Cortinarius subgenus Callistei in North America and Europe–type studies, diversity, and distribution of species

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Short title: *Cortinarius* subgenus *Callistei*

Cortinarius subgenus *Callistei* in North America and Europe—type studies, diversity, and distribution of species

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Abstract: Five species of *Cortinarius* subgenus *Callistei,* are recognized in Europe and North America. *Cortinarius callisteus*, *C*. *infucatus*, and *C*. *neocallisteus* sp. nov. have a broad distribution, extending from western North America to Europe. *Cortinarius tofaceus* is known from eastern North America and Europe, while *C*. *callistei* sp. is known only from one locality in Sweden. All five species are primarily associated with coniferous trees. Previously the species were included either in subgenus *Leprocybe* or subgenus *Cortinarius*, but recently they have been separated into subgenus *Callistei* based on molecular data. Type specimens of the names associated with this subgenus were studied and a neotype proposed for *C. tofaceus* and an epitype for *C. infucatus*. Barcodes for the species are deposited in RefSeq and UNITE.

Key words: Agaricales, Cortinariaceae, ectomycorrhiza, ITS, molecular systematics, taxonomy

INTRODUCTION

Cortinarius is the largest genus of Agaricales with a cosmopolitan distribution and over 2000 described species. All *Cortinarius* species are important ectomycorrhizal partners worldwide and associated with a range of different trees and shrubs belonging to the families Caesalpiniaceae, Cistaceae, Dipterocarpaceae, Fabaceae, Fagaceae, Myrtaceae, Rhamnaceae, Rosaceae, Pinaceae, and Salicaceae, as well as some herbaceous plants in the Cyperaceae and Polygonaceae. In recent years several molecular studies on *Cortinarius* have been published which cover studies of type material as well as comparisons of species from different areas and have provided new insight into the taxonomy, evolution, ecology, and distribution of the species (Garnica et al. 2009, 2011; Harrower et al. 2011, 2015; Niskanen et al. 2011a, 2012a, 2013a, 2013b; Ammirati et al. 2013; Dima et al. 2014; Liimatainen et al. 2014, 2015; Cripps et al. 2015).

The names for many species of macrofungi have been difficult or even impossible to interpret when only morphological characteristics are considered. This is especially challenging in large genera like *Cortinarius* that show considerable convergence in morphology, coloration, and microscopic features. For example, studies by Liimatainen et al. (2014, 2015) and Cripps et al. (2015) have shown that the same species was described from North America and Europe by different authors.

Molecular studies of *Cortinarius* from Europe and North America have revealed several patterns of species distribution. Some species have a broad distribution extending from western North America (i.e. west of the Rocky Mountains) to Europe. They mainly represent species associated with boreal/montane trees (conifers, *Betula*, *Populus*, *Salix*), but may extend into more southern areas: *C*. *hedyaromaticus* C. Cripps & O.K. Mill. and *C*. *napus* Fr. (Garnica et al. 2011, Cripps et al. 2015). Endemic species also occur both in western North America, eastern North America (east of the Rocky Mountains) and Europe: *C*. *californicus* A.H. Sm. and *C*. *xanthodryophilus* Bojantchev & R.M. Davis in western North America (Bojantchev and Davis 2011, Ammirati et al. 2013), *C*. *hesleri* Ammirati, Niskanen, Liimat. & Matheny and *C*. *harrisonii* Ammirati, Niskanen & Liimat. in eastern North America (Ammirati et al. 2013, Niskanen et al. 2013a), and *C*. *albogaudis* Kytöv., Niskanen & Liimat., and *C*. *puniceus* P.D. Orton in Europe (Niskanen et al. 2009, Niskanen et al. 2013a). The species composition of eastern North America and Europe is somewhat similar, but there appears to be less similarity between Europe and western North America (Niskanen et al. 2011b).

This study focuses on *Cortinarius* subgenus *Callistei* Liimat., Niskanen & Ammirati (Niskanen et al. 2015). Species of this subgenus feature yellowish to orange-brown basidiomata, a yellow to orange-yellow universal veil, and subglobose to somewhat elongated, <9 µm long basidiospores. The smell of the pileus is usually distinctive, like raw potatoes, hot iron, or apples. The species have previously been classified in subgenus *Leprocybe* (Moser 1983) or subgenus *Cortinarius*, for example, in section *Heterocliti* (Brandrud et al. 2012), but molecular studies have shown that they are not related to the type species of these subgenera and instead form a well-delimited clade inside *Cortinarius* (Peintner et al. 2004, Garnica et al. 2005, Stensrud et al. 2014). Species in subgenus *Leprocybe* are fluorescent and have greenish, olivaceous, or brownish tints in their basidiomata, whereas the species in subgenus *Callistei* are not fluorescent and lack greenish, olivaceous, and brownish tints. Species in section *Heterocliti*, *Cortinarius limonius* (Fr.) Fr., and *C. kroegeri* Niskanen, Liimat., Harrower, Berbee, Garnica & Ammirati, are distinguished from the species of subgenus *Callistei* by having a cylindrical, often downward tapering stipe, an orange to orange-brown pileus when young and somewhat larger basidiospores (7.5–9.5 × 6–7 μm) than the species of subgenus *Callistei*. The species of subgenus *Leprocybe* and section *Heterocliti* lack the hot iron or apple-like odor of subgenus *Callistei* although some species have a more or less strong radish-like odor.

