RESEARCH ARTICLE

Taxonomy of *Tricholoma* in northern Europe based on ITS sequence data and morphological characters

J. Heilmann-Clausen[1], M. Christensen[2], T.G. Frøslev[3], R. Kjøller[4]

Abstract   Based on molecular and morphological data we investigated the taxonomy and phylogeny of the ecto-mycorrhizal genus *Tricholoma* in northern Europe. Our phylogenetic tree confirmed the presence of at least 72 well circumscribed species within the region. Of these, three species, viz. *T. boreosulphurescens*, *T. bryogenum* and *T. ilkkae* are described as new to science, based on morphological, distributional, ecological and molecular data. Several other terminal branches represent putative cryptic taxa nested within classical species or species groups. Molecular type studies and/or designation of sequenced neotypes are needed in these groups, before the taxonomy can be settled. In general our phylogenetic analysis supported previous suprageneric classification systems, but with some substantial changes. Most notably, *T. virgatum* and allies were found to belong to sect. *Tricholoma* rather than sect. *Atrosquamosa*, while *T. focale* was found to be clearly nested in sect. *Genuina* rather than in sect. *Caligata*. In total, ten sections are accepted, with five species remaining unassigned. The combination of morphological and molecular data showed pileus colour, pileipellis structure, presence of clamp connections and spore size to be rather conservative characters within accepted sections, while the presence of a distinct ring, and especially host selection were highly variable within these.

INTRODUCTION

The genus *Tricholoma* is a classic genus of agarics already proposed as a section by Fries (1821) and subsequently erected as a genus by Staude (1857).

Over the years more than 850 species epithets have been published or combined in the genus. Many of these have since been transferred to other genera, including *Lepista*, *Leucopaxillus*, *Lyophyllum* and *Melanoleuca* based on various deviations, mainly in microscopic characters. Molecular studies have supported the segregation of most of these more modern genera, and *Tricholoma* in its narrow circumscription (e.g. Noordeloos & Christensen 1999) is supported as a monophyletic genus of ectomycorrhizal fungi within the *Tricholomataceae* (e.g. Moncalvo et al. 2002). According to Ryberg & Matheny (2012), the genus seems to have segregated from its ancestral clade some 60–90 million years ago in the late Cretaceous, possibly with *Pinaceae* as mycorrhizal partners. A recent study (Sánchez-García et al. 2014) surveyed in depth the *Tricholomataceae* based on several molecular markers and concluded that only the genera *Albomagister*, *Corneriella*, *Dennisiomyces*, *Leucopaxillus*, *Pseudotricholoma*, *Porpoloma* s.str. and *Tricholoma* belong to the family, while other previously contained genera should be assigned to families, including the *Lyophyllaceae* and a poorly resolved residual Tricholomatoid clade. Of the genera included in the *Tricholomataceae*, also *Porpoloma* s.str. is proven ectomycorrhizal, while a biotrophic lifestyle is

indicated to be probable in *Albomagister* and *Pseudotricholoma.* Only the latter genus is known to occur in Europe, were *Pseudotricholoma metapodium* is widespread.

Tricholoma has a worldwide distribution (Tedersoo et al. 2010), but seems to be most prominent in temperate and subtropical zones in both the southern and northern hemisphere. All known species are known or supposed to be ectomycorrhizal (Ryberg & Matheny 2011), mainly with trees in the *Pinaceae*, *Betulaceae* and *Fagaceae*, but the genus also contains species that are associated with *Eucalyptus*, *Dryas* and *Helianthemum* (Bougher 1996, Christensen & Heilmann-Clausen 2013). Some species form dual ectomycorrhizal and monotropoid associations linking trees and monotropoid plants (Leake et al. 2004). The centre of species richness appears to be in North America. According to Bessette et al. (2013), more than 100 species are reported from this continent while 63 to 88 species are listed from Europe (Riva 1988, Bon 1991, Kirby 2012). Several species are described or reported from Japan, New Zealand and Australia (e.g. Hongo 1988, Bougher 1996, Orlovich & Cairney 2004), but the overview of the species diversity in these regions is fragmentary due to the lack of modern comprehensive treatments.

Tricholoma species show limited microscopic variation, and are characterized by hyaline, subglobose to oblong spores, simple pileipellis structures and lack of well-differentiated sterile elements, including cystidia. Hence, species identification and partly also the infrageneric classification has mainly been based on macromorphology. Singer (1986) divided the genus in four subgenera, mainly based on pileipellis structure and the presence or absence of clamp connections. The four subgenera were further divided into nine sections, of which three (*Leucorigida*, *Iorigida* and *Adusta*) do not belong to the genus in the current circumscription. In their treatment of the genus, Noordeloos & Christensen (1999) accepted the four subgenera suggested by Singer (1986), but with a more narrow definition of sections, especially in subg. *Tricholoma*, in which seven sec-

[1] University of Copenhagen, Natural History Museum of Denmark, Center for Macroecology, Evolution and Climate, Universitetsparken 15, DK-2100 Copenhagen, Denmark;
   corresponding author e-mail: jheilmann-clausen@snm.ku.dk.
[2] Hvidtjørnevej 1, DK-4180 Sorø, Denmark.
[3] University of Copenhagen, Natural History Museum of Denmark, Center for Geogenetics, Øster Voldgade 5-7, 1350 Copenhagen, Denmark.
[4] University of Copenhagen, Institute of Biology, Section of Terrestrial Ecology, Universitetsparken 15, DK-2100 Copenhagen, Denmark.

tions were accepted. Slightly deviating classification systems have been proposed by other authors, including Bon (1984a, 1991). For a more throughout evaluation see Riva (1988) and Christensen & Heilmann-Clausen (2013).

Despite their attractive fruit bodies, and a long mycological tradition, the overall taxonomy in *Tricholoma* is still poorly resolved in Europe. Molecular data have been used to study the taxonomy and phylogeny of some species groups (e.g. Comandini et al. 2004, Jargeat et al. 2010, Ota et al. 2012, Moukha et al. 2013), typically resulting in the identification of cryptic diversity within previously accepted species. Simultaneously, several species have been proposed in recent years without a published test of taxonomic placement based on molecular markers (e.g. Kalamees 2001, Musemeci & Contu 2008, Ferrarese & Zaffalon 2010, Ludwig 2012), adding to taxonomic confusion in the genus.

Recently, Christensen & Heilmann-Clausen (2013) monographed the genus in northern Europe, backed by sequences of the nuclear ribosomal internal transcribed spacer (ITS). The main objective of the present paper is to present the results of the underlying scientific studies in a coherent form, with the following specific aims:

1. to evaluate the monophyly of proposed subgenera and sections as defined by Singer (1986) and Noordeloos & Christensen (1999);
2. to investigate the congruence between ITS and morphology in hypothesized sections; and
3. to resolve the taxonomical delimitation of *Tricholoma* species occurring in northern Europe, with a consideration of possibly related taxa occurring in other continents, especially North America.

MATERIALS AND METHODS

Studied material

Specimens studied for this paper were mainly collected by the first two authors during collection trips throughout Europe, since the early 1990s. It was the intention to obtain representative collections of all species present in northern Europe according to modern identification books (Gulden 1969, 1992, Noordeloos & Christensen 1999, Christensen & Heilmann-Clausen 2012), but in addition a number of species recorded from southern Europe were included. Generally, several collections of each species were included in the analysis, and if possible, specimens from different geographical regions were selected. In addition to own material we have studied a number of collections, including type-specimens from various public and private herbaria throughout Europe, and for the phylogenetic analyses selected relevant and trustworthy ITS sequences were downloaded from GenBank and Unite. Finally, we included a few original ITS sequences kindly provided by Tor Erik Brandrud (Norway) and Sven-Gunnar Ryman (Sweden).

Scoring of morphological characters

Macromorphological characters were mainly scored on fresh material or more rarely photographs (for details on studied collections see Christensen & Heilmann-Clausen 2013). Morphological characters were described according to the standard terminology published by Knudsen & Vesterholt (2008), while colours were recorded according to Kornerup & Wanscher (1974). Microscopical characters were recorded from rehydrated specimens in 2 % KOH or 5–10 % NH$_3$. From each collection a minimum of 20 randomly selected spores were measured, avoiding obviously malformed or unripe spores. For this study, data on pileus and gill colour, pileus surface texture, presence of a ring-zone, spore size and the presence/absence of clamp

connections were explored in more detail, but many other characters were described for accepted species in Christensen & Heilmann-Clausen (2013).

Molecular & phylogenetic methods

DNA was extracted from dried specimens by the CTAB-chloroform method described by Gardes & Bruns (1993). Usually, one lamella was taken with a flamed pair of forceps from the specimens. The internal transcribed spacer (ITS) region was amplified with the primer combination ITS1-F and ITS4 (White et al. 1990, Gardes & Bruns 1993). The PCR products were sequenced by Europhins Genomics (previously MWG-Biotech) or Macrogen (www.macrogen.com). Forward and reverse strands were sequenced using ITS1F or ITS5 (White et al. 1990) and ITS4 as sequencing primers. If sequencing of either the ITS-1 or ITS-2 region proved difficult, additional sequencing was performed using ITS2 and ITS3 (White et al. 1990) as sequencing primers. Sequence contigs were assembled using Sequencher (v. 3.1). Alignment was done with MAFFT (online v. 7) using the settings G-INS-i (Katoh et al. 2005), with minor manual adjustments in Se-Al (Rambaut 1996) for some sequences with incomplete ends or internal gaps. Two alignments were produced, one containing all sequences in the dataset, and one based on a reduced dataset containing only one representative of each of 72 end-clusters accepted to represent described or putative species present in northern Europe. For each alignment Maximum Likelihood phylogeny estimates were produced with RAxML v. 8.1.16 (Stamatakis et al. 2008) with 1 000 fast bootstrap replicates and GTR + CAT base substitution model. Both alignments were also subjected to bayesian phylogenetic analyses using MrBayes v. 3.2 (Ronquist et al. 2011) using the GTR+I+gamma model (nst = 6, rates = invgamma) with two independent runs of 4 chains for 5 000 000 generations with sampling every 1 000th generation. Trees from the last 1 000 000 generations from each run (2 000 trees from each analysis) were summed in a consensus tree with branch frequencies corresponding to bayesian posterior probabilities.

Sequences used in this study are listed in Table 1 including source information, geographic origin, and accession numbers. Alignments can be obtained from the first author.

TAXONOMIC PART

In total we obtained 217 novel ITS sequences for this study, while 84 published sequences were downloaded from GenBank (67) and Unite (17). The alignment contained 170 unique sequence reads, represented as terminal clusters in the phylogenetic tree based on maximum likelihood (Fig. 1). The Bayesian analyses did not contradict the ML phylogeny. Based on tree topology these were assigned to 108 putative species hypotheses, of which 27 were represented only by extra-continental sequences, while seven represented accepted species or species hypotheses only recorded from southern Europe. Of the 81 species hypotheses identified among European sequences, 72 were selected for scoring of morphological characters and evaluation of previously published infrageneric classification systems (Fig. 2).

Below we first evaluate the infrageneric classification system, and subsequently the species level taxonomy is reviewed. We have applied commonly used section names as practical labels for clades in order to guide readers. We have not intended to resolve the nomenclatural history of each section in depth, as this would require a deeper and quite time-consuming nomenclatural study on candidate section names. As long as the details of the infrageneric classification remain open, due to limited sapling of the genus in North America, and the use of only one molecular marker, we find the time unripe to perform

Table 1 Sequences included in this study. For sequences retrieved from genbank or unite, only accession numbers and country of origin is given, for new sequences obtained for this study, year of collection, locality and fungarium data is given. Species names are given as in Fig. 1.

