNNAN: near Yulong Xue Shan, $26^{\circ}41'8.76''$ N, $100^{\circ}1'8.26''$ E, 3300 m a.s.l., *Picea* forest intermixed with *Pinus* spp., 21 Aug 2013, G. Kost & F. Popa (MB-302015); 21 Aug 2013, G. Kost & F. Popa (MB-302067, MB-302071, MB-302074); 21 Aug 2013, F. Popa (MB-302073); and 17 Aug 2014, G. Kost & F. Popa (MB-305284);

Notes: *Tricholoma sinoportentosum* belongs to sect. *Tricholoma*. It appears to be closely related to *T. sejunctum* and allies according to its pileus color and surface structure along with the shape and size of its basidiospores. However, this association is only supported from the ML analysis (FIG. 3). *Tricholoma sinoportentosum* is characterized by the brown to black striate and viscid pileal surface, yellow stains at stipe and lamellae, and clamps at the base of the basidia. Its basidiomes resemble those of *T. portentosum* (Fr.) Quél., which also possess radiating dark fibrils, a viscid pileus, and yellow-staining basidiomes. *Tricholoma sinoportentosum* can be delimited from *T. portentosum* by the yellowish brown tones of the pileus instead of the grayish brown to almost black tones, by the broader basidiospores, and by the clamped basidia. Basidiomes of *T. viridilutescens* have a similar color but have a pileal surface that is less viscid, serrulate lamellae edges, and larger basidiospores. Basidiomes of *T. guldeniae* can also be similar in color, but its pileus is rather dry and the

basidiospores are larger. *Tricholoma sejunctum* has brighter colors on its pileus, which is greenish yellow with a darker innately fibrillose center. Its basidiospores are very similar to those of *T. sinoportentosum* in shape and size. However, *T. sejunctum* does not possess clamp connections in the hymenium. *Tricholoma subluteum* is similar because of the yellow staining of the basidiomes and the size of the basidiospores. It may also possess dark, radiating fibrils on the pileal surface (Bessette et al. 2013), but its pileus is predominantly yellow and the pileal surface is only slightly viscid when wet (Peck 1904). *Tricholoma subsejunctum* Peck is similar in the color of the pileus, the yellow staining of the basidiomes, and the size of the basidiospores, but it is described as only slightly viscid and occurring with broad-leaved evergreen and deciduous trees (Peck 1912). Moreover, clamps in the subhymenium, or at the base of the basidia, were not reported in the original description, nor in two further studies of the type (Hesler 1958; Ammirati and Ovrebo 1979). Basidiomes of *T. viridifucatum* Bon have clamps at some basidial bases of the basidia, and the basidiospores are similar in size. They differ in a squamulose stipe and bright yellowish colors.

Tricholoma olivaceoluteolum K. Reschke, F. Popa, Zhu L. Yang & G. Kost, sp. nov. (FIGS. 8C, 11)

MycoBank MB821175

Typification: CHINA. YUNNAN: Ailao Shan, $24^{\circ}32'50''$ N, $101^{\circ}1'30''$ E, 2500 m a.s.l., *Quercus-Lithocarpus*-dominated broad-leaved forest, 20 Jul 2006, G. Kost,

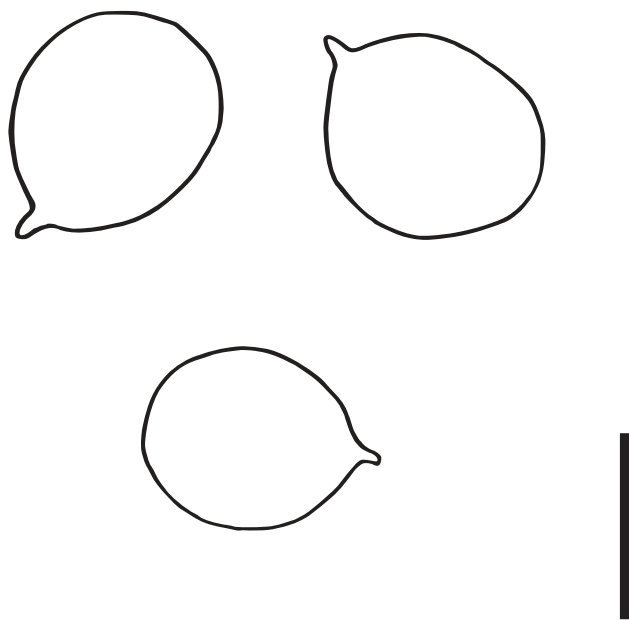


Figure 11. Spores of *T. olivaceoluteolum*, holotype (KUN-HKAS 93510). Del. K. Reschke. Bar = $5 \mu\text{m}$.

K.-H. Rexer & Z.L. Yang (**holotype** KUN-HKAS 93510). **Isotype** MB-002996.

Etymology: *olivaceus* (Latin) = olivaceous + *luteolus* (Latin) = yellowish, indicating the olivaceous and yellow coloration of the basidiomes.

Pileus 5–8 cm diam, at first conical to umbonate with involute margin, later broad umbonate to convex, when young olive brown with an orange tone getting yellow towards the margin, later yellowish brown with olive center and bright yellow towards the margin, pileal surface viscid when wet, slightly innately fibrillose. Lamellae sinuate, crowded, white to slightly cream, sometimes yellow at the very margin, with even edges. Stipe 7–12 cm, cylindrical, solid in young basidiomes, becoming stuffed to hollow, white at the base and in the upper part, yellow in the middle part, with concolorous fibrils. Basal mycelium white. Flesh white. Taste slightly bitter. No odor noticed.

Basidiospores $5.5\text{--}6.5 \times 5\text{--}6 \mu\text{m}$, $Q = 1.1\text{--}1.2$, subglobose to broadly ellipsoidal, thin-walled, hyaline, smooth, inamyloid. Basidia $26\text{--}33 \times 6\text{--}8 \mu\text{m}$, clavate, hyaline, predominantly 4-spored, sterigmata up to $5 \mu\text{m}$ long. Cystidioid cells in hymenium absent. Pileipellis an ixocutis of cylindrical $3.5\text{--}5 \mu\text{m}$ wide hyphae, with intracellular and slightly encrusting pigment, pale yellow to slightly brownish in KOH. Hyphae of stipe surface $2.5\text{--}4.5 \mu\text{m}$ wide, not distinctly pigmented. Clamps absent.

Basidiomes found scattered to gregarious, in *Quercus-Lithocarpus*-dominated broad-leaved forests at around 2500 m a.s.l. in Yunnan, China.

Additional specimens examined: CHINA. YUNNAN: Ailao Shan, $24^{\circ}32'50''\text{N}$, $101^{\circ}1'30''\text{E}$, 2500 m a.s.l., *Quercus-Lithocarpus*-dominated broad-leaved forest, 20 Jul 2006, G. Kost, K.-H. Rexer & Z.L. Yang (MB-002998, MB-002999).