The study by Garnica et al. (2005) suggests that species in subgenus *Callistei* may have a wide distribution, because *C. austrolimoneus* var. *ochrovelatus* M.M. Moser from Chile grouped together with the Northern Hemisphere materials in their phylogenetic analysis based on nuc rDNA ITS1-5.8S-ITS2 (ITS barcode) and D1-D2 domains of nuc 28S rDNA regions. The names traditionally applied in the subgenus in Northern Hemisphere include *C. callisteus* (Fr.) Fr., *C. infucatus* Fr. (= *C. citrinofulvescens* M.M. Moser), *C. tofaceus* Fr., and *C. annulatus* Peck, but the lack of type studies has led to confusing inconsistencies in application of names to DNA sequences. The purpose of this study was to examine the diversity and distribution of the species of subgenus *Callistei* in North America and Europe and to stabilize the nomenclature by studying type specimens as well as designating type specimens for Friesian names.

MATERIALS AND METHODS

DNA extraction, PCR amplification, and sequencing.—DNA was extracted from dried material (pieces of lamellae) with the NucleoSpin Plant kit (Macherey-Nagel, Düren, Germany). Primers ITS 1F and ITS 4 (White et al. 1990, Gardes and Bruns 1993) were used to amplify ITS regions, and the same primer pairs were used in direct sequencing. For problematic material the primer combinations ITS 1F/ITS 2 and ITS 3/ITS 4 (White et al. 1990, Gardes and Bruns 1993) were also used. Polymerase chain reaction amplification and sequencing followed Liimatainen et al. (2014). The type specimen of *C. croceicolor* was re-sequenced in another laboratory with the following protocol to ensure the correct result: DNA was extracted with CTAB protocol (Gardes and Bruns 1993) using the GeneCleanVR II Kit (Q-BioGene, Carlsbad, California) (Bidartondo et al. 2004). PCR was done using PicoMaxx (Agilent, Santa Clara, California) with the primers ITS1F/ITS2 and ITS3/ITS4. Sequencing followed Liimatainen et al. (2014).

Data analyses.—Sequences were assembled and edited with Sequencher 4.1 (Gene Codes, Ann Arbor, Michigan). Using a BLAST query of the public databases (GenBank: http://www.ncbi.nlm.nih.gov/ and UNITE: http://unite.ut.ee/), the presence of identical or similar sequences was checked in public databases. For *C. callisteus*, *C. infucatus*, and *C. tofaceus*, one sequence from each country was downloaded. *Hebeloma mesophaeum* (Pers.) Quél. (GenBank accession No. EF451057, epitype) and *Hebeloma* sp. (GenBank accession No. JX630953) were used as an outgroup. The ITS alignment of 37 sequences was produced with the program MUSCLE (Edgar 2004) under default settings. The alignment is composed of 710 nucleotides (including gaps) and is available at TreeBASE under S19172 (http://www.treebase.org/treebase-web/home.html). Sequences were subjected to maximum likelihood (ML) analysis as implemented in RAxML 8 (Stamatakis 2014) with 1000 bootstrap replicates under the GTRGAMMA model.

Genetic differences within and between species were calculated by dividing the number of differences (indels and/or substitutions) found in the ITS1+5.8S+ITS2 regions with the length of the region.

Morphological study.—Morphological descriptions of *C. callisteus*, *C. infucatus*, and *C. tofaceus* are based on material collected by the authors, including specimens in all stages of development. For *C. neocallisteus*, notes and photographs of fresh basidiomata were lacking and the description is based on herbarium specimen. For all species, notes on the cortina were lacking, so this characteristic is not included in the descriptions. Microscopic characteristics were observed from dried material mounted in Melzer's reagent (MLZ). Basidiospores were measured from the veil or apex of the stipe. The pileipellis structure was studied from both freehand radial and scalp sections from the pileus disc. The measurements of the elements of pileipellis were made from scalps.

RESULTS

Molecular data.—The phylogenetic tree resulting from our RaXML analysis is shown (FIG. 1). Five species in subgenus *Callistei* were recognized (BS ≥ 70): *C. callisteus*, *C. infucatus*, *C. neocallisteus*, *C. tofaceus*, and *C. callistei* sp. *Cortinarius tofaceus*, *C. callistei* sp., and *C. neocallisteus* differ from one another in the ITS region by more than 1.5%; *Cortinarius callisteus* and *C. infucatus* differ only by about 0.5%. *Cortinarius callistei* sp. is known from only one locality in Sweden. It was collected as *C. callisteus*, but only very sparse notes on the collections exist, and no photo of the specimen was made in fresh condition. In the absence of more data and collections, the species is not discussed in further detail in TAXONOMY.

The type specimen of *C. hirtipes* described from France was placed in *C. callisteus* and the type specimen of *C. croceicolor* from New York, USA in *C. tofaceus*. The sequencing of type material of *C. annulatus* was not successful.