Species	Voucher	Collection year	Locality	Origin of sequence	Herbarium	Herbarium no.	Unite accession no.	GenBank accession no.	Notes
Hypsizygus marmoreus	HM561970		Malaysia	GenBank				HM561970	Outgroup
T. 'Sp. Mex1'	AB510472		Mexico	GenBank				AB510472	
T. acerbum	AF377247		Norway	GenBank				AF377247	
	JV99-638	1999	Denmark, Jylland, Elbæk Skov	This study	C	C-F-41483	UDB001474	LT000005	
	MC00-204	2000	Slovenia, Central Slovenia, Vino	This study	C	C-F-96223	UDB002361	LT000134	
T. aestuans	JV02-540	2002	Denmark, Jylland, Sønder Herreds Plantage	This study	C	C-F-40955	UDB000779	LT000006	
	MC94-008	1994	Denmark, Jylland, Hårup Sande	This study	C	C-F-59265		LT000007	
	MC97-072	1997	Sweden, Medelpad, Harrän	This study	C	C-F-58885	UDB001434	LT000153	neotype
T. 'aff. sejunctum'	JN021102		Canada, Ontario	GenBank				JN021102	
T. 'aff. virgatum'	MC05-201	2005	Nepal, Mustang, Kunjo	This study	C	C-F-96250	UDB002370	LT000115	
T. 'albobrunneum'	MC99-060	1999	France, Provence	This study	C	C-F-96268	UDB001444	LT000077	
	UDB001218		Sweden	Unite			UDB001218		
	UDB018044		Estonia	Unite			UDB018044		
T. album	MC01-201	2001	Slovenia, Ljubljana	This study	C	C-F-96234	UDB001413	LT000135	
	MC95-159	1995	Denmark, Jylland, Skivum Krat	This study	C	C-F-96254		LT000008	
	UDB011580		Estonia	Unite			UDB011580		
T. anatolicum	AB510358		Turkey	GenBank				AB510358	
	AB699646		Morocco	GenBank				AB699646	
T. apium	JHC95-049	1995	Sweden, Medelpad, Borgsjö, Bergåsen SÖ	This study	C	C-F-35189	UDB001467	LT000154	
	JV00-215	2000	Denmark, Jylland, Skagen Klitplantage	This study	C	C-F-41884	UDB001685	LT000009	
	MC98-034	1998	Norway, Hedmark, Hornmoen	This study	C	C-F-59207		LT000118	
T. argyraceum	JHC95-112	1995	Denmark, Sjælland, Geel Skov	This study	C	C-F-35092	UDB000780	LT000010	
	JHC96-244	1996	Denmark, Sjælland, København, Botanisk Have	This study	C	C-F-96212	UDB000781	LT000011	
	JHC97-092	1997	Sweden, Värmland, Långban S of Lesjöfors	This study	C	C-F-96213	UDB000782	LT000155	
	JHC97-174	1997	Sweden, Medelpad, Bräcke, Grötingen	This study	C	C-F-96215	UDB001692	LT000156	
	MC03-251	2003	Slovakia, Presov, Snina	This study	C	C-F-96245	UDB001419	LT000127	
	MEN9491	1994	The Netherlands, Groningen, Verhildersum near Leens	This study	L	L0374886	UDB000785	LT000198	epitype
T. arvernense	MC95-102	1995	Sweden, Medelpad, Borgsjö	This study	C	C-F-59014		LT000157	
	MC98-020	1998	Norway, Hedmark, Hornmoen	This study	C	C-F-59200	UDB002362	LT000119	
	MC98-120	1998	France, Franche-Comte, St. Sifolene	This study	C	C-F-59255	UDB001438	LT000078	
T. 'atrosquamosum'	AF349701		USA, California	GenBank				AF349701	
T. atrosquamosum	O-F159872	2005	Norway, Hordaland, Granvin, Urdanes NR	This study	O	O159872		LT222019	
	O-F188799	2003	Norway, Møre og Romsdal, Norddal	This study	O	O188799		LT222024	
	O-F64018	2010	Norway, Buskerud, Øvre Eiker, Gommerud, Vestfossen	This study	O	O-64018		LT222020	
	TEB55008	2008	Norway, Aust-Agder, Evje & Hornnes, Dåsvassdalen, Husefjell SW	This study	TEB			LT222031	
T. 'atroviolaceum'	AY750166		USA, Washington	GenBank				AY750166	
T. 'aurantium'	AF377233		USA, California	GenBank				AF377233	
T. aurantium	MC96-303	1996	Italy, Toscana, Cipressa di Agnese	This study	C	C-F-59329	UDB001470	LT000100	
	MC97-227	1997	Denmark, Møn, Møns Klint	This study	C	C-F-59330	UDB001471	LT000012	
T. 'bakamatsutake'	AB036898		Japan	GenBank				AB036898	
	AB856037		Japan	GenBank				AB856037	
T. basirubens	MC01-209	2001	Croatia, Primorsko-Goranska, Krk	This study	C	C-F-96240	UDB001412	LT000001	
	TL5303	1998	Sweden, Öland, Halltorps Haga	This study	C	C-F-38408	UDB011587	LT000158	
T. batschii	AF377238		USA, California	GenBank				AF377238	
	MC01-200	2001	Croatia, Istarska, Kanegra	This study	C	C-F-96233	UDB001412	LT000002	
	UDB011587		Estonia	Unite			UDB011587		
T. bonii	AM181413		Estonia	GenBank				AM181413	
	JHC91-721	1991	Denmark, Anholt	This study	C	C-F-96201	UDB000811	LT000013	
	LUG-F8450	1996	Italy, Probe Brallo, Pavia	This study	LUG	LUG F 8450	UDB000790	LT000101	holotype
	MEN96112	1996	Italy, Trento, Spera val Campanella	This study	L	L0354472	UDB000791	LT000102	
T. boreosulphurescens	IK971187	1997	Finland, Outer Ostrobothnia, Tervola, Peura, Raemäki	This study	H	H6002040		LT000199	
	JF908737		Finland	GenBank				JF908737	

Species	Collection	Year	Locality	Source	Herb.	Voucher	UDB	GenBank	Type
T. boreosulphurescens (cont.)	SAE9507	1995	Sweden, Medelpad, Stöde, V. Västansjö, Kockerabäcken	This study	C	C-F-59441	UDB001475	LT000159	
	TROM-F21089	2007	Norway, Troms, Storfjord, Lullesletta	This study	TROM	OF21089		LT222032	
T. borgsjoeënse	O-F187683	2004	Norway, Finnmark, Alta, Kålfjordsbotten	This study	O	O187683	UDB000807	LT222023	holotype
	JHC95-067	1995	Sweden, Medelpad, Borgsjö, Julásen	This study	C	C-F-96211		LT000160	
	JV95-307	1995	Sweden, Medelpad, Borgsjö, Julásen	This study				LT000161	
T. boudieri	TEB22606	2006	Norway, Oppland, Nord-Aurdal, Mjølkebekken nordre	This study	TEB	C-F-96219		LT222030	epitype
	MC01-600	2001	Slovenia, Ljubljana	This study	C	C-F-90092	UDB001428	LT000136	
T. bresadolanum	MC95-317	1995	Denmark, Jylland, Moesgaard Skov	This study	C	C-F-59305	UDB000792	LT000014	
	CL94-166	1994	Sweden, Öland, Haltorp Hage	This study	C	C-F-59442	UDB000549	LT000162	
	MC96-264	1996	Italy, Toscana, Monte Soldano	This study	C	C-F-59341	UDB000550	LT000103	
	MC96-265	1996	Italy, Toscana, Monte Soldano	This study	C	C-F-59342		LT000104	
	TRgmb00652	2006	Italy, Sardegna, Sassari, Calangianus, Baldo	This study	TR	TRgmb00652		LT000105	
T. bryogenum	MC97-101	1997	Sweden, Jämtland, Brunflo	This study	C	C-F-59167	UDB000793	AY462034	holotype
	O-F160040	2006	Norway, Oppland, Øystre Slidre, Heggnes	This study	O	OF160040		LT222020	
	O-F52108	1979	Norway, Nord-Trøndelag, Levanger, Ytterøya	This study	O	OF52108		LT222026	
	TROM-F6702	1995	Norway, Troms, Storfjord, Lullesletta	This study	TROM	OF6702		LT222034	
T. 'caligatum'	AF309520		Costa Rica	GenBank				AF309520	
T. 'caligatum'	JV07-451	2007	Spain, Valencia, E of Gandia, N of Els	This study	C	C-F-96274	UDB001442	LT000152	
T. 'caligatum'	KC152249		Mexico	GenBank				KC152249	
T. 'cedrotorum'	KC565866		Algeria	GenBank				KC565866	
T. 'cf. japonicum'	PH99-519	1999	France, Provence	This study	C	C-F-96265	UDB001420	LT000079	
T. cingulatum	MC99049	1999	France, Provence, Massif des Cedres	This study	C	C-F-96246		LT000074	
	JN021103		Canada, Quebec	GenBank				JN021103	
	MC03-252	2003	Slovakia, Presov, Havesova	This study	C	C-F-59057	UDB000543	LT000128	neotype
	MC96-134	1996	Denmark	This study	C	C-F-59068	UDB000544	LT000015	
	MC96-170	1996	Denmark, Jylland, Borum	This study	C	C-F-96238		LT000016	
	MEN95210	1995	The Netherlands, Drenthe, Boekweitveentje	This study	L	C-F-59154		LT000200	
T. colossus	MC01-205	2001	Slovenia, Ljubljana	This study	C	C-F-58898	UDB001417	LT000137	
	MC97-047	1997	Sweden, Jämtland, Ysjö	This study	C	C-F-58886	UDB001433	LT000164	
T. columbetta	AF349693		Norway	GenBank				AF349693	
T. 'dryophilum'	MC95-181	1995	Denmark, Jylland, Skivum Krat	This study	C	C-F-96256	UDB001468	LT000017	neotype
T. dulciolens	AF377239		USA, California	GenBank				AF377239	
	AB738883		Sweden	GenBank				AB738883	holotype
	AF309523		USA, Califonia	GenBank				AF309523	
	JF908732		Italy	GenBank				JF908732	
T. equestre	MC94-027	1994	Denmark, Jylland, Hoverdal Plantage	This study	C	C-F-58890	UDB001508	LT000018	
	MC95-187	1995	Denmark, Jylland, Hoverdal	This study	C			LT000019	
	MC96-155	1996	Denmark, Jylland, Bakkerne near Ørsted	This study	C		UDB001469	LT000020	
T. filamentosum	C-F35924	1996	Sweden, Skåne, Balsberget	This study	C	C-F-35924	UDB001506	LT000165	
	JHC0-1202	2001	Slovenia, Ljubljana (exhibition)	This study	C	C-F-96191	UDB000804	LT000138	
	MC00-218	2000	Slovenia, Gorizia, Idria	This study	C	C-F-96226		LT000139	
	MC03-242	2003	Slovakia, Presov, Rozok	This study	C	C-F-96243	UDB000803	LT000129	
T. 'flavovirens'	AB036895		Japan	GenBank				AB036895	
T. 'focale'	AF458452		USA, Oregon	GenBank				AF458452	
	AF458453		USA, Oregon	GenBank				AF458453	
	AF458456		USA, Oregon	GenBank				AF458456	
	DQ822834		USA, Califonia	GenBank				DQ822834	
	AF309534		USA, Califonia	GenBank				AF309534	
	AF377236		USA, Califonia	GenBank				AF377236	
T. focale	JV97-239	1997	Sweden, Jämtland, Orrskäret	This study	C	C-F-27500	UDB001501	LT000166	neotype
	JV99-603	1999	Denmark, Læsø, Træbakke at Holtemmen	This study	C	C-F-41444	UDB001500	LT000021	
	MC98-600	1998	Denmark, Jylland, Skagen	This study	C	C-F-96260	UDB002364	LT000022	
	MC98-086	1998	France, Franche-Comte, Winkel	This study	C	C-F-59243	UDB001504	LT000075	
T. 'frondosae'	AF349689		USA, New Mexico	GenBank				AF349689	
T. frondosae type I	MC95-130	1995	Sweden, Medelpad, Borgsjö	This study	C	C-F-59031		LT000167	
	MC97-151	1997	Sweden, Jämtland, Fillstabäcken	This study	C	C-F-59188		LT000168	
T. frondosae type II	MC00-225	2000	Slovenia, Gorizia, Idria	This study	C	C-F-96227		LT000140	
	MC96-235	1996	Denmark, Jylland, Mols	This study	C	C-F-59084	UDB001509	LT000023	

Table 1   (cont.)

Species	Voucher	Collection year	Locality	Origin of sequence	Herbarium	Herbarium no.	Unite accession no.	GenBank accession no.	Notes
T. frondosae type II (cont.)	MC97-158	1997	Sweden, Jämtland, Kyckås	This study	C	C-F-59395	UDB002363	LT000169	
T. fucatum	MC97-149	1997	Sweden, Jämtland, Fillstabäcken	This study	C	C-F-58980		LT000170	neotype
	MC98-023	1998	Norway, Hedmark, Sørskogbygdn	This study	C	C-F-59201		LT000121	
T. 'fulvocastanem'	AB289668		Japan	GenBank				AB289668	
	DQ067895		Thailand	GenBank				DQ067895	
T. fulvum	JHC03-019	2003	Slovakia, Poloniny National Park, Nova Sedlica	This study	C	C-F-96193	UDB001695	LT000130	
	JHC04-251	2004	Sweden, Halland, Varberg, Akulla, Valaklitt	This study	C	C-F-96195	UDB001700	LT000171	
	MC98-078	1998	France, Franche-Comte, Winkel	This study	C	C-F-96259	UDB002365	LT000080	
T. guldeniae	JuV16997	2000	Finland, Varsinais-Suomi, Vahto, Seppälä, Ryssänvuori	This study	TURA		UDB001701	LT000070	
T. hemisulphureum	MC95-103	1995	Norway, Akershus	This study	C	C-F-96251		LT000122	
	JV08-364	2008	Estonia, Saaremaa	This study	C	C-F-96217		LT000065	
T. 'huronense'	O-F74354	2005	Norway, Hordaland, Ulvik, Finse	This study	O	O74354		LT222027	
T. 'ilkkae'	AF377229		USA, California	GenBank				AF377229	
	AB738881		Spain	GenBank				AB738881	
	AB738882		Spain	GenBank				AB738882	
T. 'imbricatum'	MC98-602	1998	Sweden, Gotland	This study	C	C-F-96261		LT000172	
	S-F173364	2007	Sweden, Uppland, Gräsö par., Djupdal 3 km NE of Gräsö church	This study	UPS	F-173364		LT222028	
	S-F513823	2000	Sweden, Gotland, Eksta par, Ekstastrand	This study	UPS	F-513823		LT222029	holotype
T. imbricatum	AF377242		USA, California	GenBank				AF377242	
	MC94-046	1994	Denmark, Jylland, Bakkerne near Ørsted	This study	C	C-F-59268	UDB001421	LT000024	neotype
	UDB000699		Sweden	Unite			UDB000699		
T. 'inamoenum'	AF377246		USA, California	GenBank				AF377246	
T. inamoenum	JHC95-042	1995	Sweden, Medelpad, Tubbobäcken	This study	C	C-F-35182	UDB001688	LT000173	
	MC95-115	1995	Sweden, Medelpad, Borgsjö	This study	C	C-F-59020	UDB001424	LT000174	neotype
T. inocybeoides	JHC95-072	1995	Sweden, Medelpad, Borgsjö, Erikslund	This study	C	C-F-35211	UDB000796	LT000175	
	MC03-229	2003	Denmark, Jylland, Århus	This study	C	C-F-96242	UDB000783	LT000025	
	MC95-152	1995	Denmark, Jylland, Aarhus	This study	C	C-F-59272	UDB000537	LT000026	
	MC96-172	1996	Denmark, Jylland, Aarhus	This study	C	C-F-59094	UDB000538	LT000027	
	MC97-060	1997	Sweden, Jämtland, Östersund	This study	C	C-F-59159	UDB000539	LT000176	
T. 'japonicum'	AB036900		Japan	GenBank				AB036900	
T. 'joachimii'	HM590876		France	GenBank				HM590876	
T. joachimii	MC98-603	1998	Sweden, Gotland	This study	C	C-F-96262		LT000177	
T. 'joachimii'	TRgmb00060	2005	Italy, Trento, Baselga di Piné, Cané	This study	TR	TR gmb 00600		LT000106	
T. josserandii	O-F167194	2004	Norway, Akershus, Bæarum, Borøya	This study	O	O167194		LT222022	
	MC99-053	1999	France, Provence, Massif des Cedres	This study	C	C-F-96266	UDB000797	LT000081	
	MC99-056	1999	France, Provence, Massif des Cedres	This study	C	C-F-96267	UDB000798	LT000082	
T. lascivum	JHC03-020	2003	Slovakia, Poloniny National Park, Rozok	This study	C	C-F-96194	UDB001696	LT000131	
	MC00-519	2000	Denmark, Sjælland, Rude Skov	This study	C	C-F-96230	UDB000005	LT000028	
	MC99-197	1999	Denmark, Sjælland, Lellinge Skovhusvænge	This study	C	C-F-59446		LT000029	
T. 'leucophyllum'	EU597086		Canada, British Columbia	GenBank				EU597086	
	JN021108		Canada, Ontario	GenBank				JN021108	
T. 'luteomaculosum'	AF458448		USA, Oregon	GenBank				AF458448	
T. 'magnivelare'	AF377224		USA, California	GenBank				AF377224	
T. matsutake	AF309538		China, Yunnan	GenBank				AF309538	
	JuV23362F	2005	Finland, Koillismaa, Oulanka national park, NWW of biological field station	This study	TURA			LT000071	
T. 'moserii'	MC03-600	2003	Sweden, Jämtland	This study	C	C-F-96247		LT000178	
	TMU62964		South Korea	GenBank				TMU62964	
T. 'mutabile'	AF377211		USA, California	GenBank				AF377211	
	AF458445		USA, Oregon	GenBank				AF458445	
T. olivaceotinctum	JHC95-070	1995	Sweden, Medelpad, Borgsjö, Julåsen	This study	C	C-F-35209	UDB000526	LT000179	
	KJ1993	1993	Sweden, Lappland, Åsele Lappmark, Risbäck, S slope of arksjöberget	This study	S		UDB000799	LT000180	
	MC95-135	1995	Sweden, Medelpad, Borgsjö	This study	C	C-F-59036	UDB000527	LT000181	
	MC97-103	1997	Sweden, Jämtland, Brunflo	This study	C	C-F-59168	UDB000525	LT000182	