Notes: *Tricholoma olivaceoluteolum* belongs to sect. *Tricholoma*, where it forms a clade with *T. sejunctum* and closely related species (FIG. 4). It is characterized by its yellow to brownish olive pileus, the viscid pileal surface, and the yellow coloration of the middle part of the stipe. It is very similar to the species invalidly described by Kawamura (1954) as *T. muscarium* in the size and color of the basidiomes and the size of the basidiospores. Kawamura's species was, however, described as having a dry pileal surface; thus, it may not be identical to *T. olivaceoluteolum*. *Tricholoma muscarium* was validated with a Latin description by Hongo (1959). It is doubtful from the basidiospore size and the shape of the basidiomes whether Hongo referred to the same species as Kawamura, but as no type was designated by Kawamura, the identity of *T. muscarium* sensu Kawamura remains obscure. Basidiomes of *T. sejunctum* are quite similar, but they can

be delimited from those of *T. olivaceoluteolum* by the more greenish pileus coloration, a white stipe, and slightly longer basidiospores with higher Q values. *Tricholoma viridilutescens* differs in having a more contrasting pileus coloration and larger basidiospores (Moser 1978). *Tricholoma luridum* differs in having gray lamellae and larger basidiospores. Basidiomes of *T. subluteum* are similar in shape but have yellow pilei without an olivaceous tinge and the basidiospores are slightly longer. Basidiomes of species of sect. *Muscaria* can be very similar in macroscopic aspects but differ in a dry pileal surface, a parenchymatoid subpellis, and ellipsoidal basidiospores. *Tricholoma viridifucatum* is similar to *T. olivaceoluteolum* in the color of the pileus and the size of the basidiospores, but it has a squamulose stipe and clamps at the base of some basidia.

Tricholoma olivaceum K. Reschke, F. Popa, Z.L. Yang & G. Kost, sp. nov. (FIGS. 8D, 12)

Mycobank MB821176

Typification: CHINA. YUNNAN: near Kunming, $25^{\circ}7'7.49''\text{N}$, $102^{\circ}52'1.6''\text{E}$, 2200 m a.s.l., mixed forest with *Pinus yunnanensis* Franch., *Cunninghamia lanceolata*, and broad-leaved trees species, 10 Aug 2013, G. Kost & F. Popa (**holotype** KUN-HKAS 93513). **Isotype** MB-301388.

Etymology: *olivaceus* (Latin) = olivaceous, referring to the color of the pileal surface.

Pileus 3–11 cm diam, convex, without umbo, margin involute when young and remaining incurved for a long time, slightly undulate and ribbed in old basidiomes, primary color bright olive, center darker, brown to almost black, towards the margin brighter olivaceous to grayish white, pileal surface glabrous with short radial and rather inconspicuous innate fibrils, particularly in the center. Lamellae sinuate, medium to rather distant, grayish white to cream, with even to distinctly serrulate edges. Stipe $4.5\text{--}8 \times 0.7\text{--}2$ cm, cylindrical to slightly clavate, tapering to a root at the base, solid in young basidiomes, becoming stuffed to hollow, white but densely overlain by dark gray to black fibrils. Slightly reddening when damaged, similar to the discoloration of *T. saponaceum*, at least in the base of bisected basidiomes. Basal mycelium white. Flesh white to pale grayish. Odor like unperfumed soap. Taste weak farinaceous to slightly bitter.

Basidiospores $4.5\text{--}6 \times 3.5\text{--}4 \mu\text{m}$, $Q = 1.3\text{--}1.6$, ellipsoidal, thin-walled, hyaline, smooth, inamyloid. Basidia $19\text{--}23 \times 5\text{--}7 \mu\text{m}$, clavate, hyaline, predominantly 4-spored, sterigmata up to $3 \mu\text{m}$ long. Cystidioid cells in hymenium absent. Pileipellis a cutis formed by cylindrical, $4\text{--}10 \mu\text{m}$ wide hyphae, with encrusting and intracellular pigment, yellowish in KOH. Hyphae of stipe

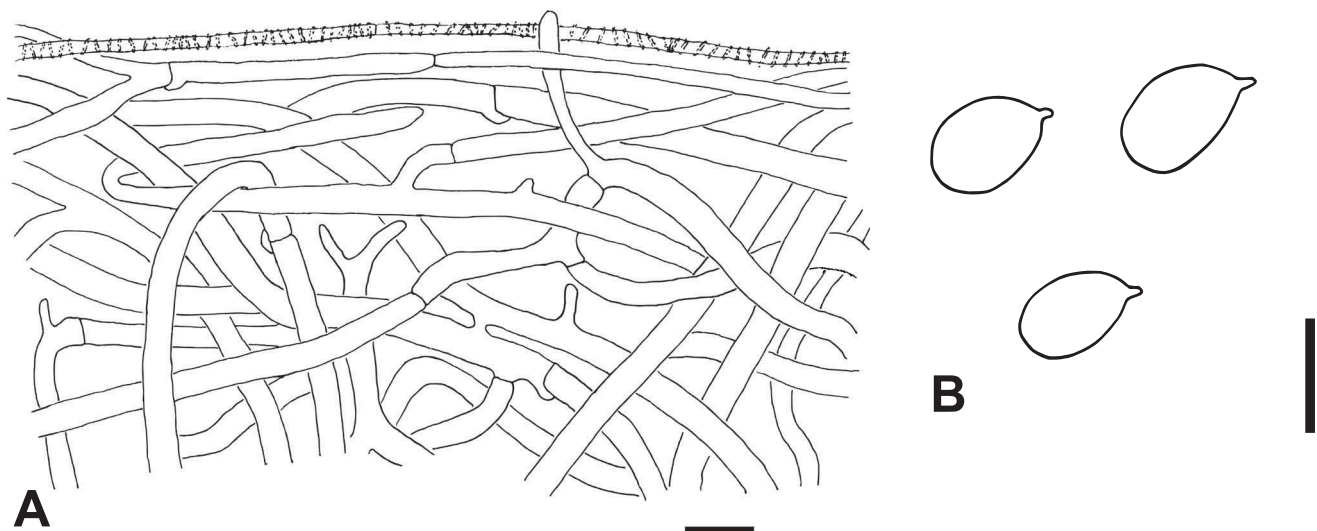


Figure 12. *Tricholoma olivaceum*, holotype (KUN-HKAS 93513). A. Pileipellis. B. Spores. Del. K. Reschke. Bars: A = 10 µm; B = 5 µm.

surface 2.5–4 µm wide, not distinctly pigmented. Clamps distinct and frequent.

Basidiomes found scattered to gregarious, also caespitose, with *Pinus* spp. and possibly other trees in *Pinus* forests and mixed forests between 2200 and 3400 m a.s.l. in Yunnan, China.