TAXONOMY

Cortinarius callisteus (Fr.) Fr. Epicr. Syst. Mycol. (Upsaliae):281. 1838. FIGS. 2a, e

Basionym: *Agaricus callisteus* Fr., Observ. Mycol. (Havniae) 2:51. 1818.

Type: SWEDEN. UPPLAND: Älvkarleby sn, Billuddens NR, in spruce forest on calcareous ground (*Picea*, *Pinus*), 10 Sep 1993, *H. Lindström et al. CFP1219* (S, **neotype**; K, **isoneotype**). GenBank accession No. KU236691.

=*Cortinarius hirtipes* Moënne-Locc. & Reumaux, in Bidaud, Moënne-Loccoz, Carteret, Reumaux & Eyssartier, Atlas des Cortinaires (Meyzieu) 15:1031. 2005.

Type: Brought to the mycological exhibiton of d'Annecy, under *Fagus*, place and collector unknown, 29 Sep 1986, *PML 362* (PC, **holotype**). GenBank accession No. KU236692.

Description: Pileus 30–90 mm diam, at first hemispherical, later low convex, margin often remaining incurved, surface smooth to very finely scaly, dull yellow to orange-yellow, soon brownish-yellow to orange-brown, somewhat hygrophanous, more yellow when dry. Lamellae medium spaced, at first pale yellow, later brownish-yellow. Stipe 40–110 mm long, 8–15 mm diam at apex, up to 25 mm diam at base, clavate, light yellow at the apex, downward yellow-brown, becoming more brownish when pressed with the thumb and with age. Universal veil yellow, soon yellow-brown, forming zones on the stipe, sometimes sparse. Context in pileus white to pale yellow to yellow, in stipe apex white at least when young, more orange-brown toward the base, becoming darker with age. Odor of pileus surface typically strong, like a recently extinguished candle (ozone), lamellae sometimes raphanoid. Exsiccatae red-brown to fairly dark yellow-brown.

Basidiospores 6.7–7.8 × 5.5–6.3 µm, Q = 1.17–1.25(–1.30), subglobose to somewhat ovoid, slightly to somewhat dextrinoid, moderately verruculose, verruculae distinct, wart-like, somewhat pointed. Basidia 4-spored, clavate, hyaline or with yellow contents. Lamellae trama hyphae smooth to finely encrusted. Pileipellis: surface layer hyphae subparallel to interwoven or entangled, cylindrical, 5–12 µm diam, golden yellow, zebra-striped encrusted. subtending layer hyphae subparallel to ±interwoven, cylindrical to enlarged, 12–20 µm diam, yellowish or hyaline, some finely encrusted. Hypoderm hyaline, hyphae up to 25 µm diam. *Ecology and distribution:* Widely distributed and found from western North America to Europe. In Europe and eastern North America in mesic coniferous forests, usually with *Picea*, sometimes with *Pinus*, on rich to calcareous soil. One collection was made under *Fagus* in France. In western North America occurring in developing to old-growth forests (*Pseudotsuga*, *Abies*). Basidiomata are produced Aug–Oct. *Cortinarius callisteus* is considered rare in hemiboreal and boreal zones as well as in montane areas and becomes rarer toward the north and in the temperate zone.

Notes: Cortinarius callisteus is a medium-sized to rather large, orange-yellow to orange-brown species with a clavate stipe and subglobose basidiospores. A distinct odor similar to a recently extinguished candle is typical and best detected from the top of the pileus. The species grows in coniferous forests, often on rich ground. A photograph published in Brandrud et al. (2012) represents easily identifiable orange-brown basidiomata, whereas this photo (FIG. 2e) represents paler basidiomata more similar to those of *C. infucatus* Fr. The sister species *C. infucatus* grows in similar habitats but is brighter yellow, the basidiospores are slightly larger, sharply verrucose, and the smell is less distinct, often faint and more like apples. Typical basidiomata of these two species can sometimes be identified in the field. However, variation in the morphological characteristics of both species exists and some specimens are not possible to identify based on morphology alone, especially herbarium specimens.

The neotype for *C. callisteus* was designated in Brandrud et al. (2012) and stabilizes the use of the name for the species traditionally called as *C. callisteus* in Nordic countries. *Cortinarius hirtipes*, described from France (Bidaud et al. 2005), was revealed to be a later synonym of *C. callisteus*. The morphology and molecular data support this conclusion.

Cortinarius callisteus and *C. infucatus* formed two separate clades in our phylogenetic analysis. These two groups can also be seen in the UNITE as species hypothesis SH261050.07FU *C. callisteus* and species hypothesis SH261049.07FU *C. infucatus*.

