NEW SPECIES AND RECORDS OF *TRICHOLOMA* (AGARICALES: TRICHOLOMATACEAE) SECTIONS *GENUINA* AND *MEGATRICHOLOMA* FROM COSTA RICA AND UNITED STATES

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ABSTRACT

Species of *Tricholoma* sections *Genuina* and *Megatricholoma* are characterized by having pilei that are some shade of brown, and by white or yellow lamellae that also discolor some shade of brown. From Costa Rica in sect. *Genuina*, we describe as new **T. luteopallidum, T. cacumense,** and **T. talamancense,** and confirm the occurrence of *Tricholoma stans*, and from the United States describe as new **Tricholoma brunneoluteum.** *Tricholoma roseoacerbum* from sect. *Megatricholoma* is confirmed for Costa Rica. Morphology as well as ITS sequences are employed to confirm the species' identifications or circumscriptions of the new species.

Key Words: Central America, Agaricomycetes, mushrooms, ITS

RESUMEN

Las especies de *Tricholoma* de las secciones *Genuina* y *Megatricholoma* se caracterizan por tener pileo de diversos tonos de marrón, y por lamelas blancas o amarillas, que también se torman marronáceas. Describimos como nuevos **T. luteopallidum, T. cacumense y T. talamanense** de Costa Rica pertenecientes a la sección *Genuina* y confirmamos la ocurrencia de *Tricholoma stans*. Además, describimos la nueva especie **Tricholoma brunneoluteum** de Estados Unidos. Se confirma *Tricholoma roseoacerbum* de la sección *Megatricoloma* para Costa Rica. Se emplean tanto la morfología como las secuencias ITS para confirmar las identificaciones de la especie o la circunscripción de la nueva especie.

INTRODUCTION

Tricholoma taxa with dry or viscid, brown pilei, white, off-white or yellow lamellae and stipes were originally placed in subg. *Tricholoma* sect. *Genuina* (Fr.) Sacc. (Singer 1986). More recent work confirmed by molecular analyses supports recognition of a second section, sect. *Megatricholoma* (Kost) M. Christensen & Noordel., that includes several species originally placed in sect. *Genuina* (Christensen & Noordeloos 1999; Heilmann-Clausen et al. 2017). Species in these sections, particularly *Genuina*, form a very complex group of taxa worldwide including North America. Many of the names of taxa in this section are of European origin making it difficult to know with reasonable certainty if the European names can be applied to North American taxa. With the publications of Christensen and Heilmann-Clausen (2013) and Heilmann-Clausen et al. (2017), especially the latter with the phylogenetic treatment which we follow, it is possible to begin analyzing and comparing species in this section that occur in North and Central America.

In this paper, we describe three new species in sect. *Genuina* from Costa Rica and one new species from the United States, and in the same section report *T. stans* (Fr.) Sacc. from Costa Rica for the first time; we also report *T. roseoacerbum* Riva, sect. *Megatricholoma,* for the first time for Costa Rica. For completeness, we provide descriptions of the latter two species. The new species all have lamellae that are light yellow to yellow as is the stipe surface pigmentation or at least the stipe context. A cladogram of the species treated is found in

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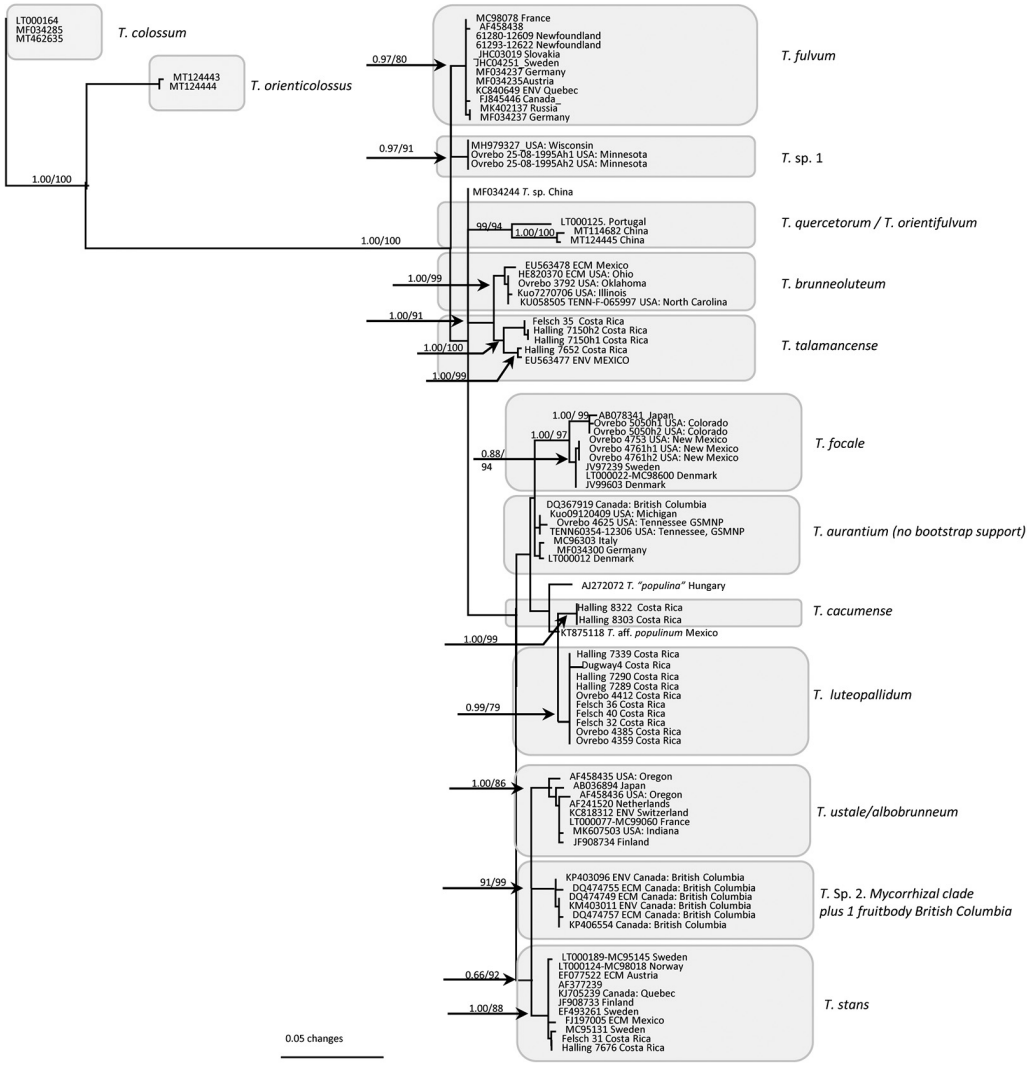

Fig. 1. PhyML tree. Node support is given to the left of the supported node. Bayesian posterior probabilities above the line; Bootstrap support based on 1000 replicates is given below the line.