Additional specimens examined: CHINA. YUNNAN: Zishi Mountain, 25°00.409'N, 101°25.214'E, 2500 m a.s.l., *Pinus*-dominated forest with old *Quercus* and *Cunninghamia* spp., 12 Jul 2007, K. Donges, G. Kost & K.-H. Rexer (MB-002991); Yulong Xue Shan, 27°0'9.4" N, 100°11'6.75"E, 2900 m a.s.l., *Pinus armandii*-dominated mixed forest, 19 Aug 2013, G. Kost & F. Popa (MB-301918);

Notes: *Tricholoma olivaceum* belongs to sect. *Rigida*. It is characterized by the olivaceous color of the pileus, dark fibrils on the stipe, a soapy odor, and clamps in all parts of the basidiome. It is very similar to *T. viridiolivaceum* G. Stev, described from New Zealand (Stevenson 1964), which is also the closest species in the molecular phylogenies. However, *T. viridiolivaceum* has larger basidiospores (6–7 × 4–5 µm) and occurs with species of *Nothofagus* and *Leptospermum* in New Zealand. An ITS sequence deposited in GenBank as “*Tricholoma viridiolivaceum*” (KJ411953), derived from a collection from India, does not represent *T. viridiolivaceum* s.s. Thus, *T. olivaceum* can be delimited against *T. viridiolivaceum* by its distribution in the Northern Hemisphere and also by its different host association. Basidiomes of *T. rapipes* also have bright colors, including olivaceous tinges; however, they differ in predominantly yellowish colors and the absence of blackish fibrils on the pileus and stipe. Basidiomes of *T. saponaceum* sensu Christensen & Heilmann-Clausen

(2013) may also be olivaceous and have blackish fibrils on the pileus and stipe. However, basidiomes of *T. saponaceum* have rather dominant grayish colors and are generally more drab. *Tricholoma sudum* lacks olivaceous colors in the pilei and has larger basidiospores.

A BLAST search on GenBank resulted in 99% similarity to an ITS sequence (JQ396486) deposited as uncultured monotropoid mycorrhiza of *Monotropa hypopitys*. The sequence was included in the *T. olivaceum* clade in all phylogenetic analyses; thus, *T. olivaceum* is most likely a host fungus for this mycoheterotrophic Ericaceae.

Tricholoma forteflavescens K. Reschke, F. Popa, Z.L. Yang & G. Kost, sp. nov. (FIGS. 8E, 13)
Mycobank MB821177

Typification: CHINA. YUNNAN: Yulong Xue Shan, 27°0'5.34"N, 100°10'47", 3500 m a.s.l., *Quercus aquifolioides* intermixed with *Pinus yunnanensis*, 20 Aug 2013, G. Kost & F. Popa FP1006 (**holotype** KUN-HKAS 93511). **Isotype** MB-301981.

Etymology: *fortis* (Latin) = strong + *flavescere* (Latin) to become yellow, indicating that the basidiomes stain yellow when old or injured.

Pileus 4–8 cm diam, convex, margin involute when young, without umbo, light gray to silver-gray, darker in the center and paler towards the margin, sometimes light red-brown in the center or reddish tinges in parts of the pileal surface, sometimes with yellow drop-like spots at the margin, pileal surface glabrous, often concentrically cracking. Lamellae sinuate, medium spaced, grayish cream to gray, staining yellow in older basidiomes or after damage, with even to slightly serrulate edges. Stipe 5–10 × 1–2.3 cm, cylindrical to clavate, often tapering to a long rooting base, solid, grayish

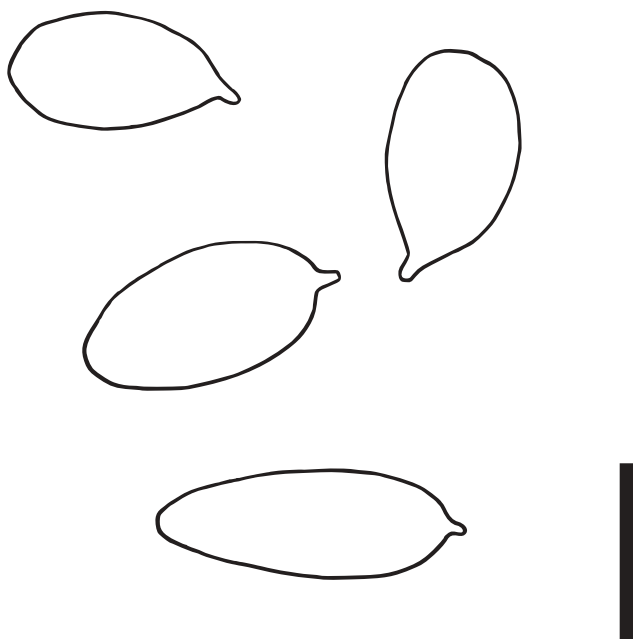


Figure 13. Spores of *T. forteflavescens*, holotype (KUN-HKAS 93511). Del. K. Reschke. Bar = 5 μ m.

white, overlain with dense gray to dark gray fibrils. Flesh white to pale grayish. All parts of the fruiting body stain citron to chrome yellow when old or after damage or touch. Odor like unperfumed soap. Taste weak.

Basidiospores 6–7(–8) \times 3–3.5 μ m, Q = 1.7–2.3(–2.7), ellipsoidal to oblong, often narrow amygdaloid, hyaline, thin-walled, smooth, inamyloid. Basidia 24–31 \times 5–6.5 μ m, clavate, hyaline, predominantly 4-spored, sterigmata up to 5 μ m long. Cystidioid cells in hymenium absent. Pileipellis a cutis formed by cylindrical, 1.5–5 μ m wide hyphae, with predominantly spirally encrusting pigment, coloration weak in KOH. Hyphae of stipe surface 3.5–6 μ m wide, not distinctly pigmented. Clamps distinct and frequent.

Basidiomes found solitary to gregarious, sometimes caespitose, close to *Quercus aquifolioides* and possibly other tree species in *Quercus aquifolioides* forests and mixed forests between 3500 and 3700 m a.s.l. in Yunnan, China.

Additional specimens examined: CHINA. YUNNAN: Yulong Xue Shan, 27°0'5.34"N, 100°10'47"E, 3500 m a.s.l., *Quercus aquifolioides* intermixed with *Pinus yunnanensis*, 20 Aug 2013, G. Kost & F. Popa (MB-301985, MB-302010) and 12 Aug 2014, G. Kost & F. Popa (MB-305034).

Notes: *Tricholoma forteflavescens* belongs to sect. *Rigida*. It is characterized by a silverish gray pileus, a strong yellowing reaction of the basidiomes, a soapy odor, and narrow basidiospores. Other species of sect.

Rigida do not stain yellow and have more broadly ellipsoidal basidiospores. *Tricholoma sulphurescens* Bres. also stains yellow but is initially white, has a strong unpleasant smell, and broadly ellipsoidal basidiospores. Other *Tricholoma* spp. with yellowing basidiomes differ by a viscid, fibrillose, felty, or squarrose pileal surface.

Tricholoma melleum K. Reschke, F. Popa, Z.L. Yang & G. Kost, sp. nov. (FIGS. 8F, G, 14)
MycoBank MB821178

Typification: CHINA. YUNNAN: near Shangri-La, 27°43'45.46"N, 99°58'43.47"E, 3700 m a.s.l., *Picea* forest with some *Quercus aquifolioides* intermixed, *Quercus* litter, 21 Aug 2014, G. Kost & F. Popa (**holotype** KUN-HKAS 93514). **Isotype** MB-305469.

Etymology: *melleus* (Latin) = color of honey, referring to the orange brown color of the pileus.