Specimens examined: EUROPE: FINLAND. VARSINAIS-SUOMI: Lohja, Hermala, takarinne, 2 Aug 2000, *I. Kytövuori 00-031* (H), GenBank accession No. KU236693. ETELÄ-SAVO: Kerimäki, Ruokojärvi, Louhi, northwest of the lime factory, dryish, partly thinned heath forest with *Betula*, *Pinus*, *Picea*, *Populus*, and *Alnus*, 8 Sep 1998, *I. Kytövuori 98-1706* (H), GenBank accession No. KU236694. Mäntyharju, Karankamäki, E-sloping grass-herb forest with *Betula, Alnus incana*, *Populus*, *Pinus*, *Picea*, *Salix*, 29 Sep 1994, *I. Kytövuori 94-1105* (H), GenBank accession No. KU236695. FRANCE. JURA: Forêt d'Arbois, *Abies* forest, 3 Oct 1998, *H. Lindström CFP1419* (S, K), GenBank accession No. KU236697. YUGOSLAVIA. SUMBER: deciduous forest, 7 Oct 1979, *M. Moser 79-656a* (IB, as *C. tophaceoides* ined.), GenBank accession No. KU236696.

NORTH AMERICA: CANADA. NEWFOUNDLAND: west coast, Gros Morne National Park, south side of the Bonne Bay East Arm, Lomond River hiking trail, 49°27′N 57°45′,46′E, mesic to damp coniferous forest (*Abies balsamea*, *Picea*) with some *Betula*, on calcareous ground, 19 Sep 2007, *K. Liimatainen & T. Niskanen 07-210*, *H7000872* (H, Gros

Morne Herbarium), GenBank accession No. KU236698. USA. WASHINGTON: Olympic Peninsula, Olympic National Park, road to Deer Park Campground, approximately 200 m south from the gate to the park, coniferous forest (*Tsuga heterophylla*, *Pseudotsuga mentziesi*, *Thuja plicata*), 47°59′N 123°19′E, 4 Oct 2007, *K. Liimatainen & T. Niskanen 07-395*, *H7001031* (H), GenBank accession No. KU236699.

Additional specimens: EUROPE: ESTONIA. SAARE: Leisi, pine alvar forest near Triigi Harbor, 21 Sep 2008, *A. Kollom TAAM128753* (TAAM), UNITE No. UDB016108 (as *C. callisteus*). FINLAND. PERA-POHJANMAA: Tervola, Raemäki Nature Reserve, 5 Sep 2013, *A. Kollom TU105433* (TU[M]), UNITE No. UDB019918. NORWAY. TELEMARK: Drangedal, Henseid, 31 Aug 1997, *K. Høiland T45* (O), UNITE No. UDB000162/GenBank accession No. KC842435 (as *C. callisteus*). SPAIN. *JB-7447/11*, GenBank accession No. JX219784 (as *C. callisteus*). NORTH AMERICA: CANADA. BRITISH COLUMBIA: *SMI19*, GenBank accession No. FJ157137 (as *C. callisteus*). *DAVFP 28810*, GenBank accession No. EU821663 (as *C. huronensis*). Interior Cedar-Hemlock forests, *OUC97063*, GenBank accession No. DQ093853 (as *C. limonius*). KISPIOX: Salmon River Road, 55°21′N 127°41′W, gregarious in mixed woods, 45 y old since fire, 7 Sep 2001, *Paul Kroeger PK 2485*, *F14447* (UBC), GenBank accession No. FJ157015 (as *C. callisteus*). USA. WASHINGTON: Skamania County, near junction of Forest Service Roads 2480 and 24, ±1300 m, mixed conifers, *Tsuga*, *Picea*, *Pseudotsuga*, *Abies* with *Vaccinium* and *Salix*, 21 Sep 2007, *J. Lindgren JEL0712*

Cortinarius infucatus Fr., Öfvers. K. Svensk. Vetensk.-Akad. Förhandl. 18:26. 1861.

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FIG. 2b, f

MycoBank MBT204733

Type: Unpublished icone (S0334) in Swedish Museum of Natural History in Stockholm (designated by Melot [2007] in Journ. J.E.C. X:117. 2007).

Epitype: FINLAND. PERÄ-POHJANMAA: Tornio, Korkeamaa, Runteli Nature Reserve, grass-herb, mesic spruce forest (*Picea abies*) with *Betula*, *Populus tremula*, and some *Pinus sylvestris*, 30 Aug 2004, *K. Liimatainen & T. Niskanen 04-531*, *H6029929* (H), designated here. GenBank accession No. KU236700.

=*Cortinarius citrinofulvescens* M.M. Moser, Fungi Non Delineati, Raro vel Haud Perspecte et Explorate Descripti aut Definite Picti. 15:40. 2001. Type: AUSTRIA. UPPER AUSTRIA: Almsee, coniferous forest (*Picea*) on calcareous soil, 28 Aug 1972, leg. *F. Speta IB19720258* (IB, **holotype** of *C. citrinofulvescens*), GenBank accession No. KU236701.

Description: Pileus 30–80 mm diam, at first hemispherical, later low convex, margin often remaining incurved, surface smooth, rarely scaly, yellow, often with an orange tint at the center, somewhat hygrophanous, bright yellow when dry. Lamellae medium spaced, pale yellow, later more brownish-yellow. Stipe 40–100 mm long, 8–13 mm diam at apex, up to 25 mm diam at base, clavate, light yellow, often almost white at the apex, downward yellow-brown, becoming more brownish when pressed with the thumb and with age. Universal veil yellow, forming incomplete zones on the stipe. Context in pileus white to pale yellow, in stipe apex and middle part white, pale orange-brown toward the base, becoming darker with age or when damaged. Odor when smelling from the top of the pileus often faint and like apples, sometimes stronger and like a recently extinguished candle. Exsiccatae paler than in *C. callisteus*, with a golden yellow to somewhat more brownish pileus.