Species	Collection	Year	Location	Herbarium	C-F no.	Source	UDB no.	Accession	Type
T. olivaceotinctum (cont.)	OP1981	1981	Sweden, Jämtland, Sällsjö	UPS		This study	UDB000800	LT000183	
T. orirubens	JHC01-200	2001	Slovenia, Idria, Mehke Dolina	C	C-F-96189	This study	UDB000524	LT000141	
	JHC93-261	1993	Denmark, Jylland, Trelde Østerskov	C	C-F-96208	This study	UDB000523	LT000030	
	MC03-243	2003	Slovakia, Presov, Rozok	C	C-F-96244	This study	UDB000801	LT000132	
	MC96-301	1996	Italy, Toscana, Cipressa di Agnese	C	C-F-59365	This study	UDB000522	LT000107	
	MC97-258	1997	Denmark, Jylland, Moesgaard Skov	C	C-F-59427	This study	UDB000521	LT000031	
	MC98-214	1998	England, Surrey, Norbury Park	C	C-F-59315	This study	UDB000520	LT000202	
T. 'palustre'	DQ494699		USA, Massachusetts			GenBank		DQ494699	
T. pardinum	JHC01-201	2001	Slovenia, Idria, Pringle	C	C-F-96190	This study	UDB000802	LT000142	
T. pessundatum	JV04-482	2004	Denmark, Jylland, Albæk Klitplantage	C	C-F-43780	This study	UDB001502	LT000032	epitype
	UDB011581		Estonia			Unite	UDB011581		
T. populinum	MC00-236	2000	Slovenia, Gorizia, Idria	C	C-F-96229	This study	UDB001410	LT000143	
	UDB011624		Estonia			Unite	UDB011624		
T. portentosum	AF349686		USA, California			GenBank		AF349686	
	JHC04-431	2004	Sweden, Halland, Hylte, Ödegärdet	C	C-F-96197	This study	UDB001698	LT000184	
	JHC92-277	1992	Denmark, Lolland, Christianssædeskovene	C	C-F-96202	This study	UDB001686	LT000033	
	MC00-206	2000	Slovenia, Central Slovenia, Vino	C	C-F-96224	This study	UDB001409	LT000144	
	MC94-082	1994	Denmark, Sjælland, Ordrup Næs	C	C-F-58959	This study		LT000034	
	MC96-156	1996	Denmark, Jylland, Bakkerne near Ørsted	C	C-F-59053	This study	UDB001429	LT000035	neotype
	MC98-116	1998	France, Franche-Comte, Doubs, St-Julien les Russey	C	C-F-59262	This study		LT000083	
T. psammopus	MC04-600	2004	Slovenia, Ljubljana	C	C-F-59248	This study		LT000145	
	MC96-345	1996	Italy, Toscana, Monte Soldano	C	C-F-59324	This study	UDB001472	LT000108	
	MC98-048	1998	Denmark, Jylland, Fløjstrup Skov	C	C-F-59212	This study	UDB001503	LT000036	
	MC99-089	1999	France, Provence	C	C-F-96273	This study		LT000084	
T. 'quercetorum'	MC99-044	1999	Portugal, Leiria	C	C-F-96263	This study	UDB000795	LT000125	
T. ramentaceum var. pseudotriste'	HQ184102		France			GenBank		HQ184102	
T. rapipes	MC03228	2003	Denmark, Jylland, Stråsø Plantage	C	C-F-96241	This study	UDB001418	LT000037	
	MC98-106	1998	France, Franche-Comte, Doubs, St-Julien les Russey	C	C-F-59258	This study	UDB001439	LT000085	epitype
T. roseoacerbum	IK881120	1988	Finland, Sompio Lapland, Sodankylä, Jeesiö-Tepsa	H	H6002032	This study		LT000072	
	IK922945	1992	Finland, Uusimaa, Hanko, Koverhar, Krogars	H	H6002034	This study		LT000073	
T. rufenum	MC96-376	1996	Italy, Lazio, Monte Rufenum	C	C-F-59393	This study	UDB001432	LT000109	
T. saponaceum	C-F23337	1992	Denmark, Lolland, Ryde Skov	C	C-F-23337	This study	UDB001499	LT000038	
	JHC00-049	2000	Norway, Sogn og Fjordane, Leikanger, Horpa	C	C-F-96188	This study	UDB001693	LT000123	
	JHC03-015	2003	Poloniny National Park, Stuzika	C	C-F-96192	This study	UDB001694	LT000133	
	JHC04-429	2004	Sweden, Halland, Hylte, Ödegärdet	C	C-F-96196	This study	UDB001697	LT000185	
	JHC04-439	2004	Sweden, Halland, Laholm, Blåalt	C	C-F-96198	This study	UDB001699	LT000186	
	JHC95-165	1995	Denmark, Sjælland, Sorø Sønderskov	C	C-F-35147	This study	UDB001505	LT000039	
	JHC97-237	1997	Denmark, Sjælland, Frederikskilde Skov	C	C-F-96216	This study	UDB001689	LT000040	
	JV87-682	1987	Denmark, Jylland, Fløjstrup Skov	C	C-F-96218	This study	UDB001507	LT000041	
	MC98-059	1998	France, Franche-Comte, Foret de Leval	C	C-F-59217	This study		LT000086	
	TF98-098	1998	France, Doubs, Forêt Valdahon	C	C-F-96276	This study	UDB001498	LT000087	
T. 'saponaceum'	DQ494700		USA, Massachusetts			GenBank		DQ494700	
T. scalpturatum	JHC93-263	1993	Denmark, Jylland, Trelde Østerskov	C	C-F-96210	This study	UDB000541	LT000042	
	JHC94-231	1994	Denmark, Fyn, Tankefuld W. of Svendborg	C	C-F-35309	This study	UDB000542	LT000043	
	MC00-207	2000	Slovenia, Ljubljana	C	C-F-96225	This study		LT000146	
	MC95-165	1995	Sweden, Jämtland, Sundsnäs	C	C-F-59399	This study		LT000187	neotype
T. 'scalpturatum forma meleagroides'	HQ184113		France			GenBank		HQ184113	holotype
T. 'scalpturatum var. atrocinctum'	JHC93-243	1993	Denmark, Jylland, Nystrup Klitplantage	C	C-F-96206	This study	UDB000784	LT000004	
T. sciodes	MC94-007	1994	Denmark, Jylland, Fløjstrup Skov	C	C-F-58902	This study	UDB000547	LT000044	
	MC95-182	1995	Denmark, Jylland, Borum Skov	C	C-F-96255	This study	UDB000548	LT000045	
T. 'sejunctum'	AB036899		Japan			GenBank		AB036899	
	AF377192		USA, California			GenBank		AF377192	
	EU819447		USA, Wisconsin			GenBank		EU819447	
T. sejunctum	MC95-187	1995	Denmark, Jylland, Enemærket Skov	C	C-F-58998	This study	UDB001431	LT000046	
	MC96-314	1996	Italy, Toscana, Cipressa di Agnese	C	C-F-58979	This study	UDB000532	LT000110	
T. squarrulosum	JHC93-224	1993	Denmark, Jylland, Trelde Østerskov	C	C-F-96205	This study	UDB000530	LT000047	
	JHC93-262	1993	Denmark, Jylland, Trelde Østerskov	C	C-F-96209	This study	UDB000786	LT000048	
	JHC95-169	1995	Denmark, Sjælland, Lellinge Skovhusvænge	C	C-F-35151	This study		LT000049	

Table 1 (cont.)

Species	Voucher	Collection year	Locality	Origin of sequence	Herbarium	Herbarium no.	Unite accession no.	GenBank accession no.	Notes
T. squarrulosum (cont.)	MC01-202	2001	Croatia, Primorsko-Goranska, Krk	This study	C	C-F-96235	UDB001414	LT000003	
	MC01-700	2001	Slovenia, Ljubljana	This study	C	C-F-96239	UDB000528	LT000147	
	MC96-269	1996	Italy, Toscana, Monte Soldano	This study	C	C-F-59343	UDB000531	LT000111	
	MC98-081	1998	France, Franche-Comte, Winkel	This study	C	C-F-59238	UDB000529	LT000088	
T. stans	MC95-131	1995	Sweden, Medelpad, Borgsjö	This study	C	C-F-59032	UDB001426	LT000188	
	MC95-145	1995	Sweden, Medelpad, Borgsjö	This study	C	C-F-59042	UDB001427	LT000189	epitype
	MC98-018	1998	Norway, Hedmark, Hommoen	This study	C	C-F-96258		LT000124	
	MC95-117	1995	Sweden, Medelpad, Borgsjö	This study	C	C-F-96252		LT000190	
T. stiparophyllum	UDB002398		Scotland	Unite			UDB002398		
	UDB011582		Estonia	Unite			UDB011582		
T. sudum	JV96-306	1996	Denmark, Læsø Klitplantage, Vester Højsandshoved	This study	C	C-F-96221	UDB001684	LT000050	
	MC98-601	1998	Denmark, Jylland, Råbjerg Plantage	This study	C	C-F-90094	UDB002366	LT000051	neotype
T. sulphurescens clade 1	MC96-296	1996	Italy, Toscana, Cipressa di Agnese	This study	C	C-F-59362	UDB000809	LT000112	
	MC99-063	1999	France, Provence	This study	C	C-F-96269	UDB002367	LT000089	
T. sulphurescens clade 2	TRgmb00062	2005	Italy, Trento, Baselga del Bondone	This study	TR	TR gmb 00062		LT000113	
	UDB011543		Estonia	Unite			UDB011543		
T. 'sulphureum'	AF377244		USA, California	GenBank		AF377244		AF377244	
	EU819448		USA, Wisconsin	GenBank		EU819448		EU819448	
	HQ650743		Canada, British Columbia	GenBank		HQ650743		HQ650743	
T. sulphureum clade 1	JHC08-049	2008	Sweden, Halland, Halmstad, Nissaström	This study	C	C-F-96200		LT000191	
	MC96-245	1996	Denmark, Jylland, Øjesø	This study	C	C-F-59115		AY462037	
T. sulphureum clade 2	JHC07-236	2007	Denmark, Lolland, Favrsted Skov	This study	C	C-F-96199		LT000053	
	MC01-204	2001	Slovenia, Ljubljana	This study	C	C-F-96237	UDB001416	LT000148	
	MC07-001	2007	Sweden, Skåne, Drakamöllan	This study	C	Missing		LT000192	
	MC94-023	1994	Denmark, Jylland, Kås Hoved	This study	C	C-F-58914		AY462036	
	MC95-188	1995	Denmark, Jylland, Enemærket Skov	This study	C	C-F-59292		AY462038	
	MC96-162	1996	Denmark, Jylland, Løvenholm Skov	This study	C	C-F-59062		AY462035	
	MC98-109	1998	France, Franche-Comte, Doubs, St.-Julien les Russey	This study	C	C-F-59260	UDB001440	LT000090	
	O-F288529	2008	Norway, Oppland, Vang, Uri	This study	O	OF288529		LT222025	
	TROM-F30019	1996	Norway, Troms, Storfjord, Lullesletta	This study	TROM	OF30019		LT222033	
T. sulphureum clade 3	AF377245		Norway	GenBank		AF377245		AF377245	
	TF06045	2006	France, Doubs, Forêt de Levier	This study	C	C-F-96275		LT000091	
T. 'terreum'	EU439339		China, Yunnan	GenBank				EU439339	
	EU439340		China, Yunnan	GenBank				EU439340	
T. terreum	JHC93-260	1993	Denmark, Jylland, Trelde Østerskov	This study	C	C-F-96207	UDB000536	LT000057	
	JHC95-118	1995	Denmark, Sjælland, Kongelunden	This study	C	C-F-35098		LT000058	
	JHC95-172	1995	Denmark, Sjælland, København, Assistens Kirkegård	This study	C	C-F-35154	UDB000812	LT000059	
	MC01-020	2001	Slovenia, Ljubljana	This study	C	C-F-96232	UDB001411	LT000149	
	MC05-200	2004	Nepal, Mustang, Lete	This study	C	C-F-96249	UDB002368	LT000116	
	MC95-119	1995	Sweden, Medelpad, Borgsjö	This study	C	C-F-96253	UDB001425	LT000193	
	MC98-209	1998	Holland, Schouwen-Duiveland	This study	C	C-F-59313	UDB000533	LT000201	
	MC99-071	1999	France, Provence, Foret des Caderach	This study	C	C-F-96271	UDB001445	LT000092	
	MC99-074	1999	France, Provence, Foret des Caderach	This study	C	C-F-96272	UDB001446	LT000093	
	MEN95192	1995	Germany, Bayern, Sperberslohe near Roth	This study	L	L0374887	UDB000813	LT000098	epitype
	O-F165767	2005	Norway, Oppland, Lunner, Grua, Olsknappen	This study	O	O165767		LT222021	
T. terreum (albinistic)	TL11317	1993	Denmark, Jylland, Klim Bjerg	This study	C	C-F-96277	UDB000808	LT000060	
	JHC93-222	1993	Denmark, Jylland, Trelde Østerskov	This study	C	C-F-96204	UDB000534	LT000061	
	JV95-519	1995	Denmark, Jylland, Staksrode Skov	This study	C	C-F-96220	UDB000535	LT000062	
T. 'tridentinum'	JV99-700	1999	France, Provence, Petit Luberon, Massif des Cedres	This study	C	C-F-96222	UDB000805	LT000076	
T. triste	E3754	1996	Germany, Baden-Württemberg, Seedorfer Wald, Schwarzwald	This study	L		UDB000814	LT000099	neotype
	JHC97-169	1997	Sweden, Jämtland, Lockna, W. of Ånge	This study	C	C-F-96214	UDB001691	LT000194	
T. 'ulvinenii'	JuV5271F	1990	Estonia, Pärnu rajooni, c. 40 km S of Pärnu, Kabli	This study	TURA			LT000066	
	IK931613	1993	Finland, Satakunta, Jämijärvi, Hämeenkangas	This study	H	H6002036		LT000067	