Pileus 4–8 cm diam, convex when young, later plane to depressed, usually with a broad umbo, margin undulating in older basidiomes and ribbed halfway to the center, orange brown in the center, breaking up into small scales on a light brown to orange background towards the margin, pileal surface dry. Lamellae sinuate, rather distant, thick and broad, grayish to cream, staining slightly yellowish, with smooth to slightly serrulate edges. Stipe 6–8 \times 1–2 cm, cylindrical to slightly clavate, solid in young basidiomes, becoming stuffed to hollow, concolorous with the pileus, fibrillose to scaly in the upper part, whitish pruinose at the tip of the stipe when young. Basal mycelium white. Flesh pale

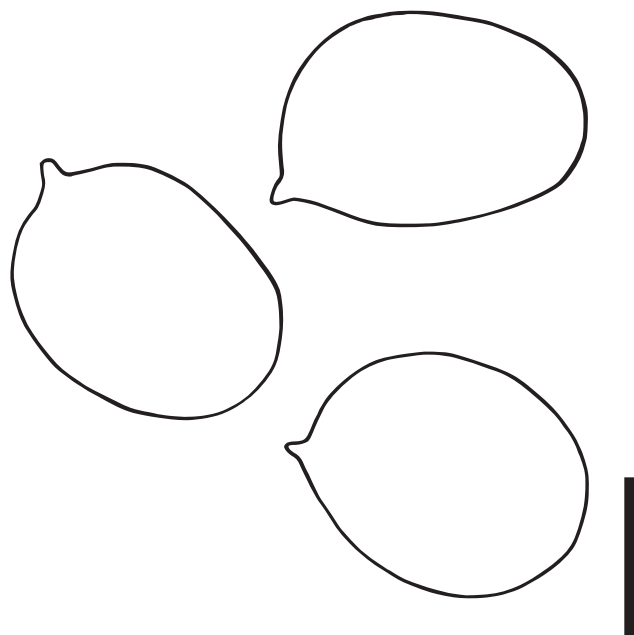


Figure 14. Spores of *T. melleum*, holotype (KUN-HKAS 93514). Del. K. Reschke. Bar = 5 μ m.

grayish to yellowish. Odor slightly sweetish aromatic, rather unpleasant. Taste not noticed.

Basidiospores $9\text{--}10.5 \times 6.5\text{--}7.5 \mu\text{m}$, $Q = 1.3\text{--}1.5$, ellipsoidal to amygdaloid, hyaline, thin-walled, smooth, inamyloid. Basidia $48\text{--}56 \times 10\text{--}11 \mu\text{m}$, clavate, hyaline, predominantly 4-spored, sterigmata up to $8 \mu\text{m}$ long. Cystidioid cells in hymenium absent. Pileipellis a cutis formed by cylindrical, $3\text{--}6 \mu\text{m}$ wide hyphae, breaking up into trichodermal scales, with mainly intracellular pigment, yellowish to pale brownish in KOH. Hyphae of stipe surface $4\text{--}8 \mu\text{m}$ wide, with intracellular and sometimes also minutely encrusting pigment, yellowish in KOH. Clamps distinct and frequent at the base of basidia and in the subhymenium, but rare to absent in other parts of the fruiting body.

Basidiomes found solitary to scattered, close to *Quercus aquifolioides* and possibly other tree species in a *Quercus aquifolioides* forest and a mixed forest at around 3700 m a.s.l. in Yunnan, China.

Additional specimen examined: CHINA. YUNNAN: Yulong Xue Shan, $27^{\circ}0'5.34''\text{N}$, $100^{\circ}10'47''\text{E}$, 3700 m a. s.l., *Quercus aquifolioides*, 12 Aug 2014, G. Kost & F. Popa (MB-305015).

Notes: *Tricholoma melleum* cannot be integrated in an existing section. It is quite different from other species in the genus. Typical basidiomes should be easy to identify in the field by the honey orange brown, fine scaly pileus, the concolorous stipe, and the broad lamellae. Additional characters are distinct clamps in the hymenium and large basidiospores. *Tricholoma psammopus* (Kalchbr.) Quél. has a dry pileus, which may be slightly scaly and of similar color, but the basidiomes are relatively small and this species is mainly associated with *Larix*. Its basidiospores are rather small, and clamps are absent in all parts of the fruiting body. *Tricholoma fucatum* also has a squamulose stipe and yellowish colors, but the basidiomes stain dark brownish, do not possess clamp connections, and have smaller basidiospores. Basidiomes of *Tricholoma coryphaum* (Fr.) Gillet sensu Riva are similar in color and a squamulose stipe. They possess clamps at the base of some basidia. However, the pileus is only squamulose in the center, the basidiospores are smaller (Riva 1988), and *T. melleum* has distinct clamps at the base of most of the basidia. Basidiomes of *T. melleum* and *Tricholoma fumosoluteum* (Peck) Sacc. may be similar to some degree. However, *T. fumosoluteum* differs by having a glabrous pileus, a white stipe, and smaller basidiospores (Peck 1875).

DISCUSSION

Diversity of *Tricholoma* species in Yunnan.—Seventy collections of *Tricholoma* spp. were made

during our field trips in Yunnan. Of these, 35 (50%) could be assigned to 14 species already described. Twenty-one collections (30%) belonged to the six newly described species. The remaining 14 collections (20%) could not be assigned to existing species; these probably include further undescribed species. An assessment of the previously published records of *Tricholoma* spp. in China (Deng et al. 2004; Deng and Yao 2005a; Yu et al. 2006; Hosen et al. 2016; Heilmann-Clausen et al. 2017; Yang et al. 2017), together with the new records and newly described species, resulted in 54 *Tricholoma* spp. that are reported from China. Of these, 38 species are reported from Yunnan. Regarding the large fraction of collections that could not be assigned to existing species and the limited range of locations sampled here, it is very likely that there still remain many *Tricholoma* spp. to be discovered in Yunnan.

Distribution of *Tricholoma* species.—Only one of the 14 identified *Tricholoma* spp., *T. aurantiipes*, is a species that is, at present, only known from Asia. All other species were originally described from Europe, whereas a distribution in North America is also known for some. None of the species found in Yunnan are distributed in the Southern Hemisphere, excluding reports of species that were introduced from the Northern Hemisphere together with host trees.

Several *Tricholoma* species were found to be distributed in Asia, Europe, and North America based on studied vouchers and comparisons of ITS sequences with sequences deposited in GenBank. *Tricholoma albobrunneum* was the most common species collected in Yunnan. It is associated with *Pinus* spp. and is rather rare in north and central Europe (Christensen and Heilmann-Clausen 2013). ITS sequences from GenBank of collections from Japan, California, and Oregon, partly deposited as *T. ustale*, along with our own data, suggest a Holarctic distribution for *T. albobrunneum*. Both *T. cingulatum* and *T. vaccinum* are reported from Europe, North America (Bessette et al. 2013), Japan (Hongo 1988), and China (Deng et al. 2004). The wide distribution of *T. cingulatum* and *T. vaccinum* is supported by the molecular and morphological data in this study.

Heilmann-Clausen et al. (2017) supposed *T. triste* to occur in Europe, North America, and China based on ITS data. This was confirmed here, including morphological analyses of the Chinese specimen (FIG. 6).

Tricholoma bonii was recently described as a new species with a white-colored pileus and lacking an inflated subpellis (Basso and Candusso 1997). However, Christensen and Heilmann-Clausen (2013)

reported a dark brown species with distinct subpellis based on analysis of the type and their own material. Just recently, *T. bonii* was reported to occur in China based on molecular data (Heilmann-Clausen et al. 2017). *Tricholoma bonii* was collected at least on three occasions in *Pinus* forests at about 2700–2900 m a.s.l. in Yunnan. Sequences derived from North American specimens form a close but separate clade to *T. bonii* and may represent another species (FIG. 6).