Basidiospores 7.0–8.2 × 5.7–6.6 µm, Q = 1.12–1.25(–1.30), subglobose to ovoid-subglobose, slightly to somewhat dextrinoid, moderately verrucose, verruculae distinct, small, warts pointed, distinctly spaced. Basidia 4-spored, clavate, hyaline or with yellow contents. Lamellae trama hyphae smooth to finely encrusted. Pileipellis: surface layer hyphae subparallel to interwoven or entangled, cylindrical, 6–13 µm diam, very pale yellow to golden yellow, majority zebra-striped encrusted, some with yellowish granulose contents.

Subtending layer hyphae subparallel to ±interwoven, cylindrical to enlarged, 7–15 µm diam, mainly hyaline, very few finely encrusted. Hypoderm hyaline, hyphae up to 25 µm diam.

Ecology and distribution: Widely distributed in North America and Europe. In Europe and eastern North America in mesic coniferous forests, often on rich to calcareous soil. In western North America, mainly in non-calcareous coniferous forests. Basidiomata produced Aug–Oct. *Cortinarius infucatus* is considered rather rare in hemiboreal and boreal zones as well as in montane areas, but becomes occasional toward the northern parts of the boreal zone at least in Fennoscandia.

Notes: Cortinarius infucatus is a medium-sized to large, bright yellow species with a clavate stipe and subglobose basidiospores. The odor when smelling the top of the pileus is often faint, like apples, or sometimes stronger, like a recently extinguished candle. The sister species *C. callisteus* is more yellow-brown and the basidiospores are slightly smaller and not as sharply verrucose.

Fries (1861) describes *Cortinarius infucatus* as a species with a yellow pileus, pale yellow, clavate stipe, yellow universal veil, and white context. Fries compared the species to *C. percomis*, which has a viscid pileus, and to *C. callisteus*, which has at first a smooth, later finely scaly pileus. Melot (2007) designated an unpublished icone (S0334) as a type of *C. infucatus* and provides a detailed discussion of the name. He also mentioned *C. citrinofulvescens* as a later synonym of *C. infucatus*. We agree with the interpretation of Melot (2007) and suggest here an epitype for *C. infucatus*.

Specimens examined: EUROPE: FINLAND. UUSIMAA: Vantaa, Kylmäoja, damp, young *Picea*-dominated forest with *Betula*, *Populus tremula*, and *Salix* spp., 6 Aug 2004, *M. Toivonen & I. Kytövuori 04-034* (H), GenBank accession No. KU236702. KAINUU: Puolanka, Pihlajavaara, herb-rich coniferous forest on calcareous ground, 7 Aug 2002, *I. Kytövuori 02-021* (H), GenBank accession No. KU236703. KOILLISMAA: Kuusamo, Oulanka National Park, Korvasvaara, herb-rich *Picea abies* forest with some *Pinus sylvestris*, *Populus tremula*, and *Betula* on calcareous ground, 30 Aug 2002, *K. Liimatainen & T. Niskanen 02-339*, *H6031441* (H), GenBank accession no. KU236704. ITALY. TRENTINO: Peneveggio ober Predazzo, under *Picea abies*, 22 Sep 1993, *M.M. Moser 93/233* (IB, as *C. tophaceoides* ined.) GenBank accession No. KU236705. SWEDEN. ÅNGERMANLAND: Häggdånger sn., Antjärn, in blueberry spruce forest, 11 Aug 1990, *H. Lindström CFP960* (S, K), GenBank accession No. KU236706. NORTH AMERICA: CANADA. NEWFOUNDLAND: west coast, Gros Morne National Park, west side of Lomond River, hiking trail to Stuckless Pond, mesic to damp coniferous forest (*Abies balsamea*, *Picea*) with some *Betula*, on calcareous ground, 20 Sep 2007, *K. Liimatainen & T. Niskanen 07-249*, *H7000912* (H).

Additional specimens: EUROPE: GERMANY. *TUB011827* (TUB, as *C. callisteus*), GenBank accession No. AY669594. ITALY. 16 Aug 1993, *E. Campo 418* (MCVE), GenBank accession No. JF907851. 16 Aug 1993, *E. Campo 3007*, GenBank accession No. JF907920. 7 Sep 1994, *E. Campo 7835* (MCVE), GenBank accession No. JF907946 (as *C. callisteus*). *IB19960100B* (IB), UNITE No. UDB001107. SPAIN. *JB-5604/06*, GenBank accession No. JX219781. *JB-4057/02*, GenBank accession No. JX219782. *JB-7417/11*, GenBank accession No. JX219783. SWEDEN. 11 Aug 2000, *A. Taylor AT2000150* (UPS), UNITE No. UDB001139 (as *C. callisteus*). 3 Sep 2005, *A. Taylor AT2005127* (UPS), UNITE No. UDB002230 (as *C. callisteus*). NORTH AMERICA: CANADA. BRITISH COLUMBIA: Smithers, McDonnell Forest Service road, 54°46′N, 127°10′W, elevation 900 m, sub-boreal spruce zone, mature forests, made up of lodgepole pine, subalpine fir and lodgepole pine, mesic soils, 22 Aug 2006, *leg. Marty Kranabetter SMI189*, *F16445* (UBC), GenBank accession No. FJ039666 (as *C. callisteus*). 9 Sep 2006, *SMIA11*, *F16446* (UBC, as *C. callisteus*), GenBank accession No. FJ039667 (as *C. limonius*).