Species	Collection	Year	Location	Source	Herbarium	Specimen no.	UDB no.	ITS accession	Notes
T. 'ulvinenii' (cont.)	JuV13229F	1997	Finland, Varsinais-Suomi, Dragsfjärd, Ölmos	This study	TURA			LT000068	
	JuV26740F	2008	Finland, Satakunta, Alastaro, Virttaankangas	This study	TURA			LT000069	
	UDB011557		Estonia	Unite			UDB011557	UDB011557	
	UDB011558		Estonia	Unite			UDB011558	UDB011558	
	UDB011559		Estonia	Unite			UDB011559	UDB011559	
T. umbonatum type I	MC00A01	2000	Denmark, Lolland, Roden Skov	This study	C	C-F-96231	UDB002369	LT000063	
T. umbonatum type II	TRgmb00651	2006	Italy, Veneto, Belluno, Meleré	This study	TR	TRgmb00651		LT000114	
T. ustale	AF377234		The Netherlands	GenBank				AF377234	
T. 'ustaloides'	JHC92-299	1992	Denmark, Sjælland, Suserup Skov	This study	C	C-F-96203	UDB000551	LT000064	
	AF377240		USA, California	GenBank				AF377240	
T. ustaloides	MC99-047	1999	Portugal, Leiria	This study	C	C-F-96264	UDB000816	LT000126	
	MC99-067	1999	France, Provence, Foret des Caderach	This study	C	C-F-96270	UDB000815	LT000094	
	UDB011564		Estonia	Unite			UDB011564	UDB011564	
T. vaccinum	MC00-229	2000	Slovenia, Gorizia, Idria	This study	C	C-F-96228	UDB001511	LT000150	
T. 'venenatum'	MC95-109	1995	Sweden, Medelpad, Borgsjö	This study	C	C-F-59017	UDB001423	LT000195	
	AF377230		USA, Califonia	GenBank				AF377230	
T. virgatum	JHC95-063	1995	Sweden, Medelpad, Björnö, Björkviken	This study	C	C-F-35203	UDB000546	LT000196	
	MC01-203	2001	Slovenia, Ljubljana	This study	C	C-F-96236	UDB001415	LT000151	
T. viridilutescens type I	MC97-164	1997	Sweden, Jämtland, Halasen	This study	C	C-F-59398	UDB000545	LT000197	neotype
	MC98-061	1998	France, Franche-Comte, Bois de la Brosse	This study	C	C-F-59219	UDB001436	LT000095	
	MC98-080	1998	France, Franche-Comte, Winkel	This study	C	C-F-59237	UDB001473	LT000096	
	MC98-093	1998	France, Franche-Comte, Bois Lachat	This study	C	C-F-59249	UDB001437	LT000097	
T. viridilutescens type II	UDB011588		Estonia	Unite			UDB011588	UDB011588	
	UDB011595		Estonia	Unite			UDB011595	UDB011595	
T. 'viridiolivaceum'	MC96-002	1996	New Zealand, Arthurs Pass National Park	This study	C	C-F-96257		LT000117	
'Uncultured ectomycorrhiza'	FJ197008		Mexico	GenBank				FJ197008	

such a study. In the section on species level taxonomy nomenclatural details are given on all species epithets.

Infrageneric classification and congruence with morphology

The phylogenetic analysis did not support a clear division of the genus in four subgenera as proposed by Singer (1986) and adopted by most subsequent authors. However, ten sections could be reasonably separated based on molecular data and scoring of morphological traits (Fig. 2), with some species remaining unclassified. Pileus colour, pileipellis structure, presence of clamp connections and spores size and shape appeared as rather constant characters supporting the validity of sections, while the presence of a distinct ring, and especially host selection was variable within sections. It is well known that the ITS region alone is poorly suited for resolving higher level phylogenies (e.g. Frøslev et al. 2005), and our infrageneric classification should be viewed as phylogenetic supported, but preliminary. However, we do trust the sections defined below as relevant hypothetical monophyletic entities that should be tested in future studies combining a global taxon sampling with multiple molecular markers.

Species with a greyish, radially fibrillose, squamulose to felty cap

Species with a dry, grey and a radially fibrillose, squamulose to felty pileipellis quite clearly represent a paraphyletic group, that we here split across four sections; *Terrea*, *Atrosquamosa*, *Tricholoma* and *Pardinicutis* (Fig. 2). Section *Terrea* contains species characterized by a dry, felty or squamulose pileipellis, predominantly greyish colours, and spores with a relatively high Q-value. Our concept of the section is narrow, and corresponds to stirps *Terrea* in Singer (1986). Most previous authors, including Noordeloos & Christensen (1999) operated with a much broader concept of the section, which included also the stirps *Virgata* and *Atrosquamosa* ss. Singer (1986). Here, we accept the latter as a separate section, although our ITS phylogeny provide only limited support for monophyly, especially in the maximum likelihood analysis (Fig. 2). The similarity in morphological traits of the assigned species is, however, striking. Species in the section are morphologically very similar to species in sect. *Terrea*, but tend to have spores with a higher Q-value, and are characterized by peculiar smells reminding of honey, ground pepper or cedar wood (compared to absent to farinaceous in sect. *Terrea*). The species belonging to stirps *Virgata* in the sense of Singer (1986) (i.e. *T. aestuans*, *T. bresadolanum*, *T. sciodes* and *T. virgatum*) were in our analysis deeply nested in sect. *Tricholoma*. As discussed later, this makes good sense morphologically. Finally, our analysis supported sect. *Pardinicutis* as a separate section. The members of this section are characterized by a grey, scaly pileipellis, large spores and the presence of clamp connections, a combination that has lead most modern authors to accept *Pardinicutis* at the subgenus level.