Tricholoma imbricatum, associated with *Pinus* spp., also reveals a wide distribution. However, the collections from Colorado form a separate, highly supported clade in the phylogeny (FIG. 3). Only the NJ analysis supports a clade formed by sequences assigned to *T. imbricatum* from Colorado, Europe, and Yunnan. This may be an effect of the large geographical gaps between the collection sites. However, a closely related, morphologically similar species cannot be excluded.

In addition, *T. populinum*, exclusively associated with *Populus* spp., is separated into two clades. Grubisha et al. (2012) reported two distinctly separate lineages of *T. populinum* from North America and Scandinavia. However, they did not consider *Tricholoma fulvimarginatum* Ovrebo & Halling, which is similar to *T. populinum* and is also associated with *Populus* spp. (Ovrebo and Halling 1986). The sequence of the *T. populinum* collection from Yunnan is included in a clade with the North American sequences. However, to date, it is the only ITS sequence available for Asia; thus, large gaps span the sampled locations. To attain an accurate estimate of the distribution of *T. populinum*, collections from further locations have to be studied.

A distribution in Asia, Europe, and North America of *T. matsutake* has already been reported by Chapela and Garbelotto (2004) and confirmed by Trudell et al. (2017) using ITS data. Carriconde et al. (2008) suggested a cosmopolitan distribution of *T. scalpturatum*, meaning a Holarctic distribution. It has been reported from North America by Ovrebo (1989), from Japan by Hongo (1988), and from China by Deng et al. (2004). However, no evidence for a distribution in Asia or America exists at the molecular level. *Tricholoma scalpturatum* may be difficult to distinguish from *T. argyraceum* (Bull.) Gillet, assumed to be a cryptic species by Carriconde et al. (2008). Both species are rather nondescript and are reported to associate with various hosts (Christensen and Heilmann-Clausen 2013). Considering the limited data and potentially unknown similar species in Asia and America, the distribution of *T. scalpturatum* is actually unknown outside of Europe.

Tricholoma viridilutescens is also reported to occur with different tree genera; however, the suggested

associations are slightly different: Moser (1978) described *T. viridilutescens* as associated with *Picea* spp. and *Pinus* spp. from Austria and Sweden, whereas Christensen and Heilmann-Clausen (2013) reported the species in Sweden and throughout the Alps and associated with *Picea* spp. and *Abies* spp. Specimen MB-002842 was collected in the north of Austria under *Picea abies*. However, its ITS sequence differs distinctly from sequence data of three specimens from France generated by Heilmann-Clausen et al. (2017). Two ITS sequences similar to that of the collection from Austria originate from Canada and from Japan. The Japanese specimen was recorded as associated with *Tsuga diversifolia* (Miyamoto et al. 2014), thus adding a further genus to the possible tree hosts. The wide distribution of *T. japonicum* indicated by ITS-data (FIG. 2) is already reported by Christensen and Heilmann-Clausen (2013).

The unclear taxonomic status and differing concepts of numerous species prevent the application of survey lists and fungal inventories for distribution assessments. Thus, knowledge of distribution patterns in *Tricholoma* so far depends on taxonomic progress in the genus.

Phylogeny.—Infrageneric ranks. Section *Tricholoma* is currently the largest section in the genus. Several species from Asia and North America are included, thus raising the number of species beyond 25. An older name for this autonym is sect. *Limacina* (Fr.) Quél. (Quélet 1872). The collection MB-305716 potentially represents a further new species in the section (FIG. 4). However, a formal description is not possible because of insufficient material.

Section *Genuina* comprises 15 species. This section also includes species from the Southern Hemisphere. Besides *T. elegans* from New Zealand, several species in the section are reported from South America by Horak (1964) and Singer (1966). The collection MB-301976 represents a potentially new species (FIG. 3).

Section *Rigida* dates back to sect. *Rigida* of *Agaricus* tribus *Tricholoma* of Fries (1838) and was combined and emended by Quélet (1872). Later synonyms are *Aggregata* Konrad & Maubl. (Konrad and Maublanc 1937) and *Contextocutis* Singer, which was described as a subgenus with a rather broad concept (Singer 1943). Species of the section are characterized by soapy odors, abundant clamp connections, and a rather weakly differentiated cutis. Singer (1943) supposed that species of the subg. *Contextocutis* have only intracellular pigment in the pileipellis. However, both species in

sect. *Rigida* described from Yunnan also have encrusting pigment.

Section *Megatricholoma* (G. Kost) Mort. Chr. & Noordel. was recently delimited to include *T. acerbum* and *T. japonicum* in addition to *T. colossus* (Heilmann-Clausen et al. 2017). Because this is not supported by our molecular analyses, this section is treated in a narrow sense here, including only *T. colossus*. The inclusion of *T. sinoacerbum* and possibly further related taxa, and the use of several molecular markers for phylogenetic analyses and a reassessment of the morphological characters, may lead to a more robust concept of this section.

Apart from sect. *Muscaria*, the sections recognized in the phylogeny are, for the most part, similar to those of Christensen and Heilmann-Clausen (2013) and Heilmann-Clausen et al. (2017). However, *T. melleum* from Yunnan and several species from North America seem to represent separate lineages that are absent or unknown in Europe. The inclusion of further species from Asia and North America and an analysis of multiple loci in molecular phylogenies may elucidate the infrageneric structure and reveal additional sections in future treatments of the genus.

Tricholoma sect. *Rigida*. *Tricholoma saponaceum* and its closely related species were the subject of taxonomic controversies since Friesian times. Until recently, only *T. saponaceum* and *T. sudum* were accepted as species. Others were interpreted at the variety rank by many mycologists (e.g., Horak 2005; Christensen and Heilmann-Clausen 2012), although Bon additionally distinguished *T. boudieri* (Bon 1984). In their monograph, Christensen and Heilmann-Clausen (2013) also recognized, in addition to the latter three, *T. rapipes* as a recombination of *T. saponaceum* var. *napipes* (Krombh.) J.E. Lange. *Tricholoma viridiolivaceum*, a species from New Zealand, is also a member of sect. *Rigida*. This species is closely related to the newly described *T. olivaceum*. Although all these species are rather well defined now, it is quite unclear what the “true” *T. saponaceum* actually is. Four supported clades that include sequences labeled as *T. saponaceum* resulted from our molecular analyses (FIG. 7). Clade I includes *T. boudieri* and the North American sequences therein may belong to that species. Clade IV is a highly supported clade of two collections from Yunnan, which potentially represent an undescribed species. Both were collected in a *Picea* forest. Further, extensive sampling is needed to clarify the taxonomic state of these clades. The macromorphology, as well as the ecology, are important characters to record in the

future, because the micromorphological differences appear to be small.