Cortinarius neocallisteus Kranab., Ammirati, Liimat. & Niskanen sp. nov. FIG. 2c, g

MycoBank MB816804

Type: CANADA. BRITISH COLUMBIA: Date Creek, Hazelton, 55°23′N, 127°41′W, gregarious in interior Cedar-Hemlock old-growth forest, moist cold variant, made up of western hemlock (*Tsuga heterophylla*) and lodgepole pine (*Pinus contorta*), on submesic soils with relatively dry and low nutrient status, 6 Sep 2002, *P. Kroeger SMI 34*, *F18486* (UBC, **holotype**). GenBank accession No. FJ157127.

Description (from the herbarium material): Pileus 20–35 mm diam (estimate ca. 25-42 mm diam fresh), surface wrinkled and shiny, no fibrils or scales including the margin, likely had a dry pileus surface, margin enrolled to incurved; deep orange to light orange or orange-brownish in the center, margin lighter colored, usually with brown tones mixed with yellowish color or more brownish, edge with more orange tones. Lamellae medium spaced, adnexed with a decurrent line, moderately thick, edges even, yellow-brown to cinnamon brown or various shades of rust brown, fairly brightly colored. Stipe 35–60 mm long, above about 6–10 mm diam, base clavate bulbous, 12–18 mm diam, base sometimes short pointed, surface shiny, above the base to about mid-stipe pale ochraceous or pale yellowish to brownish, in places with dark orange to reddish-orange areas (universal veil?), above shiny, ochraceous to pale yellowish. Basal mycelium orange, ochraceous or whitish among needles. Context in pileus pale, whitish to pale yellowish, stipe flesh where seen, pale or similar in color to surface but in base sometimes darker colored. Odor (notes from fresh basidiomata) lacking hot iron-like smell.

Basidiospores (7.4–)7.8–8.5(–8.9) × 6–6.3(–6.7) µm, Q = 1.2–1.3, subglobose to ovoid, slightly dextrinoid, moderately verrucose, verruculae small, distinct, pointed warts. Basidia 4–spored, clavate, hyaline or with yellow contents. Lamellae trama hyphae hyaline to yellowish, walls refractive, usually smooth, some slightly encrusted. Pileipellis: surface layer hyphae subparallel to interwoven or entangled (especially on disc), cylindrical to broadly cylindrical, 3–14 µm diam, hyaline to pale yellow or yellow, some with darker orange-brown pigment, walls hyaline to yellowish, refractive, encrusted, sometimes with heavier encrusting spirals. Subtending layer hyphae subparallel to ±interwoven, cylindrical to enlarged, 6–19 µm diam, yellowish or hyaline, walls refractive, some encrusted, but not as heavily as in surface hyphae.

Ecology and distribution: In coniferous forests (at least *Tsuga heterophylla*, *Picea*). Producing basidiomata Sep–Oct. Currently only known from three locations: Spain, Switzerland, and British Columbia (Canada).

Notes: All known specimens of the species were collected as *C. callisteus*, which would indicate that the fresh basidiomata are similar in color to those of *C. callisteus*. However, the lack of the typical smell of *C. callisteus* was noted in the holotype collection and might help to distinguish *C. neocallisteus* from *C. callisteus* in the field. Also the basidiospores are slightly longer than those of *C. callisteus* and *C. infucatus*. *Cortinarius tofaceus* can be distinguished from the other species by the raphanoid smell of the lamellae.

Additional specimens: SPAIN. *JB-7098/10*, GenBank accession No. JX219785 (as *C. callisteus*). SWITZERLAND. VANELWALD BEI INS: under *Picea*, 8 Oct 1965, *M. Moser IB19650251*, GenBank accession No. AY040713 (as *C. callisteus*).

Note: Specimen F18483 (UBC deposited as *C. iodes*) was studied and represents *C. subfoetidus*. The sequence in GenBank (No. FJ157120 as *C. subfoetidus*) referring to this specimen is *C. neocallisteus,* implying an error in GenBank submission.

Cortinarius tofaceus Fr., Epicr. Syst. Mycol.:28. 1838. FIG. 2d, h

MycoBank MBT204735

Type: SWEDEN. BOHUSLÄN: Kville, S Ödsmål, in dry oak-hazel forest, 21 Sep 1985, *H. Lindström et al. CFP366* (S, **neotype**; K, **isoneotype**). Neotypus here designated. GenBank accession No. KU236707.