Figure 1. There is much macromorphological diversity within sect. *Genuina* in North America so detailed documentation of both the macroscopic and microscopic morphology along with phylogenetic work will be required to understand fully the diversity of character variation and species limits within these sections.

METHODS AND MATERIALS

Macroscopic and microscopic descriptions

Macroscopic descriptions are based on field notes recorded by the authors. The color terms in parentheses are from Kornerup and Wanscher (1978), Kelley (1965), Ridgway (1912) and Anonymous (1992). The formula for PDAB can be found in Ovrebo and Smith (1979). Microscopic notes were made by Ovrebo based on sections made from dried collections and mounted in 3% KOH. Spore data are based mostly on 15 or 20 measurements per collection and Q indicates length/width ratio. The Costa Rican collections have been split between

Table 1. Collections used in the phylogenetic analysis.

GenBank No.	Name	Specimen Voucher	Isolate Number	Location
Tricholoma albobrunneum/ustale				
AF458435	*T. ustale*		trh884	USA: Oregon
AF458436	*T. ustale*		trh902	USA: Oregon
AB036894	*T. ustale*		strain 611	Japan
AF241520	*T. albobrunneum*		CBS 572.96	Netherlands
KC818312	Environmental sample		C_G12_A	Switzerland
LT000077	*T. albobrunneum*	C-F-96268	MC99060	France
JF908734	*T. albobrunneum*		17151	Finland
MK607503	*T. albobrunneum*		MyCoPortal. #4959473	USA: Indiana
Tricholoma aurantium				
MW881157	*T. aurantium*	TENN-F-060354	TFB12306	USA: Tennessee, GSMNP
MW881158	*T. aurantium*	MICH	MK09120409	USA: Michigan
MW881159	*T. aurantium*	CSU	Ovrebo 4625	USA: Tennessee, GSMNP
DQ367919	*T. aurantium*	OUC99349		Canada: British Columbia
LT000012	*T. aurantium*	C-F-59330	MC97227	Denmark
LT000100	*T. aurantium*	C-F-59329	MC96303	Italy: Toscana
MF034300	*T. aurantium*	MB<DEU-Marburg>:102121		Germany
Tricholoma brunneoluteum				
MW881161	*T. brunneoluteum*	TENN	Ovrebo 3792, holotype	USA: Oklahoma
HE820370	ECM			Not given
EU563478	ECM			Mexico: Guerrero
MW881160	*T. brunneoluteum*	MICH	MK7270706	USA: Illinois
KU058505	*T. brunneoluteum*	TENN-F-065997	TFB14052	USA: North Carolina
Tricholoma colossum				
LT000164	*T. colossum*	C-F-59154	MC97047	Sweden: Jamtland
MT462635	*T. colossum*	AMB 17237		Italy: Trentino
MF034285	*T. colossum*	MB<DEU-Marburg>:002363		Germany: Baden-Wuerttemberg
Tricholoma focale				
AB078341	*T. focale* as T. *robustum*	Not given	Not given	Japan
MW881162	*T. focale*	CSU	Ovrebo 4753	USA: New Mexico
MW881163	*T. focale*	CSU	Ovrebo 4761h1	USA: New Mexico
MW881164	*T. focale*	CSU	Ovrebo 4761h2	USA: New Mexico
MW881165	*T. focale*	CSU	Ovrebo 5050h1	USA: Colorado
MW881166	*T. focale*	CSU	Ovrebo 5050h2	USA: Colorado
LT000166	*T. focale*	C-F-27500	JV97239	Sweden
LT000021	*T. focale*	C-F-41444	JV99603	Denmark
LT000022	*T. focale*	C-F-96260	MC98600	Denmark
Tricholoma fulvum				
MW881167	*T. fulvum*	TFB12609	TENN-F-061280	Canada: Newfoundland
MW881168	*T. fulvum*	TFB12622	TENN-F-061293	Canada: Newfoundland
AF458438	*T. fulvum as T. muricatum*		TRH610	Not Given
FJ845446	*T. fulvum as T. pessundatum*	Not given	SMI303	Not given
KC840649	*T. fulvum*	"ECM, root of *Picea glauca*"	MBN0213_40	Canada: Newfoundland
LT000080	*T. fulvum*	C-F-96259	MC98078	France
LT000130	*T. fulvum*	C-F-96193	JHC03019	Slovakia
LT000171	*T. fulvum*	C-F-96195	JHC04251	Sweden
MF034235	*T. fulvum*	MB<DEU-Marburg>:002711		Austria
MF034237	*T. fulvum*	MB<DEU-Marburg>: 102827		"Germany: Bayern, Oberstdorf, Tiefebbach"
MK402137	*T. fulvum*	Culture	voucher Strain 236	Russia
Tricholoma stans				
AF377239	*T. stans* as *T. dryophilum*		KMS362	
LT000124	*T. stans*	C-F-96258	MC98018	Norway
LT000189	*T. stans*	"C-F-59042, CFT-0396"	MC95145	Sweden

Table 1. continued.