Tricholoma equestre complex. *Tricholoma equestre* and its allies are a difficult and still unresolved species complex. Although *T. flavovirens* (Pers.) S. Lundell and *T. auratum* Gillet are regarded as synonyms (Deng and Yao 2005b; Christensen and Heilmann-Clausen 2013), two new species were described by Kalamees from north Europe (Kalamees 2001): *T. frondosae* and *T. ulvenii* Kalamees. Another similar species is *T. chrysophyllum* A. Riva et al., described from Spain (Riva 1998). Christensen and Heilmann-Clausen (2013) reported at least three species within the complex: *T. equestre* s.s. and two molecularly different, but as yet unresolved, species within their concept of *T. frondosae*. They were unable to confirm *T. ulvenii*. Moukha et al. (2013) report three clades within the grouping: *T. frondosae*, *T. equestre* s.l., and a clade corresponding to four specimens from Japan labeled *T. auratum*. The inclusion of six sequences derived from specimens collected in Yunnan led to the recognition of additional clades (FIG. 5). Both *T. equestre* and *T. frondosae* appear to be complexes composed of several lineages that may represent separate species. The lineages of *T. equestre* s.l. appear to be restricted to *Pinus* spp., whereas the lineages of *T. frondosae* s.l. seem able to associate with *Populus* spp. and coniferous trees, as reported in Europe by Christensen and Heilmann-Clausen (2013). However, the plant partner often could not be determined for collections found in mixed forests in Yunnan.

ACKNOWLEDGMENTS

We thank the Sam Mitchel Herbarium of Fungi, Denver Botanic Gardens (DBG), and the National Museum of Nature and Science, Tokyo (TNS), for loans of herbarium specimens. Morten Christensen and Jacob Heilmann-Clausen kindly provided at that time unpublished ITS sequences and valuable comments. Jerry Cooper provided unpublished sequence data for comparison and important information on New Zealand *Tricholoma* species. Karl-Heinz Rexer is thanked for comments, advice, and help with loan requests. Zai-Wei Ge, Mitko Karadelev, Karin Pätzold, Matthias Theiß, and Qi Zhao provided *Tricholoma* collections to the involved herbaria, which is highly appreciated. Meike Piepenbring is thanked for numerous valuable comments on a preliminary version of the manuscript. Members working at the Ailao Shan Station for Subtropical Forest Ecosystem Research Studies, Yunnan, are acknowledged for their kind support. Björn Sandrock is thanked for help with molecular cloning. Various comments of J. Heilmann-Clausen and Clark Ovrebo considerably improved the manuscript.

FUNDING

ZLY's participation was supported by the National Natural Science Foundation of China (No. 31770032).

ORCID

Kai Reschke  <http://orcid.org/0000-0001-5790-843X>

LITERATURE CITED

- Adhikari MK. 2000. Mushrooms of Nepal. Kathmandu, Nepal: KS Adhikari. 236 p.
- Ammirati JF, Ovrebo CL. 1979. Type studies: some *Cortinarius* and *Tricholoma* species described by Charles Horton Peck [Fungi]. *Mycotaxon* 8:353–371.
- Basso MT, Candusso M. 1997. *Tricholoma bonii*. *Documents Mycologiques* 107:64–71.
- Bessette AE, Bessette AR, Roody WC, Trudell SA. 2013. *Tricholomas* of North America: a mushroom field guide. Austin, Texas: University of Texas Press. 220 p.
- Bidartondo MI, Bruns TD. 2001. Extreme specificity in epiparasitic Monotropeoideae (Ericaceae): widespread phylogenetic and geographical structure. *Molecular Ecology* 10:2285–2295.
- Bidartondo MI, Bruns TD. 2002. Fine-level mycorrhizal specificity in the Monotropeoideae (Ericaceae): specificity for fungal species groups. *Molecular Ecology* 11:557–569.
- Bon M. 1984. Les *Tricholomes* de France et d'Europe occidentale. Paris, France: Lechevalier. 324 p.
- Bon M. 1991. Les *Tricholomes* et ressemblants—Tricholomataceae (Fayod) Heim, 1^{ère} partie. *Documents Mycologiques, Mémoire Hors-Série*. 163 p.
- Carriconde F, Gardes M, Jargeat P, Heilmann-Clausen J, Mouhamadou B, Gryta H. 2008. Population evidence of cryptic species and geographical structure in the cosmopolitan ectomycorrhizal fungus, *Tricholoma scalpturatum*. *Microbial Ecology* 56:513–524, doi:10.1007/s00248-008-9370-2
- Castresana J. 2000. Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution* 17:540–552.
- Chapela IH, Garbelotto M. 2004. Phylogeography and evolution in matsutake and close allies inferred by analyses of ITS sequences and AFLPs. *Mycologia* 96:730–741.
- Christensen M, Heilmann-Clausen J. 2009. Two new boreal species of *Tricholoma* from Fennoscandia. *Mycotaxon* 107:431–440, doi:10.5248/107.431
- Christensen M, Heilmann-Clausen J. 2012. *Tricholoma* (Fr.) P. Kumm. In: Knudsen H, Vesterholt J, eds. *Funga Nordica*. Copenhagen, Denmark: Nordsvamp. p. 494–510.
- Christensen M, Heilmann-Clausen J. 2013. The genus *Tricholoma*. Tilst, Denmark: Svampetryk. 228 p.
- Christensen M, Noordeloos ME. 1999. Notulae ad floram agaricinum neerlandicam XXXVI—*Tricholoma*. *Persoonia* 17:295–317.
- Cline ET. 2004. Mycorrhizal fungus communities of Douglas-fir (*Pseudotsuga menziesii*) seedlings and trees: effects of proximity to residual trees [doctoral thesis]. Seattle, Washington: University of Washington. 164 p.
- Deng H, Yao YJ. 2005a. Revision of three species of *Tricholoma* reported from China. *Mycotaxon* 92:77–84.
- Deng H, Yao YJ. 2005b. *Tricholoma equestre*, the correct name for *T. flavovirens* (Agaricales). *Mycotaxon* 94:325–329.
- Deng H, Yao Y-J, Pegler DN. 2004. An annotated checklist of *Tricholoma* from China. *Journal of Fungal Research* 2:1–18.
- Dentinger BTM, Ammirati JF, Both EE, Desjardin DE, Halling RE, Henkel TW, Moreau P-A, Nagasawa E, Soytong K, Taylor AF, Watling R, Moncalvo J-M, McLaughlin DJ. 2010. Molecular phylogenetics of porcini mushrooms (*Boletus* section *Boletus*). *Molecular Phylogenetics and Evolution* 57:1276–1292, doi:10.1016/j.ympev.2010.10.004
- Felsenstein J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39:783–791, doi:10.2307/2408678
- Fries EM. 1821. *Systema mycologicum*, Vol. 1. Lund & Greifswald: Ex Officina Berlingiana. 520 p.
- Fries EM. 1838. *Epicrisis systematis mycologici, seu synopsis Hymenomycetum*. Uppsala: Typographia Academica. 610 p.
- Fries EM. 1874. *Hymenomycetes europaei*. Uppsala: Berling. 756 p.
- Gardes M, Bruns TD. 1993. ITS primers with enhanced specificity for basidiomycetes—application to the identification of mycorrhizae and rusts. *Molecular Ecology* 2:113–118.
- Gogoi Y, Sarma TC. 2012. An ethnomycological survey in some areas of Dhemaji district (Assam). *The Ecoscan* 1:403–407.
- Grubisha LC, Levsen N, Olson MS, Lee Taylor D. 2012. Intercontinental divergence in the *Populus*-associated ectomycorrhizal fungus, *Tricholoma populinum*. *New Phytologist* 194:548–560, doi:10.1111/j.1469-8137.2012.04066.x
- Gulden G. 1969. *Musseronflora: slekten Tricholoma* (Fr. ex Fr.) Kummer sensu lato. Oslo, Norway: Universitetsforlaget. 96 p.
- Hawksworth DL. 2001. The magnitude of fungal diversity: the 1.5 million species estimate revisited. *Mycological Research* 105:1422–1432.
- Hawksworth DL. 1991. The fungal dimension of biodiversity: magnitude, significance, and conservation. *Mycological Research* 95:641–655, doi:10.1016/S0953-7562(09)80810-1
- Heilmann-Clausen J, Christensen M, Frøslev TG, Kjølner R. 2017. Taxonomy of *Tricholoma* in northern Europe based on ITS sequence data and morphological characters. *Persoonia* 38:38–57.
- Hesler LR. 1958. Southeastern Agaricales II. Studies of *Tricholoma* types. *Journal of the Tennessee Academy of Science* 33:186–191.
- Hongo T. 1959. The Agaricales of Japan 1. *Memoirs of the Faculty of Liberal Arts and Education, Shiga University Natural Science* 9:47–94.
- Hongo T. 1968. *Notulae Mycologicae* (7). *Memoirs of the Faculty of Liberal Arts and Education, Shiga University Natural Science* 18:47–52.
- Hongo T. 1983. *Notulae Mycologicae* (18). *Memoirs of the Faculty of Education, Shiga University Natural Science* 33:37–41.