=*Cortinarius croceicolor* Kauffman, Bull. Torrey Bot. Club 32:323. 1907 (1905). Type: USA. New York, Ithaca, Coy's Glen and Mich., gregarious or solitary in mixed woods, hollow swamp, Aug 1904, *C. H. Kauffman MICH10341* (MICH, **lectotype** designated here). GenBank accession No. KU236708.

Description: Pileus 40–110 mm diam, hemispherical, then low convex to almost plane, distinctly and minutely scaly to almost tomentose, golden to orange-yellow, scales and later the whole cap orange-brown, not hygrophanous. Lamellae medium spaced to distant, yellowish-brown to more brown with age. Stipe 40–100 long, 7–15 mm diam at apex, 10–20 mm diam at base, cylindrical to clavate, rarely bulbous, pale yellow, with age more brownish. Universal veil yellow to orange-yellow, later more brownish, forming incomplete girdles on stipe. Basal mycelium white. Context in the pileus white to ochre yellow with age, in the stipe base pale yellow-brown to orange-brown. Odor of lamellae like raw potatoes or old cellar. Exsiccatae with orange-brown pileus, brown lamellae, and yellow-brown stipe.

Basidiospores (7–)7.5–8(–8.5) × 5.8–6.5 µm, Q = 1.20–1.30, subglobose to somewhat elongate, moderately verrucose, moderately dextrinoid. Basidia 4-spored, clavate, hyaline or with yellow contents. Lamellae trama hyphae smooth to finely encrusted. Pileipellis: Epicutis hyphae 5–10(–15) µm diam, strongly encrusted and with yellow pigment. Hypocutis not well developed, hyphae 15–25 µm diam, with thin pale walls.

Ecology and distribution: Cortinarius tofaceus grows in deciduous forests with *Fagus*, *Quercus*, and *Corylus*, often on mull soil but also occurs in coniferous forests on rich to calcareous ground. Basidiomata occur in Aug and Sep in loose groups or solitary. *Cortinarius tofaceus* is rare in temperate and hemiboreal zones. The species is known in Europe and eastern North America from New York to Newfoundland. In most of the Nordic countries the species has been included on the national red lists: Denmark (EN), Norway (EN), Sweden (NT) (Niskanen et al. 2012b).

Notes: Cortinarius tofaceus is characterized by the golden to orange-brown, scaly pileus, yellowish, cylindrical to clavate stipe, yellow universal veil, and white context in pileus and upper part of the stipe. The odor of raw potatoes or old cellar of the lamellae and subglobose to somewhat elongate basidiospores are also characteristic. The closely related *C. callisteus* and *C. infucatus* have smooth or a very finely scaly pileus, clavate to bulbous stipe, smell like a recently extinguished candle (ozone) or apples, and have more subglobose basidiospores Qav < 1.25.

The description of *C. tofaceus* by Fries (1838) “pileo carnoso obtuso ochraceo-fulvo villoso-squamoso, carne alba … in fagetis raro” fits our species well. The collection of Lindström et al., CFP366, is typical of *C. tofaceus*, and we propose it as a neotype for the species. A possible sister species of *C. tofaceus*, named *C. callistei* sp. in our phylogenetic tree (AY040714, Sweden, Småland), might also occur in northern Europe. Thus far, it is only known based on a single collection.

The North American name *C. croceicolor* Kauffman was long interpreted as a species close to *C. clandestinus* Kauffman, a species in subgenus *Leprocybe* (Ammirati et al. 2012). The study of the type specimen, however, showed that it is a synonym of *C. tofaceus*. Morphology, molecular data, and the original description support this conclusion. Another North American name, *Cortinarius annulatus* Peck, was described as a species close to *C. tofaceus* and *C. callisteus* with a raphanoid smell. The current interpretation of the name (GenBank accession No. KJ705130) and the odor would suggest it to be a synonym of *C. tofaceus*, but unfortunately the sequencing of the type specimen was not successful, and the identity of the name could not be fully resolved.

Specimens examined: EUROPE: ESTONIA. SAAREMAA: western part, Viidumäe Nature Reserve, rich pine-spruce forest with *Quercus*, *Corylus*, and other deciduous trees and bushes, 13 Sep 1993, *I. Kytövuori 93-1089* (H), GenBank accession No. KU236709. FINLAND. VARSINAIS-SUOMI: Vihti, Salmenkartano, herb rich *Picea abies* forest with some *Populus* and *Betula*, 30 Aug 2005, *I. Kytövuori H6032405* (H), GenBank accession No. KU236710. NORTH AMERICA: CANADA. NEWFOUNDLAND: west coast, Gros Morne National Park, south side of the Bonne Bay East Arm, Lomond River hiking trail, mesic to damp coniferous forest (*Abies balsamea*, *Picea*) with some *Betula*, on calcareous ground, 49°27′N 57°45′,46′E, 19 Sep 2007, *Liimatainen & Niskanen 07-208*, *H7000870* (H, Gros Morne Herbarium), GenBank accession No. KU236711. QUEBEC: Rivière-à-Pierre, south entrance of the Réserve faunique de Portneuf, conifer-dominated (*Tsuga*, *Abies*, some *Picea*) forest with some *Betula* and *Populus*, 31 Aug 2010, *Paul, Lebeuf & Liimatainen 10-061* (H), GenBank accession No. KU236712.