GenBank No.	Name	Specimen Voucher	Isolate Number	Location
EF077522	ECM			Austria
KJ705239	*T. stans*		#4510, "Quebec Mushroom Project"	Canada: Quebec
JF908733	*T. stans*		17133	Finland
EF493261	*T. stans*	UP604		Sweden
FJ197005	ECM		Ovrebone M42E4	Mexico: Guerrero
LT000188	*T. stans*	C-F-59032	MC95131	Sweden
MW881169	*T. stans*	USJ 66013, NY	Felsch 31	Costa Rica: San Jose Prov.
MW881170	*T. stans*	USJ 66082, NY	Halling 7676	Costa Rica: San Jose Prov.
Tricholoma orienticolossus				
MT124443	*T. orienticolossus*	HAKS99341		China
MT124444	*T. orienticolossus*	HAKS98645		China
Tricholoma quercetorum/T. orientifulvum				
LT000125	*T. quercetorum*	C-F-96263	MC99044	Portugal
MT114682	*T. orientifulvum*	HAKS107157		China
MT124445	*T. orientifulvum*	HAKS107156		China
Tricholoma luteopallidum				
MW881171	*T. luteopallidum*	USJ 109575, NY	Duguay 4	Costa Rica
MW881172	*T. luteopallidum*	USJ 65978, NY	Felsch 32	Costa Rica
MW881173	*T. luteopallidum*	USJ 65980, NY	Felsch 36	Costa Rica
MW881174	*T. luteopallidum*	USJ 66022, NY	Felsch 40	Costa Rica
MW881175	*T. luteopallidum*	USJ 53355, NY	Halling 7289	Costa Rica
MW881176	*T. luteopallidum*	USJ 53347, NY	Halling 7290	Costa Rica
MW881177	*T. luteopallidum*	USJ 53780, NY	Halling 7339	Costa Rica
MW881178	*T. luteopallidum*	USJ 109576, CSU	Ovrebo 4359	Costa Rica
MW881179	*T. luteopallidum*	USJ 109574, isotype NY	Ovrebo 4385 Holotype	Costa Rica
MW881180	*T. luteopallidum*	USJ 109577, NY	Ovrebo 4412	Costa Rica
Tricholoma cacumense				
MW881182	*T. cacumense*	USJ 109578, isotype, NY	Halling 8303 Holotype	Costa Rica
MW881183	*T. cacumense*	USJ 109579, NY	Halling 8322	Costa Rica
Tricholoma talamancense				
MW881184	*T. talamancense*	USJ 65976, NY	Felsch 35	Costa Rica
MW881185	*T. talamancense*	USJ 53447, isotype, NY	Halling 7150h1 Holotype	Costa Rica
MW881186	*T. talamancense*		Halling 7150h2 Holotype	Costa Rica
MW881187		USJ 66066, NY	Halling 7652	Costa Rica
EU563477	ECM		Ovrebone M60D4	Mexico
***Tricholoma* sp. 1**				
NW881188	*T.* sp. 1	CSU	Ovrebo25-08-1995A-h1	USA: Minnesota
NW881189	*T.* sp. 1	CSU	Ovrebo25-08-1995A-h2	USA: Minnesota
MH979327	*T.* sp 1 as *T. ustale*	NAMA 2017-381	North American Project; Mycoflora MyCoPortal.org #4952132	USA: Wisconsin
***Tricholoma* sp. 2 (Predominantly ECM environmental isolates)**				
KP403096	Environmental sample		Ovrebone 46C	Canada: British Columbia
DQ474755	ECM		Ovrebone SWUBC176	Canada: British Columbia
DQ474757	ECM		Ovrebone SWUBC169	Canada: British Columbia
KM403011	Environmental sample			Canada: British Columbia
KP406554	*T.* sp 2 as *Tricholoma stans*	UBC F28495		Canada: British Columbia
DQ474749	ECM			Canada: British Columbia
***Tricholoma* spp. (unplaced)**				
AJ272072	*T. populinum*		strain 99/150 culture	Hungary
KT875118	*T.* aff. *populinum*	HC-PNNT-278		Mexico: Mexico State
MF034244	*Tricholoma* sp.		MB<DEU-Marburg>:301976	China: Yunnan
Tricholoma* Section *Megatricholoma				
MW881190	*T. roseoacerbum*	USJ 72053, NY	Halling 8000	Costa Rica

herbaria at the Universidad de Costa Rica (USJ followed by an accession number) and the New York Botanical Garden (NY) or the University of Central Oklahoma (CSU). Barcodes were previously designated for several of the cited collections and are searchable at the Mycology Collections data Portal (https://mycoportal.org/portal/). These barcode numbers are preceded by "barcode."

Molecular methods

Collections used for phylogenetic analysis are given in Table 1. Taxa were included in the phylogeny based on preliminary trees showing relative placements of taxa within *Tricholoma*. A subset of the larger phylogeny was used in this manuscript. For highly speciose taxa, a geographically divergent subset of isolates was included. Outgroup taxa were selected from an adjacent clade within section *Genuina* but outside the highly speciose *T. fulvum* clade. Procedures for DNA extractions, PCR amplification and dideoxy sequencing of the ribosomal ITS region (Fungal barcode; Schoch et al. 2012) were performed as described in Ovrebo and Hughes (2018) using primers ITS1F or ITS5 and ITS4 (White et al. 1990; Gardes & Bruns 1993). ITS sequences were obtained as part of a broad survey of 350 *Tricholoma* isolates in 2007. Later attempts to amplify these DNAs for additional genes were unsuccessful. NrITS sequences were manually aligned with an internal *Tricholoma* ITS database in GCG (2000) to evaluate putative associations. Where indels prevented recovery of a complete ITS sequence, alignment of forward and reverse nrITS sequences were used to deduce the individual sequences at the insertion/deletion point. No cloning was performed. Alignments were exported to Geneious version R11 (Geneious 2017). PhyML was performed in Geneious with 1000 bootstrap replications using estimated transition/transversion rates, proportion of invariable sites and gamma distribution parameter. The number of substitution rate categories was 4 (Guindon & Gascuel 2008). Bayesian analysis was performed using Mr. Bayes in Geneious Rll. The substitution model was GTR, Rage Variation was "gamma." There were 4 heated chains with a total chain length of 1,100,000. Burn-in was 100,000. Branch lengths were unconstrained. Outgroups were chosen from the most closely related ITS sequences in GenBank (Table 1).

RESULTS

Descriptions of Costa Rican Taxa

Sect. *Genuina* (Fr.) Saccardo

Tricholoma luteopallidum Ovrebo, Halling, & Hughes, **sp. nov.** (**Figs. 2–3**). TYPE: COSTA RICA. SAN JOSE PROV. Dota Co.: San Gerardo, ± 5 km SW of Cerro de la Muerte, Albergue de la Montaña, Savegre, 9°33'N, 83°48'28"W, 4 Jun 2004, *Ovrebo 4385* (HOLOTYPE: USJ 109574, ISOTYPE: NY, Mycobank no. 840677; GenBank MW881178).

Diagnosis.—Characterized by the very light yellow, narrow, crowded lamellae, brownish orange to orange-brown pilei, bitter farinaceous taste, and by the small spores and presence of cheilocystidia, Also differs from other species in section *Genuina* by the ITS sequence.

Etymology.—*luteus* (L.) yellow, *pallidus* (L.) pale, referring to the very light-yellow lamellae.

Pileus 40–110 mm wide, convex when young, expanding to broadly convex to nearly plane, margin inrolled on buttons, down-curved or straight when mature, occasionally wavy or lobed, occasionally ribbed at edge, viscid, at center matted-fibrillose or with scattered small squamules, glabrous elsewhere, occasionally with areolate squamules near edge, brownish orange, orange-brown to brown overall (5C–D6–5, 6–7–EDF–8, 2.5 YR–5YR–4/6, 55 S. Br–56 deep Br) but generally with center darker brown and margin often lighter yellowish tan (5C7–6), orange buff to cinnamon buff, occasionally with darker brown streaks, occasionally with brown watery spots near the edge; context 5–12 mm thick, buff to pale yellow, not discoloring, odor farinaceous and taste bitter-farinaceous.