- Hongo T. 1988. On the genus *Tricholoma* of Japan. *Transactions of the Mycological Society of Japan* 29:441–447.
- Hongo T. 1991. Materials for the fungus flora of Japan, 45. *Transactions of the Mycological Society of Japan* 32:463–465.
- Horak E. 1964. *Fungi Austroamerici I - Tricholoma*. *Sydowia* 17:153–167.
- Horak E. 2005. *Röhrlinge und Blätterpilze in Europa*. Munich, Germany: Elsevier, Spektrum Akademischer Verlag. 555 p.
- Hosen MI, Li T-H, Li T, Zhong X-J, Chen Y. 2016. *Tricholoma sinoacereum*, a bitter species from Guangdong Province of China. *Mycoscience* 57:233–238, doi:10.1016/j.myc.2016.02.002
- Huelsenbeck JP, Ronquist F. 2001. MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* 17:754–755.
- Jones MD, Twieg BD, Durall DM, Berch SM. 2008. Location relative to a retention patch affects the ECM fungal community more than patch size in the first season after timber harvesting on Vancouver Island, British Columbia. *Forest Ecology and Management* 255:1342–1352.
- Kalamees K. 2001. Taxonomy and ecology of the species of the *Tricholoma equestre* group in the Nordic and Baltic countries. *Folia Cryptogamica Estonica* 38:13–23.
- Katoh K, Standley DM. 2013. MAFFT: Multiple Sequence Alignment Software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 30:772–780, doi:10.1093/molbev/mst010
- Kawamura S. 1954. *Icones of Japanese fungi*. Vol. IV. Tokyo, Japan. Kazamashobo. 199 p.
- Khaund P, Joshi SR. 2013. Wild edible macrofungal species consumed by the Khasi tribe of Meghalaya, India. *Indian Journal of Natural Products and Resources* 4:197–204.
- Kiet TT. 1998. Preliminary checklist of macrofungi of Vietnam. *Feddes Repertorium* 109:257–277, doi:10.1002/fedr.19981090309
- Kikuchi K, Matsushita N, Guerin-Laguette A, Ohta A, Suzuki K. 2000. Detection of *Tricholoma matsutake* by specific ITS primers. *Mycological Research* 104:1427–1430, doi:10.1017/S0953756200002653
- Kikuchi K, Matsushita N, Suzuki K. 2007. Discrimination of *Tricholoma* species by species-specific ITS primers. *Mycoscience* 48:316–320, doi:10.1007/s10267-007-0368-2
- Konrad P, Maublanc A. 1937. *Icones selectae fungorum*. Tome VI. Paris: Paul Lechevalier. 558 p.
- Kost G. 1981. Vergleichende morphologische, anatomische und feinstrukturelle Merkmalsstudien an Arten der Gattung *Tricholoma* (Fr.) Staude, Sektion *Genuina* (Fr.) Sacc. [PhD dissertation]. Tübingen, Germany: Eberhard-Karls-Universität. 152 p.
- Kranabetter JM, Friesen J, Gamiet S, Kroeger P. 2009. Epigeous fruiting bodies of ectomycorrhizal fungi as indicators of soil fertility and associated nitrogen status of boreal forests. *Mycorrhiza* 19:535–548, doi:10.1007/s00572-009-0255-0
- Mandel M, Higa A. 1970. Calcium-dependent bacteriophage DNA infection. *Journal of Molecular Biology* 53:159–162, doi:10.1016/0022-2836(70)90051-3
- Matheny PB, Curtis JM, Hofstetter V, Aime MC, Moncalvo J-M, Ge Z-W, Yang Z-L, Slot JC, Ammirati JF, Baroni TJ, Bougher NL, Hughes KW, Lodge DJ, Kerrigan RW, Seidl MT, Aanen DK, DeNitis M, Daniele GM, Desjardin DE, Kropp BR, Norvell LL, Parker A, Vellinga EC, Vilgalys R, Hibbett DS. 2006. Major clades of Agaricales: a multilocus phylogenetic overview. *Mycologia* 98:982–995, doi:10.3852/mycologia.98.6.982
- McNeill J, Barrie FR, Burdet HM, Demoulin V, Hawksworth DL, Marhold K, Nicolson DH, Prado J, Silva PC, Skog JE, Wiersema JH, Turland NJ. 2006. *International Code of Botanical Nomenclature* (Vienna Code). Ruggell, Liechtenstein: ARG Ganter Verlag. 568 p.
- Miller M, Pfeiffer W, Schwartz T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: *Gateway Computing Environments Workshop (GCE)*, 2010. IEEE. p. 1–8.
- Miyamoto Y, Nakano T, Hattori M, Nara K. 2014. The mid-domain effect in ectomycorrhizal fungi: range overlap along an elevation gradient on Mount Fuji, Japan. *ISME Journal* 8:1739–1746, doi:10.1038/ismej.2014.34
- Morris MH, Pérez-Pérez MA, Smith ME, Bledsoe CS. 2009. Influence of host species on ectomycorrhizal communities associated with two co-occurring oaks (*Quercus* spp.) in a tropical cloud forest. *FEMS Microbiology Ecology* 69:274–287, doi:10.1111/j.1574-6941.2009.00704.x
- Moser MM. 1978. *Fungorum rariorum icones coloratae—pars VII*. Vaduz, Liechtenstein: J. Cramer. 48 p.
- Moukha S, Férandon C, Beroard E, Guinberteau J, Castandet B, Callac P, Creppy E, Barroso G. 2013. A molecular contribution to the assessment of the *Tricholoma equestre* species complex. *Fungal Biology* 117:145–155, doi:10.1016/j.funbio.2013.01.003
- Murata H, Ota Y, Yamada A, Ohta A, Yamanaka T, Neda H. 2013a. Phylogenetic position of the ectomycorrhizal basidiomycete *Tricholoma dulciolens* in relation to species of *Tricholoma* that produce “matsutake” mushrooms. *Mycoscience* 54:438–443, doi:10.1016/j.myc.2013.02.003
- Murata H, Ota Y, Yamaguchi M, Yamada A, Katahata S, Otsuka Y, Babasaki K, Neda H. 2013b. Mobile DNA distributions refine the phylogeny of “matsutake” mushrooms, *Tricholoma* sect. *Caligata*. *Mycorrhiza* 23:447–461, doi:10.1007/s00572-013-0487-x
- Murrill WA. 1913. The Agaricaceae of the Pacific Coast: IV. New Species of *Clitocybe* and *Melanoleuca*. *Mycologia* 5:206–223, doi:10.2307/3753386
- Murrill WA. 1938. New Florida agarics. *Mycologia* 30:359–371.
- Murrill WA. 1942. New fungi from Florida. *Lloydia* 5:136–157.
- Murrill WA. 1945. More fungi from Florida. *Lloydia* 7:303–327.
- Murrill WA. 1949. Florida *Tricholomas*. *Lloydia* 12:62–69.
- Myers N, Mittermeier RA, Mittermeier CG, Fonseca GAB da, Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853–858, doi:10.1038/35002501
- Noordeloos ME, Christensen M. 1999. *Tricholoma*. In: Bas C, Kuyper TW, Noordeloos ME, Vellinga EC, eds. *Flora Agaricina Neerlandica*. Rotterdam, The Netherlands: A.A. Balkema. p. 107–148.
- Ovrebo CL. 1989. *Tricholoma*, subgenus *Tricholoma*, section *Albidogrisea*: North American species found principally in the Great Lakes region. *Canadian Journal of Botany* 67:3134–3152, doi:10.1139/b89-393