Species with a reddish brown cap

For the reddish brown species our ITS phylogeny showed a division in three relatively well-supported sections, sect. *Caligata*, sect. *Genuina* and sect. *Megatricholoma* (Fig. 2). The members of sect. *Caligata* are characterized by an annulate stipe, a whitish, pale brown to dark reddish brown squamose pileus, rather large spores with low Q-value, and a strong perfumed smell. All European species are associated with conifers, but according to Murata et al. (2013) basal members of the clade from other parts of the world associate with deciduous hosts. The annulate species *T. focale* has traditionally been included in the section (e.g. Noordeloos & Christensen 1999), but the current study shows it to be deeply nested in sect. *Genuina*,
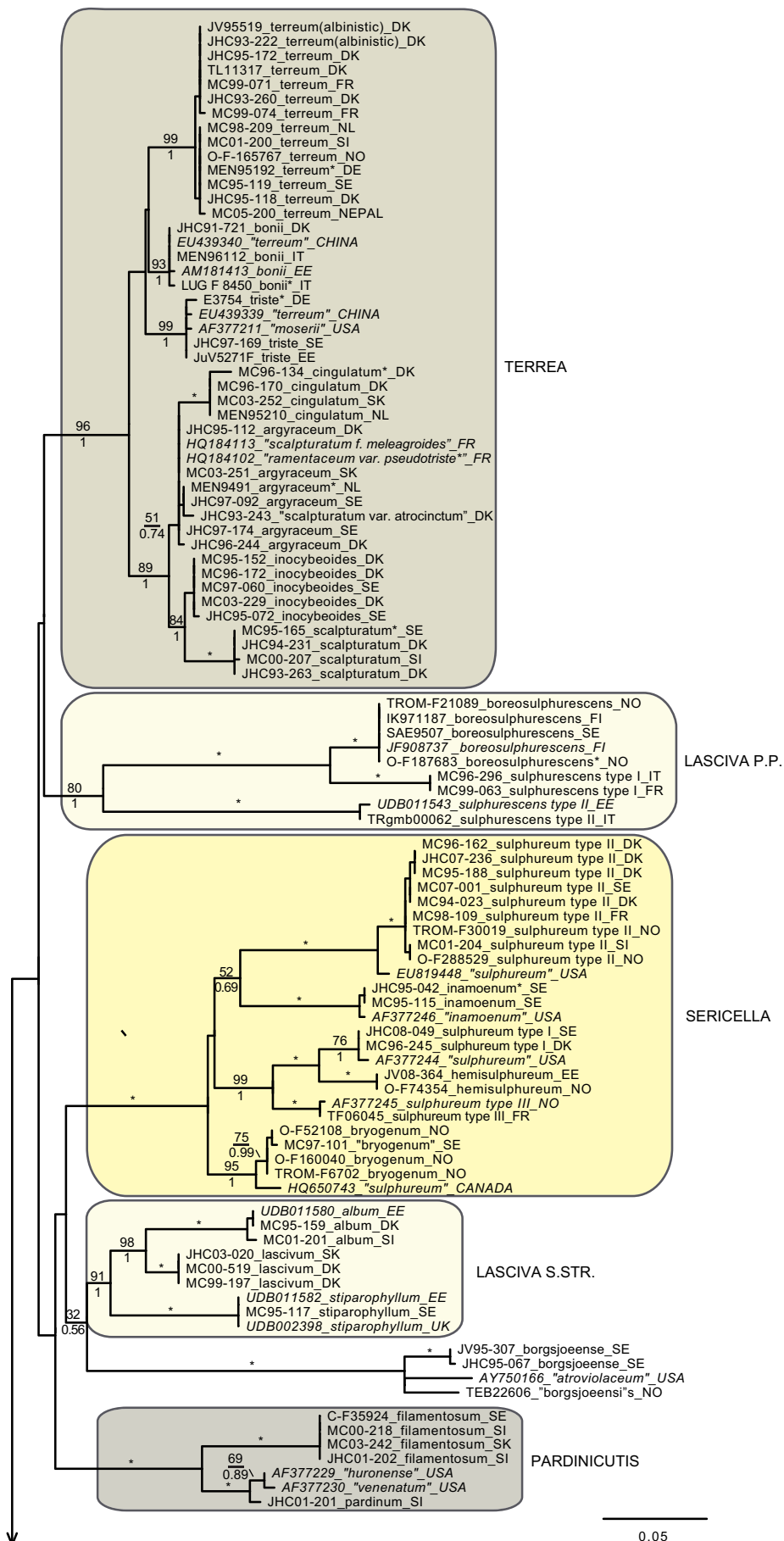
Fig. 1 Phylogeny inferred from ITS regions for the full dataset, with branch lengths based on the Maximum Likelihood analysis. No notable differences in branching patterns were observed between the Bayesian and the Maximum Likelihood analysis. Maximum Likelihood bootstrap values are indicated above branches, while Bayesian posterior probabilities are indicated below branches. * Denotes 100 % support in both analyses. New sequences obtained for this study are indicated in regular letters, while sequences obtained from GenBank or Unite are given in *italics*. Species names without quotes represent our interpretation of relevant taxa as discussed in this paper. Names in quotes are not interpreted by us, but are given as in the original source, or by the collector. Hypothesized sections are indicated by background shadings with names in capital letters.
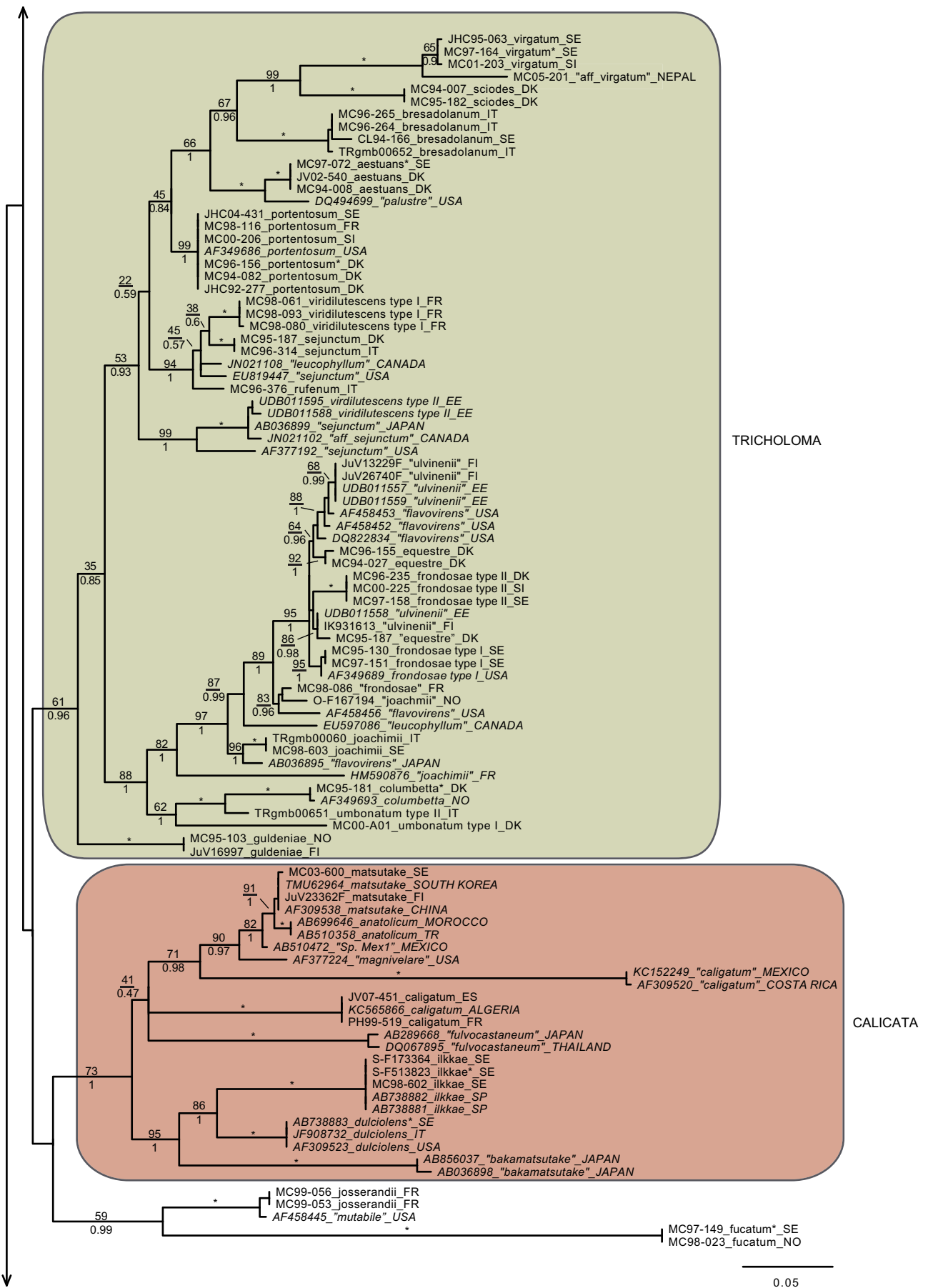
Fig. 1 (cont)
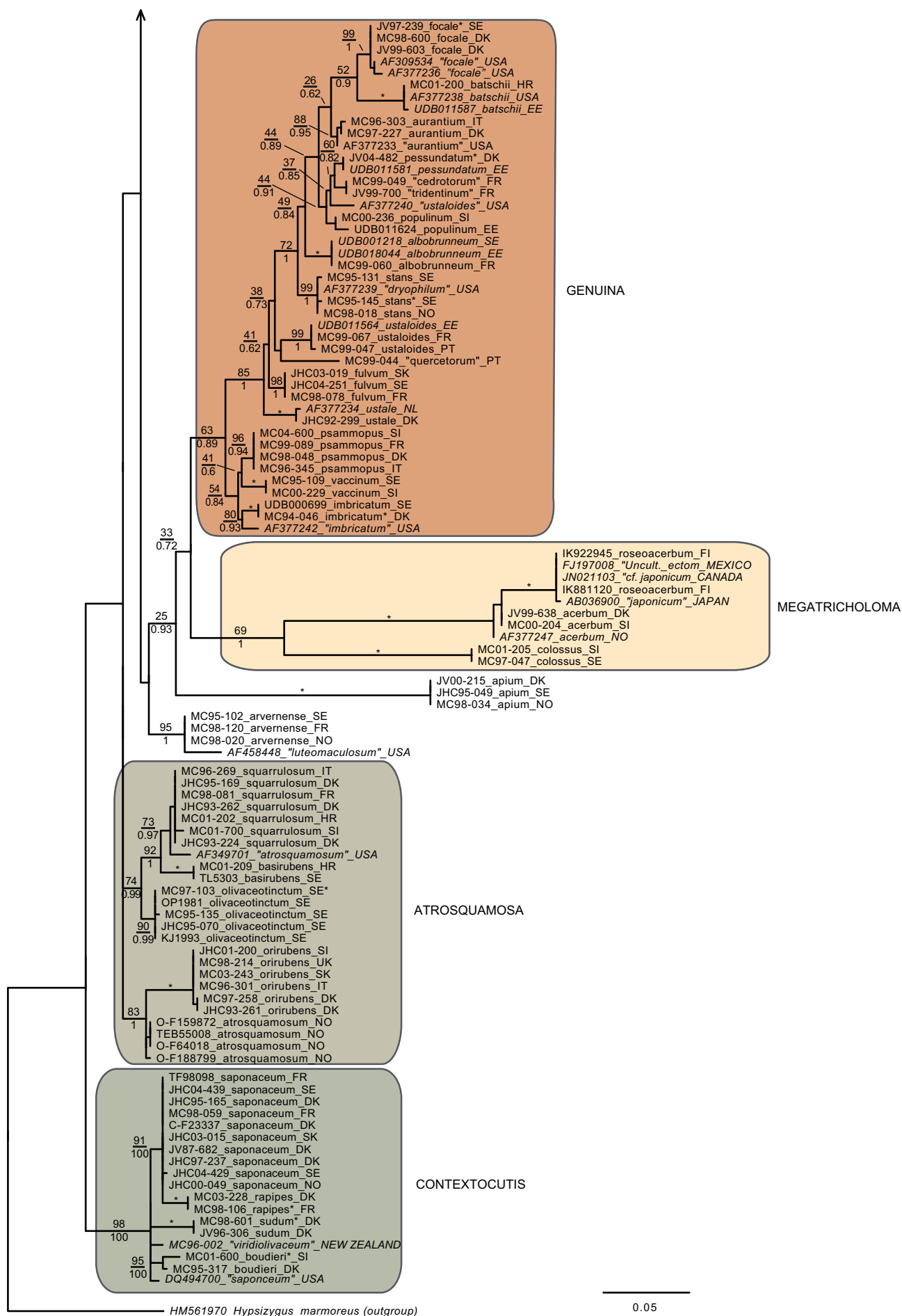
Fig. 1   (cont)

close to the subannulate *T. batschii* (Fig. 2). The species lack a perfumed smell and has no broad scales on the pileus so this makes sense morphologically. Section *Megatricholoma* was originally erected as a monotypic genus to accommodate *T. colossus* (Kost 1984). Based on detailed morphological and ontological studies the genus was by its author suggested to be only distantly related to *Tricholoma* s.str., a view that was challenged by Christensen & Noordeloos (1999) who recombined *Megatricholoma* as a section in *Tricholoma.* Our study supports this disposition, and gives reasonable support for the inclusion of *T. acerbum* and *T. roseoacerbum* in the section (Fig. 2). In the preliminary phylogeny presented in Christensen & Heilmann-Clausen (2013) there was no support for this, but the broader taxon sampling and more careful alignment in the current analysis has changed this. All three species share a very robust and short stipe, close lamellae, and an involute pileus margin, but *T. colossus* stands apart by its annulate stipe, and large spores. Section *Genuina* in our circumscription include species with a reddish brown and glutinous pileipellis, as well as several species with paler brown colours and/or a dry squamulose pileus. Noordeloos & Christensen (1999) divided these in sect. *Imbricata* (with a dry fibrillose to squamulose pileipellis) and sect. *Albobrunnea* (with glutinous pelipellis). Both are moderately well supported in our ITS phylogeny, but at present we prefer to treat them as entities below the section level.

Species with a smooth, white to yellowish cap

Species with a smooth, white to yellowish, dry pileipellis and presence of clamp connections were divided across four clades in our tree, which we here assign to three sections; *Contextocutis*, *Sericella* and *Lasciva* (Fig. 2). Members of sect. *Contextocutis* are characterized by reddening flesh, a soapy odour, greenish to greyish colours and small spores, and the section has long been recognized as a separate entity, often at the subgenus level (e.g. Singer 1986, Noordeloos & Christensen 1999). In contrast most previous authors have not separated *Sericella* and *Lasciva* at the section level (e.g. Bon 1984a, Singer 1986, Riva 1988, Noordeloos & Christensen 1999). However, Bon (1984a) and Riva (1988) distinguished two subsections, *Sulphurea* (corresponding to our sect. *Sericella*) and *Lasciva.* Our analysis do not suggest the two sections to be closely related, and they are morphologically well differentiated. Thus, species in sect. *Sericella* are characterized by very large spores, a strong gas-like odour and white to yellow colours, while members of sect. *Lasciva* have small spores, initially whitish to yellowish grey pileus colours, and a strong, complex odour combining aromatic flowery, gas-like and rancid components. A single member of sect. *Sericella*, i.e. *T. inamoenum*, was by Noordeloos & Christensen (1999) assigned to a separate sect. *Inamoena*, but our analysis clearly shows this section to be redundant. The species assigned to sect. *Lasciva* is in our analysis divided among two terminal clades (Fig. 2), one containing species with non-yellowing context close to *T. lascivum*, the other species with yellowing context. Based on morphological similarities, we expect that future multigene phylogenies will show the two clades to be more closely related than our current analysis proposes, and at present we prefer to keep sect. *Lasciva* as a single taxonomic unit.

Species with a radially fibrillose, whitish, greyish, greenish or yellow cap

The great majority of species characterized by an innately fibrillose to squamulose pileipellis and whitish, greyish, greenish or yellow colours, were joined in one terminal clade in our tree. These are here assigned to sect. *Tricholoma* in accordance with Noordeloos & Christensen (1999). The *T. equestre* group including *T. columbetta* and *T. umbonatum* form a well-supported core clade. *Tricholoma columbetta* has traditionally

been assigned to the separate sect. *Albata* (e.g. Noordeloos & Christensen 1999), but this is not supported by our analysis. Two less well-supported subclades are formed by *T. sejunctum* and allied species, and by sect. *Virgata* in the sense of Singer (1986) with *T. portentosum* taking up an intermediate position. *Tricholoma guldeniae* appears to be the most deviant and basal member of the section. We previously did not consider it as a member of this section (Christensen & Heilmann-Clausen 2013), but our current phylogenetic analysis gives reasonable support for its inclusion.
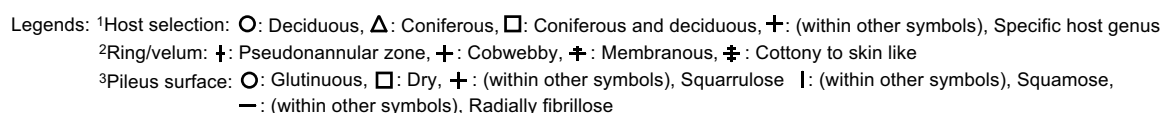
For five species, viz. *T. apium*, *T. avernense*, *T. borgejoensis*, *T. fucatum* and *T. josserandii*, our analysis do not support a clear assignment to traditionally accepted sections (Fig. 1, 2), and appear to represent deviant lineages. These species are discussed further in the next section.

Species level taxonomy

Below we give an overview of the accepted sections, and their circumscribed species accepted by us to occur in northern Europe. We compare our results with earlier studies and comment on further taxa revealed by the analysed ITS data. For further details on the ecology, morphology and practical differentiation of discussed taxa we refer to Christensen & Heilmann-Clausen (2013).