Lamellae narrow, 2–5 mm wide, sinuate, very light yellow (4A2, 3A3–4A3), developing small (± 1 mm) reddish brown to dark brown spots on edge and face in age and often extensively when over-mature, older ones often brownish marginate, crowded, 2–3/mm on mature basidiomes, entire, often forked; lamellulae present and in numerous tiers.

Stipe 40–100(–150) mm long, 8–20 mm thick, equal to subclavate, often bent, base rounded or abruptly tapered, terete or flattened, surface glabrous but often roughened with loosened surface fibrils which often are clumped into minute squamules, buff to yellowish buff, generally developing orange-brown to brown tones in

Fig. 2. Basidiomata and microscopic section. A. *Tricholoma luteopallidum* (*Halling 7339*). **B.** Microscopic section through pileus surface of *Tricholoma luteopallidum* (holotype). **C.** *Tricholoma talamancense* (*Halling 7652*). **D.** *Tricholoma stans* (*Halling 7676*). **E.** *Tricholoma roseoacerbum* (*Halling 8000*). **F.** *Tricholoma brunneoluteum* (*TFB 14052*). Scale bar=20 mm for basidiomata; 10 µm for 2.B.

streaks and sometimes becoming light brown overall with the apex remaining yellowish buff; context solid but soon hollow, buff to very pale yellow, often orange-tan to brown when older. Basal mycelium white.

Spores white in deposit, 5–6 × 3.5–4(4.5) µm (mean = 5.33 × 4.0 µm, Q = 1.25–1.5, mean Q = 1.33), elliptic to broadly elliptic in profile and face view, smooth, thin-walled, hyaline, inamyloid. Basidia 20–30 × 5.5–7 µm, clavate, 4-sterigmate, hyaline. Cheilocystidia present but abundance varying among collections, sometimes most evident where the lamellar edge is brown-stained, 25–35 × 5.5–8 µm, cylindric, ventricose-rostrate, fusiform-ventricose, often capitate, smooth, thin-walled, hyaline. Hyphae of lamellar trama 3–10 µm wide, parallel, hyaline, but often yellowish brown near lamellar edge. Hyphae of subhymenium 2 µm wide, hyaline. Pileipellis hyphae narrow, 1.5–4 µm wide, loosely interwoven in a gelatinous matrix, smooth or rarely faintly

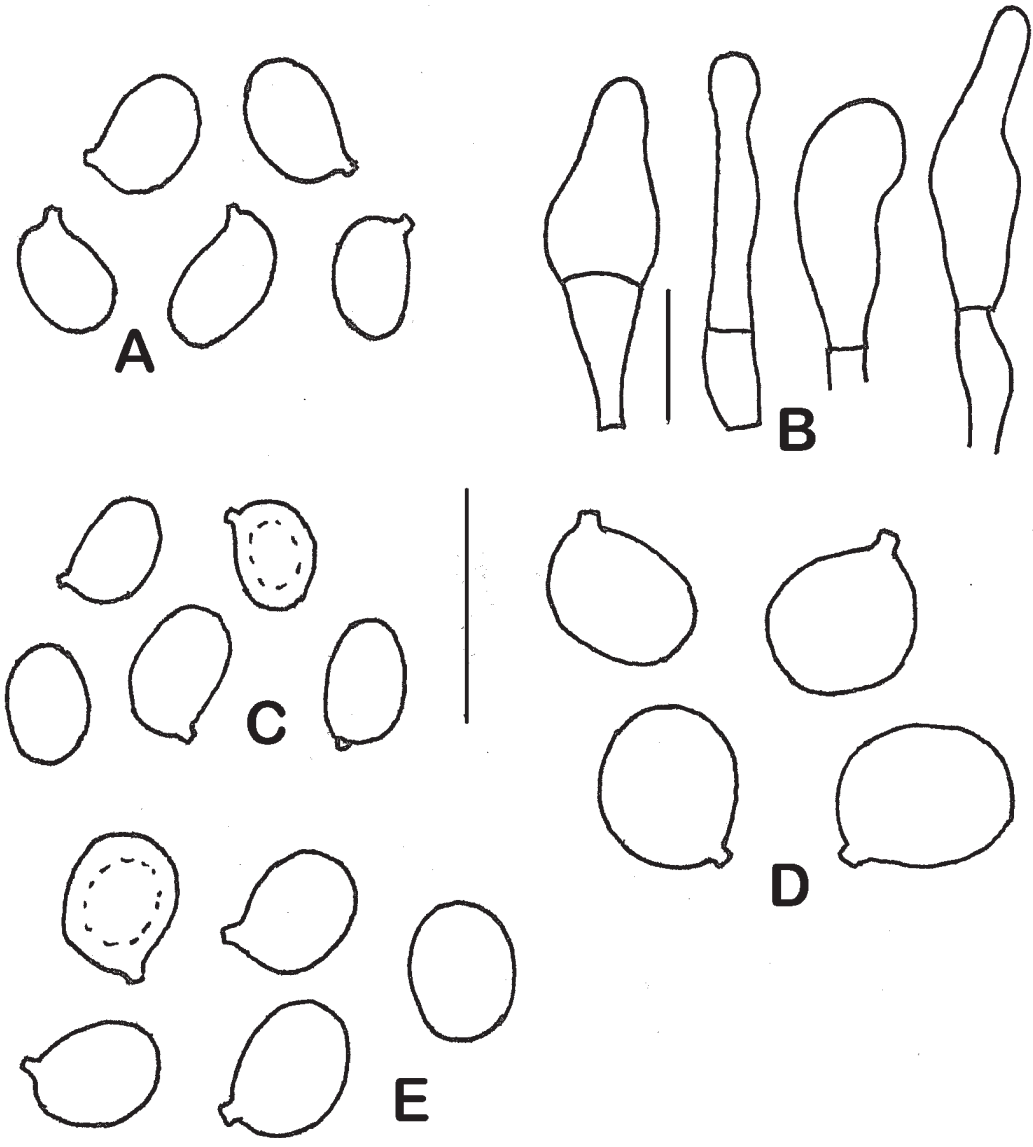

Fig. 3. Microscopic structures. **A.** Basidiospores of *Tricholoma luteopallidum* (holotype). **B.** cheilocystidia of *T. luteopallidum* (holotype). **C.** Basidiospores of *Tricholoma cacumense* (holotype). **D.** Basidiospores of *Tricholoma talamancense* (holotype). **E.** Basidiospores of *Tricholoma brunneoluteum* (holotype). Scale bar=10 µm.

incrusted, thin-walled, hyaline to pale yellow in outer region and pale yellowish brown to reddish brown at base where intergrading with pileus trama. Hyphae of pileus trama 4–13 µm wide, hyaline. Stipitipellis hyphae 3–5 µm wide, hyaline, cylindric, smooth thin-walled. Hyphae of stipe trama 5–15 µm wide, hyaline. Caulocystidia present at stipe apex, in the form of long cylindric projecting or entangled hyphae, up to 150 µm long and 3–4 µm wide, or in the form of cystidioid recurved end-cells, 20–35 × 3–5 µm, clavate, fusiform-ventricose, smooth, thin-walled, hyaline. Clamp connections absent.