- Ovrebo CL, Halling RE. 1986. *Tricholoma fulvimarginatum* (Tricholomataceae): a new species from North America associated with cottonwood. *Brittonia* 38:260–263, doi:10.2307/2807351
- Peck CH. 1875. Report of the State Botanist. Annual Report of the State Museum of Natural History 27:73–116.
- Peck CH. 1891. Report of the Botanist (1890). Annual Report on the New York State Museum of Natural History 44:117–187.
- Peck CH. 1900. New species of Fungi. Bulletin of the Torrey Botanical Club 27:609–613, doi:10.2307/2477998
- Peck CH. 1904. Report of the State Botanist 1903. Bulletin of the New York State Museum 75:1–68.
- Peck CH. 1912. Report of the New York State Botanist 1911. New York State Museum Bulletin 157:5–139.
- Pickles BJ, Genney DR, Anderson IC, Alexander IJ. 2012. Spatial analysis of ectomycorrhizal fungi reveals that root tip communities are structured by competitive interactions. *Molecular Ecology* 21:5110–5123.
- Quélet L. 1872. Les champignons de Jura et des Vosges. Montbéliard: Imprimerie et Lithographie de Henri Barbier. 424 p.
- Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA. 2018. Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* syy032, doi:10.1093/sysbio/syy032
- Riva A. 1988. Fungi Europaei Vol. 3, *Tricholoma* (Fr.) Staude. Alassio, Italy: Edizioni Candusso. 618 p.
- Riva A. 1998. Fungi non delineati V: *Tricholoma* (Fr.) Staude. Alassio, Italy: Mykoflora. 44 p.
- Riva A. 2003. *Tricholoma* (Fr.) Staude. Alassio, Italy: Candusso. 201 p.
- Ronquist F, Teslenko M, Mark P van der, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP. 2012. MrBayes 3.2: efficient bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539–542, doi:10.1093/sysbio/sys029
- Sambrook J, ed. 2012. Molecular cloning: a laboratory manual. Cold Spring Harbor, New York: Cold Spring Harbor Laboratory Press. 1333 p.
- Sánchez-García M, Matheny PB, Palfner G, Lodge DJ. 2014. Deconstructing the Tricholomataceae (Agaricales) and introduction of the new genera *Albomagister*, *Corneriella*, *Pogonoloma* and *Pseudotracheloma*. *Taxon* 63:993–1007, doi:10.12705/635.635.3
- Sanmee R, Dell B, Lumyong P, Lumyong S. 2007. First record of *Tricholoma fulvocastaneum* from Thailand. *Mycoscience* 48:131–133, doi:10.1007/s10267-006-0341-5
- Singer R. 1943. Das System der Agaricales III. *Annales Mycologici* 41:1–189.
- Singer R. 1966. Monographs of South American Basidiomycetes, especially those of the east slope of the Andes and Brazil. IX. *Tricholoma* in Brazil and Argentina. *Darwiniana* 14:19–35.
- Singer R. 1986. The Agaricales in modern taxonomy. Koenigstein, Germany: Koeltz Scientific Books. 981 p.
- Stamatakis A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30:1312–1313, doi:10.1093/bioinformatics/btu033
- Stevenson G. 1964. The Agaricales of New Zealand: V. *Kew Bulletin* 19:1–59, doi:10.2307/4108283
- Stöver BC, Müller KF. 2010. TreeGraph 2: combining and visualizing evidence from different phylogenetic analyses. *BMC Bioinformatics* 11:7, doi:10.1186/1471-2105-11-7
- Takahashi H. 2001. Notes on new Agaricales of Japan 3. *Mycoscience* 42:355–360, doi:10.1007/BF02461218
- Talavera G, Castresana J. 2007. Improvement of phylogenies after removing divergent and ambiguously aligned blocks from protein sequence alignments. *Systematic Biology* 56:564–577, doi:10.1080/10635150701472164
- Tamura K, Stecher G, Peterson D, Filipski A, Kumar S. 2013. MEGA6: Molecular Evolutionary Genetics Analysis version 6.0. *Molecular Biology and Evolution* 30:2725–2729.
- Tanti B, Lisha G, Chandra SG. 2011. Wild edible fungal resources used by ethnic tribes of Nagaland, India. *Indian Journal of Traditional Knowledge* 10:512–515.
- Teasdale SE, Beulke AK, Guy PL, Orlovich DA. 2013. Environmental barcoding of the ectomycorrhizal fungal genus *Cortinarius*. *Fungal Diversity* 58:299–310.
- Trudell SA, Xu J, Saar I, Justo A, Cifuentes J. 2017. North American matsutake: names clarified and a new species described. *Mycologia* 109:379–390.
- Wan J, Koike A, Yamanaka K, Sotome K, Morinaga T, Tanaka C, Terashima Y, Aimi T. 2012. Genetic diversity of *Tricholoma matsutake* and close allies associated with broad-leaved trees in Asia. *Mushroom Science and Biotechnology* 19:167–174, doi:10.24465/msb.19.4_167
- White TJ, Bruns T, Lee S, Taylor JW. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ, eds. PCR protocols: a guide to the methods and applications. New York: Academic Press. p. 315–322.
- Yang Y, Tian K, Hao J, Pei S, Yang Y. 2004. Biodiversity and biodiversity conservation in Yunnan, China. *Biodiversity and Conservation* 13:813–826, doi:10.1023/B:BIOC.0000011728.46362.3c
- Yang ZL, Ding X-X, Kost G, Rexer K-H. 2017. New species in the *Tricholoma pardinum* complex from Eastern Himalaya. *Phytotaxa* 305:1–10.
- Yu FQ, Wang Y, Liu PG. 2006. *Tricholoma lavendulophyllum*, a new species from Yunnan, China. *Mycotaxon* 95:305–308.