Section Terrea

Our detailed phylogenetic tree supports the presence of seven well-differentiated terminal clades in this section, viz. *T. argyraceum*, *T. cingulatum*, *T. scalpturatum*, *T. inocybeoides*, *T. terreum*, *T. bonii* and *T. triste* (Fig. 1). All of these are known from northern Europe. Many authors (e.g. Huijsman 1968, Krieglsteiner 1982, Clémençon 1983, Riva 1988) accepted *T. gausapatum* and *T. myomyces* as distinct species close to *T. terreum*, differing by small differences in pileipellis structure, veil development and colouration. Based on our quite intensive sampling, we have found no congruence between variation in these traits and ITS phylogeny, and we doubt that *T. gausapatum* and *T. myomyces* as typically interpreted auct. are taxonomically different from *T. terreum.* Also material fitting with *T. leucoterreum* show no ITS difference to typical *T. terreum*, and we interpret this taxon to represent an albinistic form of *T. terreum.* In fact, albinism seems to be rather common in the section, with albinistic forms and varieties described also in *T. cingulatum* and *T. scalpturatum* (Hermosilla & Sánchez 1994, Bidaud & Thévenard 2003). Also *T. bonii* was originally described as a species with whitish colours (Basso & Candusso 1997), but the type shows 100 % ITS sequence similarity with collections with greyish pileus colours. The taxonomy and phylogeny of the species group around *T. argyraceum* was studied in great detail by Jargeat et al. (2010) using three molecular markers. The study found very consistent phylogenies for all markers, supporting the clear delimitation of *T. argyraceum*, *T. inocybeoides*, *T. cingulatum* and *T. scalpturatum* as biological species. Especially *T. argyraceum* was shown to encompass forms and varieties described to differ in colouration from pure white to strongly coloured. Two recently described species from Europe, *T. urbicum* and *T. distantifoliaceum*, have been assigned to the section. They are unknown to us, and type-material should be sequenced to compare their relatedness to more classical species. *Tricholoma moseri* described from North America clearly also belongs to this section, and is close to or even conspecific with *T. triste*, as suggested by our ITS analysis. Both species share small fruit bodies and very long elongate spores. Based on ITS data *T. triste* is also present in China, which is also the case for *T. bonii* (Fig. 1).

Legends: [1]Host selection: O: Deciduous, △: Coniferous, □: Coniferous and deciduous, ✚: (within other symbols), Specific host genus
        [2]Ring/velum: ⊹: Pseudonannular zone, ✚: Cobwebby, ✛: Membranous, ⊞: Cottony to skin like
        [3]Pileus surface: O: Glutinous, □: Dry, ✚: (within other symbols), Squarrulose, ▮: (within other symbols), Squamose,
           —: (within other symbols), Radially fibrillose

Section Atrosquamosa

Our analysis supports the presence of five well-circumscribed European species in this section, viz. *T. atrosquamosum*, *T. orirubens*, *T. basirubens*, *T. squarrulosum* and *T. olivaceotinctum* (Fig. 1). The European species fall in two distinct clades with *T. squarrulosum* and *T. orirubens* as central species, respectively. As discussed thoroughly by Christensen & Heilmann-Clausen (2009) we use the name *T. atrosquamosum* differently than done by Noordeloos & Christensen (1999), and apply it for a taxon close to *T. orirubens*, but mainly associated with conifers and lacking yellow mycelia. Conversely *T. basirubens*, that was first described as a variety to *T. orirubens* (Bon 1975), is closely related to *T. squarrulosum* based on our data. The section appears to be well represented, but poorly resolved in North America. *Tricholoma michinganense* clearly belongs to this section but appears to be poorly represented in modern literature. Bessette et al. (2013) presented three photographs labelled as *T. squarrulosum*, which appear to be somewhat deviant from our concept of this species, based on the slender stipe and occurrence under conifers. The included American sequence labelled as '*T. atrosquamosum*' in our tree, is clearly deviant from included European taxa, but it is unknown if it corresponds to *T. michinganense* or *T. squarrulosum* in the sense of Bessette et al. (2013).

Section Pardinicutis

Our analysis supports five species in this section (Fig. 1), of which only two, i.e. *T. filamentosum* and *T. pardinum*, are known with certainty from Europe. Bon (1991) included a number of additional taxa in his treatment of the section, including *T. tumidum*, *T. cookeanum* and *T. cedrorum*, the latter two being described from Morocco. All are unknown to us. At least three North American taxa are described in this section, viz. *T. huronense*, *T. venenatum* and *T. vernaticum*. Our tree supports the two former as distinct species, assuming that the two sequenced specimens have been correctly labelled.

Section Caligata

Our analysis supports at least ten species in this section (Fig. 1), of which only two are known to occur in northern Europe, viz. *T. matsutake* and *T. dulciolens*. Two further species, viz. *T. caligatum* and *T. anatolicum* occur in southern Europe or adjacent regions. Kytövuori (1988) made a careful taxonomic treatment of the section in Europe, and described *T. dulciolens* as new to science based on collections from Fennoscandia, while *T. anatolicum* was recently described from *Cedrus* forests in Turkey (Intini et al. 2003). This species has since been recorded from Morocco (Ota et al. 2012), and might well occur in southern Europe. A fifth species, *T. ilkkae*, is here described as new to science. It has long been known from the Swedish island of Gotland in the Baltic Sea, but has been identified as either *T. dulciolens* or *T. caligatum*. *Tricholoma ilkkae* share small spores with the first mentioned species, and general colouration with the latter, so the confusion is not surprising. ITS data, however, show that *T. ilkkae* is clearly differentiated from both species, showing most affinity to *T. dulciolens*. We have studied material of the species only from Sweden, but have seen photographs of the species from Norway, and ITS sequence data show that it is also present in Spain (Murata et al. 2013) and Turkey (unpubl. data from Nicklas Bergius). Most likely it

is widely distributed but rare in Europe. Quite likely, *Armillaria caligata* forma *gracilis* represent an earlier synonym, but as the name has not been combined in *Tricholoma* or proposed at the species level, it has limited nomenclatural relevance.

The global phylogeny of the section has been studied rather intensively (Chapela & Garbelotto 2004, Ota et al. 2012, Murata et al. 2013, Gulden et al. 2014). These studies show *T. matsutake* (possibly as a species complex) to be present in both Europe, Asia and North America, while *T. dulciolens* so far is confirmed from Europe and North America. The other recognized species appear to be restricted to smaller biogeographic regions, i.e. *T. anatolicum*, *T. caligatum* and *T. ilkkae* to Europe (including adjacent North Africa and Asia Minor), *T. bakamatsutake*, *T. fulvocastaneum* to eastern Asia and *T. magnivelare* and at least two undescribed lineages (one denoted as 'Mexican magnivelare' in Gulden et al. (2014), and one or two labelled as *T. caligatum*) in Chapela & Garbelotto (2004), to North America. These taxa are represented in our dataset, as '*T. sp. Mex1*.' from Mexico and '*T. caligatum*' from Mexico and Costa Rica, respectively.

Section Genuina

Our analysis supports the presence of at least 18 species in this section in Europe, which fall in two more or less well-supported subclades (Fig. 1).

The largest subclade contains species with reddish brown colours and a glutinous pileipellis, i.e. *T. focale*, *T. batschii*, *T. pessundatum*, *T. populinum*, *T. stans*, *T. aurantium*, *T. albobrunneum*, *T. fulvum*, *T. ustale* and *T. ustaloides*, all known from northern Europe. Many authors have accepted *T. pseudonictitans* as a separate species close to *T. fulvum*, but differing by less pronounced yellow tinges in the gills and flesh of the stipe, and by the association with conifers. Our ITS data do not support this separation (JHC04-251 and MC98-078 were collected under *Picea* and *Abies*, respectively, while JHC03-109 was collected under *Betula*), and hence we treat *T. pseudonictitans* as a synonym to *T. fulvum* (see also Christensen & Heilmann-Clausen 2013). On the other hand, collections from southern Europe identified as *T. cedretorum* and *T. quercetorum* appear to represent distinct species based on ITS, but we have studied too little material and literature to have any opinion on the correct nomenclatural judgments regarding these. Further European taxa characterized by a reddish brown and glutinuous pileus include *T. tridentinum*, *T. ustale* var. *rufoaurantiacum*, *T. ustaloides* var. *aurantiodes* and *T. ezcarayense*. The latter taxon, *T. ezcarayense*, however possesses clamp connections (Hermosilla & Sánchez 1994), which are otherwise absent in the section and is probably unrelated. The North American sequences included in the tree suggest that *T. aurantiacum*, *T. batschii*, *T. focale* and *T. stans* are present also on this continent, with *T. zelleri* and *T. dryophilum* being potential synonyms to the two latter species. In contrast, the included American sequence assigned to *T. ustaloides* represents a distinct taxon not closely related to our concept of this species. Judging from photos and descriptions in Bessette et al. (2013) *T. muricatum*, *T. pudorinum* ined. and *T. transmutans* are further North American taxa in this group, with *T. fulvum*, *T. pessundatum*, *T. populinum* and *T. ustale* being also recorded as North American. Grubisha et al. (2012) investigated the phylogeography of *T. populinum* in Scandinavia and North America, and found no signs

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Fig. 2 Phylogeny inferred from ITS regions for a reduced dataset, based on representative sequences for 72 well-circumscribed species or species hypotheses. Branch lengths and branching patterns are based on the Maximum Likelihood analysis. Branching patterns were similar in the Bayesian analysis, except for sect. *Atrosquamosa*, were the alternative configuration is shown as an insert. Maximum Likelihood bootstrap values are indicated above branches, while Bayesian posterior probabilities are indicated below branches for proposed sections indicated with background shadings and names in capital letters. * Denotes 100 % support in both analyses. Coloured bars show the affiliation to subgenera in the sense of Singer (1986). Host selection and six different morphological traits are scored using different symbols, to illustrate their distribution across the phylogeny, and to the proposed sections.

of recent intercontinental gene flow in this specific partner of *Populus* spp. Based on the molecular clock approach they estimated divergence between European and American populations to have happened between 1 and 1.7 million years ago.

A smaller, and slightly less well-supported subclade contain species with a dry, squamulose pileus. Our analysis include only three European species in this group, viz. *T. psammopus*, *T. vaccinum* and *T. imbricatum*, but Moreau (2011) presented and discussed two additional central-European taxa, viz. *T. inodermeum* and *T. subfusipes*. Both appear to be well delimited species, close to *T. imbricatum* and *T. vaccinum*, respectively, but with slightly different macroscopic characters (Moreau 2011) and deviant ITS data (P.-A Moreau pers. comm.). Ecologically, *T. subfusipes* differs from *T. imbricatum* by being associated with *Larix* rather than *Pinus*. A third species, *T. pseudoimbricatum*, described from Denmark is by us regarded as a synonym to *T. imbricatum* (for details see Christensen & Heilmann-Clausen 2013). The included North American sequence of *T. imbricatum* is quite deviant from the two European sequences, and might represent a distinct species. Both *T. imbricatum* and *T. vaccinum* are illustrated with several photographs from various American states in Bessette et al. (2013). The variation in colouration, stature and pileipellis structure is quite striking, and suggests the presence of several additional species on the continent.

Section Megatricholoma

This relatively well-supported section was not accepted in Christensen & Heilmann-Clausen (2013) but as mentioned above the present analysis has lead us to treat it in a wider sense than done previously, by including the non-annulate species *T. acerbum* and *T. roseoacerbum* beside the types species *T. colossus*. Thus, our concept of the section includes three well known species in Europe (Fig. 1, 2), with *T. robustum* representing a tentative fourth, badly known member (see Christensen & Heilmann-Clausen 2013). *Tricholoma roseoacerbum* appears to be remarkably widely distributed, with almost perfect ITS sequence matches connecting collections and environmental samples from Finland, Japan, Canada and Mexico. *Tricholoma japonicum* probably represents the oldest valid name for this species, with *T. radotinense* representing a further potential synonym. Also *T. manzanitae* described from North America belongs to this group, judging from the presentation in Bessette et al. (2013).

Section Sericella

This section contains six well-separated European end-clusters in our tree. Two additional sequences appear to represent distinct taxa occurring in Canada and the USA (Fig. 1). Across continents, only three of these can be assigned to well-known species, i.e. *T. inamoenum*, *T. hemisulphureum* and *T. sulphureum*, while a forth, *T. bryogenum* is described as new to science in this paper. Already Comandini et al. (2004) reported the presence of cryptic diversity within the section, but mainly concluded that *T. bufonium*, described to differ from *T. sulphureum* by more reddish to purplish pileus colours, could not be readily separated from *T. sulphureum.* Our studies partly confirm pileus colours to be poorly suited to differentiate taxa within the section (Christensen & Heilmann-Clausen 2013), but we are not convinced that the cryptic taxa detected by the phylogenetic analysis are truly indistinguishable from *T. sulphureum* s.str. The colours of the lamellae and basal mycelium appear to be promising characters in this respect, but we also expect differences in ecology and biogeography. At least this is the case for *T. bryogenum* that differs from *T. sulphureum* s.lat. by its habitat in boreal coniferous forests, the dull yellow colours and the whitish basal mycelium. No modern type exists of *T. sulphureum*, and hence it remains

unknown which of the three additional lineages in our tree corresponds to *T. sulphureum* s.str. Hence they are labelled as type I to III in correspondence with Comandini et al. (2004) and Christensen & Heilmann-Clausen (2013). A large number of varieties have been described in *T. sulphureum* (see Bon 1991 for an overview). Some of these might correspond to the presently cryptic species in our tree. According to our phylogenetic tree, *T. inamoenum* occurs also in North America, at least based on ITS data. Another species from this continent that clearly belongs to this section is *T. odorum*.

Section Contextocutis (= section Rigida)

This section contains at least four European taxa in our tree, viz. *T. saponaceum*, *T. sudum*, *T. rapipes* (comb. nov.) and *T. boudieri* (Fig. 1, 2). Of these, the two latter are normally not differentiated from *T. saponaceum* at the species level, but we find that differences in morphology and ITS sequence data warrant their distinguishing. A large number of further varieties have been described in the section, mainly based on pileus colours and surface texture of the stipe (see Bon 1991). Our studies indicate that these characters are quite plastic characters with limited taxonomic relevance (Christensen & Heilmann-Clausen 2013). Based on the collections studied by us, *T. saponaceum* and *T. boudieri* are associated with deciduous hosts, while *T. rapipes* and *T. sudum* are associated with conifers (Christensen & Heilmann-Clausen 2013). We are far from convinced that these preferences are strict, and await future studies testing host selection and taxonomy in the group. Our current analysis indicates that our concept of *T. boudieri* could cover more than one species, and we would not be surprised if more dedicated studies would prove the existence of additional species in the section in Europe. The two included extralimital sequences from New Zealand and North America represent further independent species in the section, which judging from the photographs given in Besseette et al. (2013) contains several different species in North America.