Scattered, gregarious, on soil, presumed ectotroph of plants listed among collections cited below.

Additional collections studied: **COSTA RICA. San Jose Prov. Dota Co.:** San Gerardo, ± 5 km SW of Cerro de la Muerte, Albergue de la Montaña, Savegre, 9°33'N, 83°48'28"W, 2200–2600 m, 23 Jun 1994, *Halling 7339* (USJ 53780, NY with barcode 47741; GenBank MW881177); 17 Oct 1999, *Duguay 4* (USJ 109575, NY; GenBank MW881171); 1 Jun 2004, *Ovrebo 4359* (USJ 109576, CSU; GenBank MW881178); 8 Jun 1997, *A.-G. Felsch 27* (USJ 66017, NY); Los Robles trail, 7 Jun 2004, *Ovrebo 4412* (USJ 109577, NY; GenBank MW881180) previous four found under *Quercus copeyensis*; 1.5 km from Interamerican Hwy on road to San Gerardo, under *Q. costaricensis*, 9°35'47"N, 83°47'55"W, 2860 m, 9 Jun 1997, *A.-G. Felsch 32*, (USJ 65980, NY; GenBank MW881172); Jaboncillo, 3.2 km along road from Interamerican Hwy toward San Gerardo, 9°35'21"N, 83°47'58"W, 2740 m, 12 Jun 1996, *Halling 7677* (USJ 66081, NY); 7 Jun 1997, *A.-G. Felsch 23* (USJ 65978, NY); 10 Jun 1997, *A.-G. Felsch 36* (USJ 65983, NY; GenBank MW881173); last three under *Q. copeyensis, Q. seemannii,* or *Q. costaricensis*. **Cartago Prov.:** Estrella, 5 km E of km 31 of Interamerican Hwy, near town of Estrella, 9°46'4"N, 83°57'19"W, 1685 m, under *Q. oocarpa*, 12 Jun 1997, *A.-G. Felsch 40* (USJ 66022, NY; GenBank MW881174); 13 Jun 1994, *Halling 7289* (USJ 53355, NY with barcode 47746; GenBank MW881174) & *7290* (USJ 53347, NY with barcode 47747; GenBank MW881176).

Chemical color reaction.—PDAB light pistachio green after a few minutes (recorded for *A.-G. Felsch 23, 32, 40*).

Tricholoma luteopallidum is characterized by having pale yellow, very crowded, narrow lamellae, stipe that start out pale yellow, and by the presence of cheilocystidia. The bitter farinaceous taste is also distinctive. For several of the collections studied the cheilocystidia were rare and may be missed if several sections are not checked. Cheilocystidia are most likely very rare among species of sect. *Genuina* and none of the species included in Christensen and Heilmann-Clausen (2013) from Northern Europe mentions their presence. Shanks (1997) mentions two species with cheilocystidia from California: *T. aurantium* (Schaeff.) Ricken with occasional filamentous hyphae, 3–4 µm wide, on the lamellar edge, although Ovrebo (unpublished data) has not confirmed their presence in material from Tennessee, Michigan or Illinois; *T. dryophilum* (Murr.) Murr. with cheilocystidia 30–62 × 2.4–3.4 µm although a study of the holotype by Ovrebo (unpublished data) did not confirm their presence. Compared to *T. luteopallidum*, *Tricholoma aurantium* has lamellae with off-white color, and distinct bands of tiny orange-brown squamules on the stipe; *T. dryophilum* has white or pale cream lamellae and the spores are larger (from holotype, 5.7–6.7 × 4.3–5.3 µm, Ovrebo unpublished data). Also interesting for *T. luteopallidum* are the very narrow hyphae that are mainly unincrusted in the outer layer of the pileipellis (Fig. 2B) which may be a good species characteristic, as compared to most species in this section that have brown walls with either hyaline or brownish incrustations or walls that fracture in the outer part resulting in uneven, banded pattern. A similar situation of narrow, scarcely incrusted pileal hyphae was found in *Tricholoma terriferum* Peck described from New York (Ammirati & Ovrebo 1979), but that species has buff colors to the lamellae and stipe.

Tricholoma fulvum (DC.) Bigeard & H. Guill. has been the name generally applied to the species in sect. *Genuina* with yellow lamellae and stipe. This species, based on the description of Christensen and Heilmann-Clausen (2013), has darker brown pileal coloration and lamellae that are medium broad and medium spaced, cheilocystidia are absent, and the ITS sequences do not match with *luteopallidum*. Specific details concerning the walls of the pileipellis hyphae are not given by Christensen and Heilmann-Clausen (2013). The spores of the Costa Rican fungus are also narrower than those of *T. fulvum*, the latter averaging 4.3–5.1 µm wide (Christensen & Heilmann-Clausen 2013).

Tricholoma cacumense Ovrebo, Halling, & Hughes, **sp. nov.** (**Fig. 3**). Type: COSTA RICA. San Jose Prov.: Cerro de la Muerte, 9°33'16"N, 83°45'18"W, 3491 m, 7 Nov 2002, *Halling 8303* (holotype: USJ 109578; isotype: NY, Mycobank no. 840678: GenBank MW881182).

Diagnosis.—Characterized by the dark brown, viscid pileus, pale yellow lamellae and stipe, dark brown pileipellis hyphae and by the ITS sequence.

Etymology.—cacumen (L.), summit, peak, referring to the high elevation in the Talamanca Mountains where the fungus was collected.

Pileus 30–90 mm wide, convex, plano-convex to plane, surface dry to subviscid or viscid, appressed fibrillose, sometimes developing areolate squamules at the margin, dark brown (7F6, 7F8) at first, fading to light brown (6D6–5), margin paler brown (7E8); context 10 mm thick, white, odor and taste farinaceous.