Section Lasciva

In our tree this section is split across two subclades, containing a total of five species (Fig. 1, 2) in northern Europe, viz. *T. lascivum*, *T. album*, *T. stiparophyllum*, *T. sulphurescens* and *T. boreosulphurescens*. The latter is described as new to science in this paper. A sequence labelled a *T. sulphurescens* from Estonia, appears to represent a further, undescribed species. The taxonomy of the section was discussed in detail by Christensen & Noordeloos (1999) who neotypified *T. lascivum*, *T. album* and *T. stiparophyllum. Tricholoma albidum* and *T. farinaceum* in the sense of Bessette et al. (2013) appear to represent North American members of this section.

Section Tricholoma

This section contains at least 13 species in northern Europe, viz. *T. virgatum*, *T. sciodes*, *T. bresadolanum*, *T. aestuans*, *T. portentosum*, *T. sejunctum*, *T. viridilutescens*, *T. equestre*, *T. frondosae*, *T. joachimii*, *T. columbetta*, *T. umbonatum* and *T. guldeniae*, but several included subclades have complex ITS sequence patterns, and remain poorly resolved in our tree. This is especially the case in the *T. equestre* group, but also *T. sejunctum/viridilutescens* and *T. umbonatum* represent species complexes based on our phylogeny. The complex phylogeny of *T. equestre* s.lat. was noted previously by Horton (2002) based on North American specimens, and have been confirmed by subsequent studies, dealing with the group across the northern hemisphere (Moukha et al. 2013). Even before molecular phylogenies were available, a number of taxa were proposed but often synonymized in this group, with *T. equestre*, *T. auratum* and *T. flavovirens* representing classical names. Kalamees (2001) studied the group based on ecological and morpho-

logical characters. He described two new species, *T. frondosae* and *T. ulvinenii*, and at the same time assigned *T. auratum* and *T. flavovirens* as synonyms to *T. equestre*. The study was not supported by molecular sequences, and unfortunately we have been unsuccessful in our attempts to extract DNA from the types of the two new species. In our analysis collections labelled as *T. frondosae* form three groupings in the tree, but we are quite convinced that *T. frondosae* type I match the type, as all collections have been characterized by warm colours and small spores as emphasized in the diagnosis. *Tricholoma frondosae* type II have larger spores and more greenish colours and seem to represent an undescribed species. A further collection from France (MC98-086) is only distantly related to the *T. equestre* core group based on ITS data.

Collections labelled as *T. ulvinenii* fall in two distinct clusters within the poorly resolved core *T. equestre* clade, and it is unknown if any of these represent the type concept of this species. Collections identified as *T. ulvinenii* by Kuulo Kalamees (viz. UDB011557–UDB011559) are separated on both groups, indicating them to be difficult to separate based on morphological characters. In our simplified overview tree (Fig. 2) *T. ulvinenii* is represented by the upper terminal clade containing four collections labelled with this name, and illustrated in Christensen & Heilmann-Clausen (2013: 103).

Collections labelled as *T. joachimii* appear on three widely divided branches in the tree. We have not studied the type of this species, and as far we know no type sequence is available to test the correct position of this species in the phylogeny.

The included extra-liminal sequences add to the complexity of the groups. A global analysis including multiple genetic markers, and renewed attempts to sequence type collections is needed to resolve the taxonomy of the group, which also contains *T. chrysophyllum*, described from southern Europe (Riva 1988), and *T. intermedium*, described from North America. Somewhat surprisingly, the two whitish species with radially fibrillose pileipellis, *T. columbetta* and *T. umbonatum* seem to have a basal position to the *T. equestre* complex. As already emphasized by Christensen & Heilmann-Clausen (2013) collections labelled as *T. umbonatum* fall in two distinct subclades. We are quite convinced that type II, as illustrated in Christensen & Heilmann-Clausen (2013), corresponds to the original concept of this species as presented by Clémençon & Bon in Bon (1984b). Judging from Bessette et al. (2013) also *T. subresplendens* belongs to this species group.

The *T. sejunctum/viridilutescens* group is another poorly resolved subclade in sect. *Tricholoma*. Except for the South-European taxon *T. rufenum* that has a grey pileus, the European members of this group are characterized by greenish to yellowish pileus colours. In our recent monograph, we accepted only two species viz. *T. sejunctum* and *T. viridilutescens* to occur in northern Europe, but the current analysis shows that our concept of *T. viridilutescens* as presented in Christensen & Heilmann-Clausen (2013) circumscribes two well separated species based on ITS. These are here denoted as *T. viridilutescens* type I and II, respectively. Further collections from North America labelled as *T. sejunctum* and *T. leucophyllum* represent further distinct terminal branches. In our data *T. viridilutescens* type I is represented by two collections from France, quite close to the type locality in the Austrian Alps, and it might well represent *T. viridilutescens* s.str. Type II is represented by two collections from Estonia, that have high ITS similarity to collections from Canada and Japan. *Tricholoma subsejunctum* described from eastern North America is a relevant candidate name for these collections. We have studied the type collection of *T. subsejunctum* which is in poor condition and unlikely to yield usable ITS data. *Tricholoma eosinobasis* and *T. clavocystis*

are additional European species described in this group and represent further candidate names (or synonyms) for *T. viridilutescens* type I and II. Types of the mentioned taxa have not been studied by us.

Also *T. viridifucatum* and *T. luridum* are characterized by greenish to olivaceous pileus colours and both may belong to this group, even if the squamulose stipe in the former and the greyish lamellae in the latter are deviant. We have been unsuccessful in obtaining sequence data for these two taxa. Chapon (2011) compared *T. viridifucatum* with a further taxon denoted as *T. coryphaeum*. This species might well belong to this group but could also be part of the *T. equestre* complex. For a nomenclatural discussion on this name see Christensen & Heilmann-Clausen (2013). Judging from descriptions and photos in Bessette et al. (2013), also the North American taxa *T. davisiae* and *T. subluteum* belong to this group, probably together with *T. muscarium* described from Japan (e.g. Hongo 1988). Comprehensive studies using a global sampling strategy, type studies and multiple molecular markers are needed to resolve the taxonomy of this difficult species complex.

Species with a grey or yellow, radially fibrillose dry pileus (sect. *Virgata* ss. Singer 1986) form a relatively well-resolved subclade in our tree, with the glutinous *T. portentosum* having a more distant position. According to our data, *T. bresadolaum* is heterogeneous in the ITS region, and in general we would not be surprised if a more comprehensive sampling would show the subclade to contain more species in Europe. Several additional species have been described in the group, including *T. lilacinocinereum*, *T. sciodellum* and *T. vinaceogriseum*, and some authors also distinguish *T. hordum* as a separate species close to *T. sciodes* (but see Christensen & Heilmann-Clausen 2013). The subclade seems to be richly represented in North America. Judging from Bessette et al. (2013) at least *T. acris*, *T. argenteum*, *T. atrodiscus*, *T. palustre* and *T. pullum* belongs here. The included sequence of the latter species is close to *T. aestuans.* Finally, the sequence of *T.* aff. *virgatum* from Nepal clearly represent a separate taxon close to *T. virgatum.*

Unassigned species

Apart from the species that are assigned to the ten hypothesized sections discussed above, five sequenced North-European species, viz. *T. arvernense*, *T. josserandii*, *T. fucatum*, *T. borgsjoeënse* and *T. apium*, remain unclassified at section level (Fig. 2). Despite the presence of clamp connections, *T. arvernense* has traditionally been assigned to the clampless sect. *Tricholoma* (e.g. Riva 1988, Noordeloos & Christensen 1999), but in our tree it forms an isolated cluster with a sequence identified as *T. luteomaculosum* from North America (Fig. 1). This species is characterized by a greyish, fibrillose to squamulose pileus and yellowing flesh and in contrast to *T. arvernense*, it is described to lack clamp connections (Ovrebo 1986). Smith (1942), who described the species, pointed out its similarity with *T. scalpturatum*, which lead Singer (1986) to regard it as a possible member of sect. *Terrea*. This placement is not supported by our analysis. The second unclassified species, *T. josserandii*, has traditionally been considered as a close relative to *T. virgatum* (Bon 1984a, Riva 1988), but this is disapproved by our analysis. Instead, the species clusters closely with two sequences from North America identified as *T. mutabile*, and more distantly so with a third unassigned species, *T. fucatum*, that has traditionally been assigned to sect. *Tricholoma* (e.g. Riva 1988, Noordeloos & Christensen 1999). All three species are characterized by slender fruit bodies with a cylindrical stipe, a radially fibrillose pileipellis and large spores. Based on photographs and descriptions in Bessette et al. (2013), the North American *T. aurantio-olivaceum* appears to be a close relative of *T. fucatum*, together with *T. olivaceobrun-*

neum. All the above species might form an evolutionary lineage worth accepting at the section level. A further deviant lineage is formed by *T. borgsjoeënse* that clusters closely with a sequence of *T. atroviolaceum* from North America. Both species share a dark grey, felty to squamulose pileus, greyish lamellae and large spores. When describing *T. borgsjoeënse*, Jacobsson et al. (2006) assigned the species to sect. *Terrea*, but the current phylogenetic analysis indicates it to be only distantly related to this section. The large spores and the quite special pileipellis structure (see Christensen & Heilmann-Clausen 2013: 20) support the isolated position among European *Tricholoma* species. Interestingly, our analysis points to substantial variation in the ITS region in *T. borgsjoeënse*, with the Norwegian collection deviating considerably from the two Swedish collections that both stem from the type locality.

Finally, *T. apium* appears to be isolated among the species analysed. Noordeloos & Christensen (1999) classified it in sect. *Imbricata* (here a part of sect. *Genuina*). The species do show some morphological resemblance to species in this section, and might have a basal position in it, as suggested by the maximum likelihood analysis.

NEW COMBINATIONS

Tricholoma rapipes (Krombh.) Heilm.-Claus. & Mort.Chr., *comb. nov.* — Mycobank MB816908

Basionym. Agaricus rapipes Krombh. (1836: 22).

Description in Christensen & Heilmann-Clausen (2013).

DIAGNOSES AND DESCRIPTIONS OF NEW SPECIES

Tricholoma ilkkae Mort.Chr., Heilm.-Claus., Ryman & Niclas Bergius, *sp. nov.* — MycoBank MB816909; Fig. 3a, b

Etymology. Latin 'ilkkae' in honour of the Finnish mycologist Ilkka Kutövuori.

Holotype. SWEDEN, Gotland, Eksta par, Ekstastrand, coniferous forest dominated by *Pinus sylvestris*, with scattered *Picea abies* on old beach ridges, 21 Sept. 2000, leg. *Svengunnar Ryman* 9080 (UPS, F-513823).

Diagnosis — A medium-sized to large *Tricholoma*, with a distinct ring, and fawn to dark brick, confluent fibrillose patches on the pileus and girdles on the stipe. Mycorrhizal with *Pinus* and possibly *Picea*.

Pileus 40–100 mm, at first hemispherical to convex with involute margin, later convex to flattened, often with low, broad umbo, in central part soon breaking up into appressed, ± confluent scales, which are fawn, orange brown to dark brick, on a cream to straw yellow background; scales gradually or more abruptly thinning out towards the marginal zone, which is typically white to straw yellow or pale mouse grey; margin in young fruit bodies shaggy due to remnants of veil, but soon ± smooth to somewhat felty-costate. *Lamellae* emarginate, with even to somewhat eroded edges, whitish, with age sometimes with orange brown spots, rather close to medium spaced. *Stipe* 50–100 × 15–25 mm, cylindrical or tapering downwards, often somewhat rooting, with a distinct, persistent, cuff-like, cottony-woolly ring, whitish and granulose or slightly fibrillose above ring, below ring with irregular, fawn, orange brown to dark brick confluent girdles and patches on a whitish background, basal part occasionally with a weak greenish tinge. *Flesh* whitish; smell sweetish, perfumed fruity, similar to *Inocybe corydalina* or *Hemipholiota heteroclita*; taste unknown. *Spores* 4.5–6.7 × 3.9–5.5 µm, average 5.1–6.0 × 4.4–4.9 µm, predominantly broadly ellipsoid, Q = 1.0–1.5, average 1.15–1.31. Basidia 30–40 × 6–8 µm, 4-spored. *Cheilocystidia* not observed. *Pileipellis* cutis made up of cylindri-cal, warm brown hyphae, 50–300 × 5–15(–20) µm, pigment not incrusting. *Clamp connections* absent.

Ecology & Habitat — Ectomycorrhizal with *Pinus* and possibly *Picea*, mainly in forests on calcareous ground.

Known distribution — Central Sweden (holotype), Norway, Spain and Turkey; most likely widespread in Europe.

Additional material examined. SWEDEN, Gotland, Eksta Par., Ekstastrand, coniferous forest on old beach walls, 9 Oct. 1998 (MC98-602, C-F-96261); ibid., 18 Sept. 2000 (UPS-F013888); ibid., associated with *T. aurantium*, *T. fracticum*, *Hydnum albidum*, *Hygrophorus latitabundus* and *Sarcodon fuligineoviolaceous*, 3 Oct. 2009, *Irene Anderson & Michael Krikorev* (MKR 091003-4, IMG: 100/1208-11); ibid., 29. Sept. 2011 (TF2011-201); Uppland, Gräsö par., Djupdal 3 km NE of Gräsö church (Grid: RN1648667 x 6697072), in needle bed under *Picea abies* in old *Picea / Pinus* forest, 2 Oct. 2007, *Gillis Aronsson* (UPS-F173364); Uppland, Börstil par., the turnaround on NW Tvärnö (Grid: RN1648788 x 6681279), under *Picea abies* and *Pinus sylvestris* in older, grass-dominated forest on old slag heap, 13 Sept. 2007 (UPS-F173264); ibid., 24 Sept. 2009, *Gillis Aronsson* (UPS-F173265).