Lamellae adnexed-emarginate, white to off-white or yellowish white (4A2, 4A3), developing reddish brown stains in situ with age, close to crowded, edges entire or uneven.

Stipe 30–100 mm long, 5–15 mm thick, equal, clavate or gradually tapered toward base, strict or curved, terete, flattened or cleft, sometimes contorted at the base, dry, fibrillose-striate to finely squamulose-striate, yellowish white with brown fibrils and squamules, developing light brown stains from handling, context becoming hollow. Base with whitish mycelium.

Spores 5–5.5(6) × 3.5–4 µm, (mean = 5.2 × 3.84 µm, Q = 1.25–1.43, mean Q = 1.36), elliptic in profile and face view, smooth, thin-walled, hyaline, inamyloid. Basidia 23–27 × 5–6 µm, 4-sterigmate, clavate, hyaline. Hymenial cystidia absent. Hyphae of lamellar trama 5–15 µm wide, parallel, hyaline. Hyphae of subhymenium 2–3 µm wide, hyaline. Pileipellis hyphae 2.5–7 µm wide with widest hyphae towards the base, interwoven in a gelatinous matrix, smooth and thin-walled or roughened due to incrustations or because of fracturing and separation of the outer part of the wall, hyphae reddish brown throughout the layer but darkest where intergrading with pileus trama. Hyphae of pileus trama 4–15 µm wide, hyaline. Stipitipellis hyphae 3–5 µm wide, appressed, smooth, thin-walled hyaline to yellow-ochre. Hyphae of stipe trama 5–13 µm wide, hyaline. Caulocystidia present at stipe apex, 18–40 × 3–10 µm, formed from recurved end-cells, cylindric, clavate, versiform, smooth, thin-walled, hyaline. Clamp connections absent.

Gregarious, on soil, beneath *Comarostaphylis arbutoides, Vaccinium consanguineum, Pernettya prostata.*

Additional collection studied: **COSTA RICA. San Jose Prov.:** Cerro de la Muerte, south slope of summit, 9°33'16"N, 83°45'18"W, 3532 m, 13 Nov 2002, *Halling 8322* (USJ 109579, NY; GenBank MW881183).

Tricholoma cacumense is similar to *T. luteopallidum* in lamellar coloration and crowdedness, but differs by having darker, duller brown pileal colors, more darkly pigmented hyphae in the outer layers of the pileipellis, by the lack of cheilocystidia and by the ITS analysis. The host specificity may be different as well because *T. luteopallidum* was collected under *Quercus* spp. whereas the plant associates indicated for *T. cacumense* are ericoid plants. *Comarostaphylis arbutoides* (Ericaceae) is a confirmed ectotroph associate for *Leccinum monticola* Halling & G.M. Mueller (Osmundson et al. 2007) and the authors of that paper also suggest that *Tricholoma*, along with several other ectotroph fungal genera, should be considered as likely associates of *C. arbutoides* as well.

Tricholoma talamancense Ovrebo, Halling, & Hughes, **sp. nov.** (**Figs. 2–3**). TYPE: COSTA RICA. San Jose Prov.: Villa Mills, C.A.T.I.E. Experimental Forest of Villa Mills, 9°33'0"N, 83°41'0"W, 2880 m, 11 Aug 1993, *Halling 7150* (HOLOTYPE: USJ 53447; ISOTYPE: NY with barcode 473560; Mycobank no. 840679; GenBank MW881185).

Diagnosis.—Characterized by the dark brown, viscid pileus, light yellow lamellae, buff to pinkish cinnamon stipe, yellowish mycelium at the stipe base, and by the ITS sequence.

Etymology.—named for the Talamanca mountains of Costa Rica where the species was collected.

Pileus 10–70 mm wide, conic-convex or flattened conic when young, convex to plano-convex or plane when mature, sometimes with a low broad umbo, margin incurved when young, straight and often upcurved and undulating when mature, surface viscid but soon dry, matted-fibrillose over disc, finely appressed-fibrillose toward the margin or glabrous, often with scattered squamules, dark reddish brown overall or with dark brown or fuscous at the disc and lightening to light brown or yellowish brown toward the margin, near the margin sometimes cinnamon buff; context 8–10 mm thick, white but with yellowish and pinkish tones, with reddish brown stains, odor and taste farinaceous.

Lamellae adnexed to emarginate, ivory, yellowish white to pale yellow (4A3, 4B3), developing reddish brown stains, close to crowded, edge even to uneven.

Stipe 30–60(140) mm long, 5–11 mm thick, equal to somewhat broader below, often bent, the lower half often flattened and bumpy, dry, appressed fibrillose-striate, light buff or pinkish cinnamon at first with reddish brown surface fibrils, becoming darker reddish brown with handling; context solid at first, becoming hollow, light yellow, discoloring cinnamon to brown especially at base. Base with yellow mycelium (3A4) and yellow mycelial strands attached.

Chemical Color Reaction.—PDAB no reaction (*A.-G. Felsch 35*).

Spores 6–7 × (4.5)5–5.5 µm (mean = 6.65 × 5.17 µm, Q = 1.2–1.3, mean Q = 1.29, broadly elliptic in profile

and face view, smooth, thin-walled, hyaline, inamyloid. Basidia 25–41 × 7–8 µm, 4-sterigmate, clavate, hyaline, but often yellowish brown in mass when seen under low power. Lamellar edge in one collection with filamentous, often flexuous hyphae like elements projecting, 20–55 × 2–4 µm, occasionally branched, tapering gradually to a rounded apex, widest at base, often several-celled and with a short basal cell that can reach 7 µm in dia, smooth, thin-walled, hyaline or sometimes translucent-brown. Hyphae of lamellar trama 3–17 µm wide, parallel, in mass hyaline or yellowish to orange-brown. Hyphae of subhymenium 2.5–3 µm wide, hyaline. Pileipellis hyphae 3–8 µm wide, radially interwoven to slightly interwoven in a gelatinous matrix, some hyphae smooth but most often with brown incrustations, a slightly pigmented banding pattern seen due to fracturing and separation of outer part of the wall, hyphae reddish brown, both as a layer and individual hyphae. Hyphae of pileus context 4–15 µm wide, hyaline. Stipitipellis hyphae 3–5 µm wide, appressed, light reddish brown to reddish brown as a layer as individual hyphae, pale yellowish brown at stipe apex, smooth, thin- to slightly thick-walled. Hyphae of stipe trama 4–20 µm wide, slightly inflated, hyaline. Caulocystidia occasional at stipe apex, 20–40 × 2.5–4 µm, filamentous-cylindric or clavate, thin-walled, hyaline. Clamp connections absent.

Gregarious, on soil, under *Quercus costaricensis*.

Additional collections studied: **COSTA RICA. San Jose Prov.:** Villa Mills, C.A.T.I.E. Experimental Forest of Villa Mills, 9°33'3"N, 83°40'55"W, 2880 m, 9 Jun 1996, *Halling 7652* (USJ 66066, NY; GenBank MW881187), 10 Jun 1997, *A.-G. Felsch 35* (USJ 65976, NY; GenBank MW881184).

Tricholoma talamancense is a third Costa Rican species with pale yellow lamellae. The stipe is buff to pinkish cinnamon and discolors brown although the stipe context is light yellow. Also potentially diagnostic is the yellowish mycelium and strands at the stipe base which were reported for the collections cited. For one collection (*Halling 7150*) the basal hyphae started out white and became yellow, and also had elements projecting from the lamellar edge that could be considered as cheilocystidia but they more resemble very narrow hyphal end-cells, as compared to the more typical cheilocystidia that tend to be inflated cells. *Tricholoma talamancense* has larger spores than either *T. luteopallidum* or *T. cacumense*.

***Tricholoma stans* (Fr.) Sacc. (Fig. 2)**

Pileus 20–80(130) mm wide, convex when young, expanding to plano-convex to plane, margin incurved when young, straight and sometimes partly uplifted when mature, surface tacky or subviscid to viscid, soon dry, matted fibrillose to matted fibrillose-scaly at first, when mature to matted-glabrous over central area and with scattered squamules toward and on the margin with age, reddish brown (7–8E8) mostly overall with a white margin at first, medium brown (6C–D7–6) with age and margin lighter brown; context up to 10–15 mm thick, white, unchanging or with orange-brown discoloration below the surface, odor and taste farinaceous.

Lamellae adnate, adnexed or emarginate, medium width (not narrow) white to off-white, discoloring fulvous to brown when mature, close, edges even.

Stipe 20–50 mm long, 5–20 mm thick, equal, surface dry, striate-fibrillose to coarsely fibrillose with abundant recurved reddish brown squamules on white ground color that abruptly end near apex and possible remains of a veil, sometimes brown in areas, apex white and subfibrillose: context white to light buff, becoming hollow.

Spores 6–7 × 4.5–5 µm (mean = 6.5 × 4.9 µm, Q = 1.3–1.4, mean Q = 1.33), elliptic in profile and face view, smooth, thin-walled, hyaline, inamyloid. Basidia 27–36 × 7–8 µm, clavate, 4-sterigmate, hyaline. Hymenial cystidia absent. Hyphae of lamellar trama 4–12 µm wide, parallel, hyaline. Hyphae of subhymenium 2.5–3 µm wide, hyaline. Pileipellis hyphae 3–8 µm wide, radially interwoven in a gelatinous matrix, often clumped into recurved squamules, brownish red as a layer, individual hyphae hyaline to translucent brownish red to yellowish brown, smooth, thin-walled or roughened and thickened with hyaline incrustations. Hyphae of pileus trama 4–15 µm wide, hyaline. Stipitipellis hyphae between squamules 4–8 µm wide, appressed, hyaline to brownish yellow, smooth, thin-walled or slightly incrusted, with scattered caulocystidia formed from recurved end cells or intercalary, 20–120 × 3–5 µm, filamentous, hyaline; squamules most obvious and

well-developed on young basidiomes, composed of bundles of recurved hyphae, cells 5–12 µm wide, yellowish brown, slightly thick-walled, sometimes emanating from bundle are thin-walled, hyaline hyphae 30–120 × 3–5 µm. Hyphae of stipe trama 5–18 µm wide, parallel, hyaline. Clamp connections absent.

Gregarious, on soil, under *Quercus costaricensis* and *Comarostaphylis arbutoides*.

Collections studied: **COSTA RICA. San Jose Prov.:** San Gerardo, ± 500 m along road from Interamerican Highway toward San Gerardo, 9°36'13"N, 83°47'26"W, 3000 m, 12 Jun 1996, *Halling 7676* (USJ 66082, NY; GenBank MW881170); 1.5 km from Interamerican Highway toward San Gerardo, 9°35'47"N, 83°47'55"W, 2860 m, 9 Jun 1997, *A.-G. Felsch 31* (USJ 66013, NY: GenBank MW881169).

Tricholoma stans is a European species and the ITS sequences of the Costa Rican material match those as published by Heilmann-Clausen et al. (2017). Christensen and Heilmann-Clausen (2013) indicate that the European *T. stans* is characterized by robust basidiomata, a brownish cap with a pale ribbed margin, and association with *Pinus*. For the Costa Rican material, the ribbed margin was not evident and the collections were associated with hardwoods. *Tricholoma stans* belongs to a complex of species with brown, viscid pilei and pale white to off-white (non-yellow) lamellae and stipe. A name commonly associated with fungi with these colors is *T. pessundatum* (Fr.: Fr.) Quél., a name frequently assigned to fungi with these features in North America, but for which there are likely undescribed species in this region. See Christensen and Heilmann-Clausen (2013) for a discussion of species in this group for European taxa, and Bessette et al. (2013) for taxonomic issues of North American taxa in this group. The notes with collection *Halling 7676* suggest the possibility of a veil but additional young specimens need to be collected to confirm its presence.

Section *Megatricholoma* (G. Kost) M. Christensen & Noordeloos

Tricholoma roseoacerbum A. Riva (Fig. 2)

Pileus 30–50 mm wide, convex to plano-convex, dry, matted tomentose to matted subtomentose, subviscid, mottled brownish orange to clay color (5C–D6–5) over most areas, staining dark brownish orange, with bright pastel yellow (2A4–3A4) at the inrolled and thick cottony margin; context white, unchanging but brown around larval tunnels, 8–10 mm thick, odor and taste mild.

Lamellae adnexed, white to yellowish white to pale yellow, developing brown stains, with uneven margins.

Stipe 30–50 mm long, 10–20 mm thick, equal, dry, strict or curved, white with pastel yellow squamulose scales, to fibrillose, staining orange to brownish orange; context solid, white, unchanging; context solid, white, unchanging.

Chemical color reaction.—PDAB: no reaction.