Notes — According to the phylogenetic analysis the new species is close to *T. dulciolens*. Both species share small spores, but *T. ilkkae* is easily distinguished from *T. dulciolens* by the shorter stem and much darker pileus scales and stipe girdles. Another similar species is *T. caligatum*, which is distinguished by larger spores and by slightly darker, more contrasting pileus scales and stipe girdles. In addition, the two species differ in habitat and distribution, as *T. caligatum* seems to be a strictly Mediterranean species, in contrast to *T. ilkkae*, which so far is known from more temperate environments. Finally, *T. matsutake* differs by duller colours, larger fruit bodies and larger spores. *Armillaria caligata* var. *gracilis*, as illustrated by Bresadola (1927), matches well with *T. ilkkae*, but we don't know if authentical material exists that could prove this. A potential synonymy will not have nomenclatural consequences as *Armillaria caligata* var. *gracilis* has never been combined as a species epithet.

Tricholoma bryogenum Mort.Chr., Heilm.-Claus. & Vauras, *sp. nov.* — MycoBank MB816910; Fig. 3c

Etymology. From Greek 'βρύον' (moss) and 'γεννώ' (born), referring to the habitat in mossy *Picea*-forests.

Holotype. SWEDEN, Jämtland, Brunflo, under *Picea abies* on rich soil, among mosses, 4 Sept. 1997, *Morten Christensen* MC97-101 (C-F59167).

Diagnosis — A small to medium-sized *Tricholoma*, with dull yellow colours on stipe, lamellae and pileus margin and a strong, chemical smell. Differing from the closely related *T. sulphureum* by the duller colours, white basal mycelium and by the occurrence in mossy *Picea* forests.

Pileus 30–100 mm, at first conical, bell-shaped or convex, soon low convex to plane, with or without a low umbo, smooth, glossy, at margin whitish chrome to pale chrome, with age and towards centre darker, pinkish buff to ochraceous orange. *Lamellae* adnate to deeply emarginate, rather broad and thick, medium spaced to rather distant, lemon yellow to lemon chrome or honey, more saturated than the margin of the pileus. *Stipe* 50–130 × 8–25 mm, cylindrical or slightly club-shaped, smooth or more often distinctly fibrillose, at base often with white tomentum, straw yellow, pale yellow to light chrome, darkest and most yellow towards base, with age often duller, pale cream to cream, with a ± fibrillose brownish covering; basal mycelium whitish to faintly yellowish. *Flesh* rather firm, coloured more or less like the surface; smell strong, tar- or gas-like as in *T. sulphureum*, after cutting more farinaceous; taste unpleasant, mild, farinaceous-rancid to slightly bitter. *Spores* 8.2–14.4 × 4.7–8.4 µm, average 9.4–12.3 × 5.6–7.5 µm, ellipsoid to elongate or amygdaliform, Q = 1.3–2.0, average 1.62–1.69. *Basidia* 35–60 × 7.5–10.0 µm, mainly 2-spored. *Cheilocystidia* not observed. *Pileipellis* an interwoven cutis with individual hyphal elements generally

Fig. 3 Fruitbodies of *Trichloma* species. a. *Tricholoma ilkkae* (holotype); b. *Tricholoma ilkkae*, older specimens (UPS-F173364); c. *Tricholoma bryogenum* (holotype); d. *Tricholoma boreosulphurescens* (holotype). — Scale bars = 1 cm.

50–150 × 3–6 µm; subpellis poorly differentiated. *Clamp connections* not observed, apparently absent.

Ecology & Habitat — Ectomycorrhizal with *Picea* and possibly *Pinus*, mainly in rich, mixed forests on calcareous soils. Most records are from moist, eutrophic depressions, or spring-fed slopes with abundant bryophytes, but there are also some records from drier soils.

Known distribution — Central Sweden, Norway and Finland; most likely widespread in Fennoscandia, and possibly in the mountains of central Europe.

Additional material examined. Finland, Koillismaa, Kuusamo, Iivaara, E slope, S of Saunakunnas, near Isokorpi, forest with mainly *Picea abies* and scattered *Pinus sylvestris*, *Alnus incana* and *Betula*, eutrophic depression, 29 Aug. 2007, *Jukka Vauras* (25068, TURA); Perä-Pohjanmaa, Rovaniemi rural commune, Jaatila, Jaatilanvaara, near Kylmäojao brook, fairly rich, gently W-sloping, spring-fed forest with *Picea abies*, *Betula*, *Alnus incana*, *Populus tremula* and *Pinus sylvestris*, 11 Aug. 1999, *Jukka Vauras* (15082F, TURA); ibid., 19 Aug. 1999, *Jukka Vauras* (15223F, TURA).

Notes — The new species is distinguished from *T. sulphureum* mainly by its habitat, the dull yellow colours and the whitish basal mycelium. The difference in coloration is distinct even in exsiccata, which are typically pale buff in *T. bryogenum*, but cinnamon to greyish brown in *T. sulphureum*. A further difference may be the absence of clamp connections in *T. bryogenum*, but we are not certain if this character difference is truly stable. *Tricholoma bryogenum* is quite similar to *T. odorum* described from North America, but the latter taxon has more crowded lamellae.

Tricholoma boreosulphurescens Mort.Chr. & Heilm.-Claus., *sp. nov.* — MycoBank MB816911; Fig. 3d

Etymology. From latin 'borealis' (northern) combined with the species epithet of *Tricholoma sulphurescens*, a closely related and morphologically almost similar relative with a southern distribution in Europe.

Holotype. Norway, Finnmark, Alta, Kåfjordsbotten, S of Hesteskovattnet, under *Betula*, 18 Aug. 2004, *Per Marstad* 197-04 (O-F187683).

Diagnosis — A medium-sized to large *Tricholoma*, with whitish colours and strongly yellowing context. Mycorrhizal with *Betula* and possibly *Picea* in boreal and subalpine forests on calcareous soils. Morphologically very similar to *T. sulphurescens*, but with substantial differences in the mitochondrial ITS region and a different ecology and distribution range.

Pileus 30–100 mm, at first bell-shaped to convex, soon low convex to plane or slightly depressed, often irregularly wavy, with or without a low umbo, dry and dull, very finely velutinate, without radial structure, white when young, becoming pale chrome, ochraceous or yellowish brown with age, especially in central part, strongly yellowing when touched, after some time fading to ochre. *Lamellae* adnate to emarginate, medium broad, medium spaced to rather crowded, whitish to cream or pale chrome, with age becoming lemon yellow to honey, especially near the edges or when damaged. *Stipe* 50–100 × 10–20 mm, ± cylindrical, mostly widened at base, more rarely tapering, smooth, but mostly finely floccose to squamulose at top, at base often velutinate, at first white to whitish chrome, staining lemon yellow to pale chrome, especially when touched, slowly fading to clay buff reddish brown. *Flesh* rather firm, white to cream, staining lemon yellow to sulphur yellow after cutting; smell strong, at first recalling lemons, then complex nauseating, combining aromatic flowery, gas-like and rancid components; taste first mild, but after a while somewhat acrid to bitter. *Spores* 4.5–7.6 × 3.9–6.0 µm, average 5.6–6.4 × 4.2–5.1 µm, predominantly broadly ellipsoid, Q = 1.0–1.5, average 1.20–1.25. *Basidia* 25–35 × 5.5–8 µm, mainly 4-spored. *Cheilocystidia* not observed. *Pileipellis* an irregularly interwoven cutis with individual hyphal elements generally 50–200 × 4–10 µm; subpellis poorly differentiated. *Clamp connections* present at some septa.

Ecology & Habitat — Ectomycorrhizal with *Betula* and possibly *Picea* on calcareous soils in rich, mixed *Picea* dominated forests and in subalpine *Betula* forests near the timber line.

Known distribution — Seemingly with an eastern distribution in Fennoscandia; known from several localities in the northern part of Finland, but only from scattered localities in Sweden and Norway. Probably distributed eastwards in Russia, and perhaps even present in other parts of Europe, e.g. in subalpine forests in central European mountain chains.

Additional material examined. Finland, Outer Ostrobothnia (PeP/Obu), Tervola, Peura, Raemäki, E of the forest road to Syvälampi, between the pond Pikku-Ruuntana and Raemäenjänkä, S-sloping, grass-herb spruce forest with spring-fed depressions on calcareous ground, 11 Oct.1997, *Ilkka Kytövuori* 97-1187 (H6002040); Koillismaa, Kuusamo, Oulanka National Park, N of the biological field station, E of Puukkosuo, herb rich forest with *Picea abies*, *Pinus sylvestris*, *Betula*, *Populus tremula* and *Salix*, eutrophic depression with *Daphne mezereum*, *Filipendia ulmaria*, *Goodyera repens*, *Cirsium helenoides* and *Elymus caninus*, 4 Sept. 2005, *Jukka Vauras* (23414F, TURA); Koillismaa, Kuusamo, Oulanka National Park, Ampumavaara, E of Puukkosuo, S of the main road, margin of eutrophic depression with *Picea abies*, *Pinus sylvestris*, *Alnus incana*, *Betula* and *Salix*. 30 Aug. 2007, *Emanuele Campo & Jukka Vauras* (25089F, TURA).

Notes — *Tricholoma sulphurescens* has long been known as rare but easily identified species characterized by whitish colours and strongly yellowing context. While working with the volume on *Tricholoma* in Fungi of Northern Europe (Christensen & Heilmann-Clausen 2013) we realized that collections from boreal to subalpine Fennoscandia represented a clearly different lineage, than collections from southern Europe that are typically associated with *Fagus* and *Quercus*, on warm calcareous soils. Since *T. sulphurescens* was originally described from Italy (Bresadola 1905) we here describe the new species as *T. boreosulphurescens* emphasizing its boreal distribution. The new species is very similar to *T. sulphurescens* in all important morphological characters. Our updated phylogeny presented here strongly indicates the presence of a third cryptic taxon in the group represented by one collection from Italy and one from a boreonemoral forest with *Quercus* and *Tilia* in Estonia. It remains to be determined which of the two non-boreal lineages corresponds to the type specimen of *T. sulphurescens* originally described by Bresadola, and the degree to which they are separable based on morphological or ecological characters.

DISCUSSION

With the present study we have provided a first comprehensive phylogenetically supported taxonomic overview of the genus *Tricholoma* in northern Europe. Based on this we consider sections *Caligata*, *Atrosquamosa* and *Terrea* as rather well evaluated taxonomically on the European continental scale. All three sections have been sampled intensively in this or other studies, and we would be surprised if future studies will change fundamentally with the species delimitations presented here and elaborated in more detail by Christensen & Heilmann-Clausen (2013). For all other sections our sampling is limited and additional European species are likely to occur, not least in southern Europe. The sections *Genuina*, *Contextocutis*, *Sericella* and *Tricholoma* in particular are in need of further phylogenetic studies with *T. equestre* s.lat., *T. sulphureum* s.lat. and *T. viridilutescens/sejunctum* representing species complexes with considerable cryptic diversity. These are all represented across the northern hemisphere and future studies addressing these two groups should apply a comprehensive sampling strategy and apply multiple genetic markers to unravel the complex phylogeography of both groups.

Many *Tricholoma* species appear to have a circumboreal distribution based on the data presented in our study. At least

T. aurantium, *T. batschii*, *T. bonii*, *T. dulciolens*, *T. focale*, *T. frondosae*, *T. inamoenum*, *T. matsutake*, *T. portentosum*, *T. roseoacerbum T. stans* and *T. triste* have almost exact ITS similarity across two or three continents, and according to Jargeat et al. (2010) the same applies for *T. argyraceum* and *T. cingulatum*. Most extreme in this respect is *T. roseoacerbum*, which according to our data, is present in Finland, Canada, Japan and Mexico. In Europe it is considered a rarity (Riva 1988, Christensen & Heilmann-Clausen 2013), making the wide distribution particularly intriguing. The above-mentioned species with an intercontinental distribution are all associated with widely distributed boreal host tree genera: *T. dulciolens* and *T. inamoenum* are primarily associated with *Picea*, *T. frondosae* with *Populus*, *T. cingulatum* with *Salix*, while *T. aurantium* and *T. argyraceum* have a broad host selection. The remaining species are associated primarily or exclusively with *Pinus*. Thus, none of the species associated exclusively with nemoral deciduous hosts, including *Fagus* and *Quercus* occurs across continents based on our data. Grubisha et al. (2012), investigated in more detail the phylogeography of *T. populinum* and found substantial divergence between North American and Fennoscandian populations, pointing to a reproductive isolation established 1–1.7 million years ago. Similar studies investigating the phylogeography of the apparently circumboreal species mentioned above would be interesting.

Regarding the higher level taxonomy, our study has provided support for several classical sections accepted in *Tricholoma*, but with some modifications. Most importantly our data showed *T. focale* to be a member of sect. *Genuina*, rather than sect. *Caligata*, while *T. sciodes* and allied taxa were shown to belong to sect. *Tricholoma* rather than to sections *Terrea* or *Atrosquamosa*. While ITS appears to be a stable marker for species delimitations in *Tricholoma* (Mouhamadou et al. 2008, Jargeat et al. 2010) there are no reasons to believe that the region can resolve higher taxonomic relationships at a sufficiently detailed level (e.g. Frøslev et al. 2005). Hence the here suggested infrageneric classification should be viewed as preliminary, and we encourage further studies using multiple molecular markers to investigate the infrageneric phylogeny of the genus. As the majority of known species in *Tricholoma* occurs in North America it is obvious that a careful sampling of North American taxa should be part of such a study, but even Asia, Australia, New Zealand and southern South America host *Tricholoma* species that are highly relevant to include in future attempts to unravel the biodiversity, evolution and phylogeography of this important ectomycorrhizal genus.

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