Spores 5–5.5 × 3.5–4 µm (mean = 5.1 × 3.83 µm, mean Q = 1.34), broadly elliptic in profile and face view, smooth, thin-walled, hyaline, inamyloid. Basidia 24–27 × 6–6.5 µm, 4-sterigmate, clavate, hyaline. Hymenial cystidia absent. Hyphae of lamellar trama parallel, hyphae 3–8 µm wide, hyaline to yellowish in mass. Hyphae of subhymenium 2–2.5 µm wide, hyaline. Pileipellis hyphae 3–5 µm wide, embedded in a weak gelatinous matrix, hyphae smooth, thin-walled, hyaline to light yellowish brown in outer region and sometimes translucent, toward base becoming browner due to density of hyphae. Hyphae of pileus trama up to 15 µm wide, hyaline. Stipitipellis hyphae 4–7 µm wide, with scattered loosely interwoven clumps, smooth, thin-walled, hyaline to pale yellowish brown. Hyphae of stipe trama to 10 µm wide, hyaline. Clamp connections absent.

Gregarious, on soil, under *Quercus seemannii* and *Q. copeyensis*.

Collection studied: **COSTA RICA: San Jose Prov.:** Dota, San Gerardo, about 5 km SW of Cerro de la Muerte, Albergue de la Montaña, Savegre, 9°32'02"N, 83°48'27"W, 2220 m, 10 Jul 2000, *Halling 8000* (USJ 72053, NY; GenBank MW881190).

Tricholoma roseoacerbum Riva described from Switzerland is regarded as being similar to *T. acerbum* (Bull.: Fr.) Vent. The latter has a lighter cream to pinkish buff pileus surface coloration (Christensen & Heilmann-Clausen 2013), compared to the more darkly pigmented *T. roseoacerbum*. The inrolled pileus margin when young is characteristic of both species. The ITS sequence of the Halling collection cited here aligns with European sequences (not shown) so we are confident in applying this name to the Costa Rican material.

New species in section *Genuina* from United States

Tricholoma brunneoluteum Ovrebo, Kuo, & Hughes, **sp. nov.** (**Fig. 2–3**). TYPE: OKLAHOMA. Atoka Co.: Boehler Seeps, Nature Conservancy property, SE of Lane, 34°10.317'N, 95°52.317"W, 9 Oct 1999, *Ovrebo 3792* (HOLOTYPE: TENN, Mycobank no. 840680; GenBank MW881161).

Diagnosis.—Characterized by the viscid, brown pileus that is frequently brownish yellow on the margin, yellow lamellae and by the ITS sequence.

Etymology.—*brunne* (L.) brown, referring to the brown pileus, *luteus* (L.) yellow, referring to the yellow lamellar color.

Pileus 40–80 mm wide, convex when young, broadly convex at maturity, surface tacky to viscid, glabrous, matted-fibrillose at center, with scattered innate radiating fibrils elsewhere, occasionally pitted on margin, light brown (Ochraceous Tawny), medium reddish brown to brown and the margin often with yellowish ground color showing through giving a lighter brownish yellow tone (Ochraceous Buff); context 8–11 mm thick, very light yellowish buff, odor and taste farinaceous.

Lamellae 3–9 mm wide, adnate to sinuate, yellow (Amber-Yellow), discoloring brown on edge or in larger areas on face and extensively brown when older, close to crowded, entire, lamellulae in numerous tiers.

Stipe 50–70 mm long, 7–20 mm wide, equal, terete, glabrous, silky appearing and often with loosened surface fibrils projecting, light yellowish buff, discoloring brown in areas or eventually overall (Ochraceous-Tawny); context solid or hollow, very light yellowish buff; basal mycelium white (recorded for one collection).

Chemical color reaction.—3% KOH on cap reddish brown (recorded for one collection).

Spores white in deposit. Spores 5.5–6.5 × 4.5–5.5 µm (mean = 5.95 × 4.91 µm, Q = 1.1–1.3, mean Q = 1.21), broadly elliptic to nearly subglobose in profile and face view, smooth, thin-walled, hyaline, inamyloid. Basidia 25–30 × 6–8 µm, 4-sterigmate, hyaline individually but hymenium as a layer orangish-cinnamon or brown. Hymenial cystidia absent. Hyphae of lamellar trama parallel, 3–13 µm wide, hyaline to pale yellow. Hyphae of subhymenium 2–3 µm wide, hyaline. Pileipellis hyphae 3–6 µm wide, interwoven in a weakly to strongly developed gelatinous matrix, walls smooth or incrusted with hyaline to brownish incrustations, hyphae light yellowish brown, orange-brown to brown, darkest where seen in mass, often translucent and opaque where densely pigmented. Hyphae of pileus trama up to 15 µm wide, hyaline. Stipitipellis hyphae 4–5 µm wide, smooth, thin-walled or in mass light brown. Caulocystidia scattered among surface hyphae at apex, clavate, hyaline. Hyphae of stipe trama 5–18 µm wide, hyaline to pale yellow. Clamp connections absent.

Scattered, on soil, under mixed hardwoods.

Additional collections studied: **U.S.A. ILLINOIS. Coles Co.:** Fox Ridge State Park, 27 Jul 2007, *Kuo 07270706* (MICH; GenBank MW881160). **NORTH CAROLINA. Macon Co.:** Highlands, Horse Cove, Walkingstick Rd, Double Bridges, 35.01527778, -83.16611111, 31 Jul 2012, *TFB* (Tennessee Field Book) *14052* (TENN, barcode TENN-F-065997; GenBank KU058505).

Tricholoma brunneoluteum also has the brown pileus coloration and the yellow lamellae and stipe.

The lamellae have brighter yellow pigmentation compared to the species described from Costa Rica. Fungi with these colorations have frequently been referred to as *Tricholoma fulvum* (DC.) Bigeard & H. Guill. or *T. flavobrunneum* (Fr.) Kumm. in North American field guides (*T. flavobrunneum* is considered a synonym of *T. fulvum,* Christensen & Heilmann-Clausen 2013). The ITS sequence indicates that the fungus described here is not the same as the European *fulvum* (Fig. 1). *Tricholoma transmutans* Peck is another species name to consider in this complex. As pointed out by Ammirati and Ovrebo (1979), the lamellar color is difficult to interpret. Peck in the protologue gave the lamellar color as being whitish or pale yellow with no indication that there is a color change from white to yellow as they mature. Peck also described the stipe of *T. transmutan*s as white which would distinguish it from *T. brunneoluteum* which has a pale yellow stipe. Moving forward, molecular comparisons and determinations should be easier to make because it is now possible to anchor the name *fulvum* based on both the description provided by Christensen and Heilmann-Clausen (2013) and the molecular analysis of Heilmann-Clausen et al. (2017). Tricholomas with brown pilei and yellow lamellae and stipes, along with species that have whitish lamellae and stipes, are commonly collected throughout North

America and there are very likely more species in this complex and are in desperate need of study. Many of the species may be cryptic so molecular analyses will be an important part of their documentation.

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