Additional specimens: EUROPE. ESTONIA. SAARE: Kihelkonna, in the spruce-pine alvar forest, 19 Sep 2009, *Anu Kollom TAAM128740* (TAAM), Unite accession No. UDB017021. SWEDEN. GOTLAND: Fleringe Parish, near lake Bästerträsk, pine forest with *Juniperus communis*, 26 Sep 2011, *Anu Kollom TU105213* (TU), Unite accession No. UDB017019. NORTH AMERICA: CANADA. QUEBEC: Saint-Emile-De-Suffolk, *2217-QFB-25972*, GenBank accession No. KJ705130.

DISCUSSION

Currently five species are recognized in subgenus *Callistei* from North America and Europe. Three of them, *Cortinarius callisteus*, *C. infucatus*, and *C. neocallisteus*, are known from western North America and Europe, while *C. tofaceus* is known from eastern North America and Europe. All species grow with coniferous trees, and in Europe and eastern North America several of them occur in calcium-rich soil. *Cortinarius tofaceus* also grows with deciduous trees in the southern parts of its range, at least in Europe. A fifth putative species, *C. callistei* sp., is known from only one locality in Sweden. Given the existence of only a single specimen for this putative new taxon, we refrain from formally proposing it as new to science until a more complete picture of its variation can be documented.

This study emphasizes the importance of molecular studies of species (including types) with similar characteristics. Without these studies, distinctions between species are difficult to resolve across a broad geographical region spanning two continents. ITS sequences of type specimens are essential for reliable identification, especially because they allow the identification of the species in all stages of its life history. The importance of type studies has also been emphasized in recent papers by Schoch et al. (2014), Liimatainen et al. (2014, 2015), and Cripps et al. (2015). The barcodes produced in this study are deposited in the RefSeq database (Schoch et al. 2014) and used as a basis to name Species Hypothesis in UNITE (Kõljalg et al. 2013). The RefSeq database currently includes ITS sequences of more than 300 *Cortinarius* species based on studies of type specimens. These databases provide an excellent way to unambiguously identify species for use in ecological, environmental, or further taxonomic research.

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LEGENDS

FIG. 1. Phylogram resulting from the RaXML analysis of ITS regions. Bootstrap values greater than 50% are indicated above branches. The names of the species recognized in subgenus *Callistei* are shown in boldface.

FIG. 2. Basidiospores of a. *C*. *callisteus* (CFP1219, S, **neotype**), b. *C*. *infucatus* (TN 04-531, H, **epitype**), c. *C*. *neocallisteus* (F18486, UBC, **holotype**), and d. *C*. *tofaceus* (CFP366, S, **neotype**). Basidiomata of e. *C*. *callisteus* (TN 07-395, H), f. *C*. *infucatus* (TN 04-531, H, **epitype**), g. *C*. *neocallisteus* (F18486, UBC, **holotype**), and h. *C*. *tofaceus* (TN10-061, H). (Photographs a, b, d by Tuula Niskanen; c, g by Joseph Ammirati; and e, f, h by Kare Liimatainen). Scale bars: a–d = 10 mm, e–h = 10 µm.

FOOTNOTES

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100
Hebeloma mesophaeum EF451057 TYPE
Hebeloma sp. JX630953
52
C. clandestinus GQ159862 Canada BC
C. parkeri JN976987 USA WA TYPE
C. venetus AF389167
C. cotoneus KC842423
C. aureopigmentatus NR131794 TYPE
subgenus Leprocybe
100
C. vespertinus AF389137
/Vespertini
81
C. infucatus TN04-531 Finland TYPE
70
C. infucatus JX219782 Spain
C. infucatus FJ039666 Canada BC
C. citrinofulvescens 1972/0258MM Austria TYPE
C. infucatus IK02-029 Finland
C. infucatus TN02-339 Finland
68
C. infucatus CFP960 Sweden
C. infucatus 93/233MM Italy
100
C. infucatus AY669594 Germany
C. infucatus IK04-034 Finland
93
C. neocallisteus AY040713 Switzerland
C. neocallisteus FJ157127 Canada BC TYPE
C. callistei sp. AY040714 Sweden
89
C. tofaceus CFP366 Sweden TYPE
100
C. croceicolor MICH10341 USA NY TYPE
C. tofaceus TN10-061 Canada QC
C. tofaceus IK93-1089 Estonia
C. tofaceus TN07-208 Canada NL
subg. Callistei
71
C. callisteus IK98-1706 Finland
C. callisteus IK00-031 Finland
73
C. callisteus UDB000162 Norway
C. callisteus UDB016108 Estonia
C. callisteus TN07-395 USA WA
C. callisteus FJ157015 Canada BC
C. callisteus CFP1219 Sweden TYPE
C. hirtipes PC362 France TYPE
C. callisteus IK94-1105 Finland
C. callisteus TN07-210 Canada NL
C. callisteus CFP1419 France
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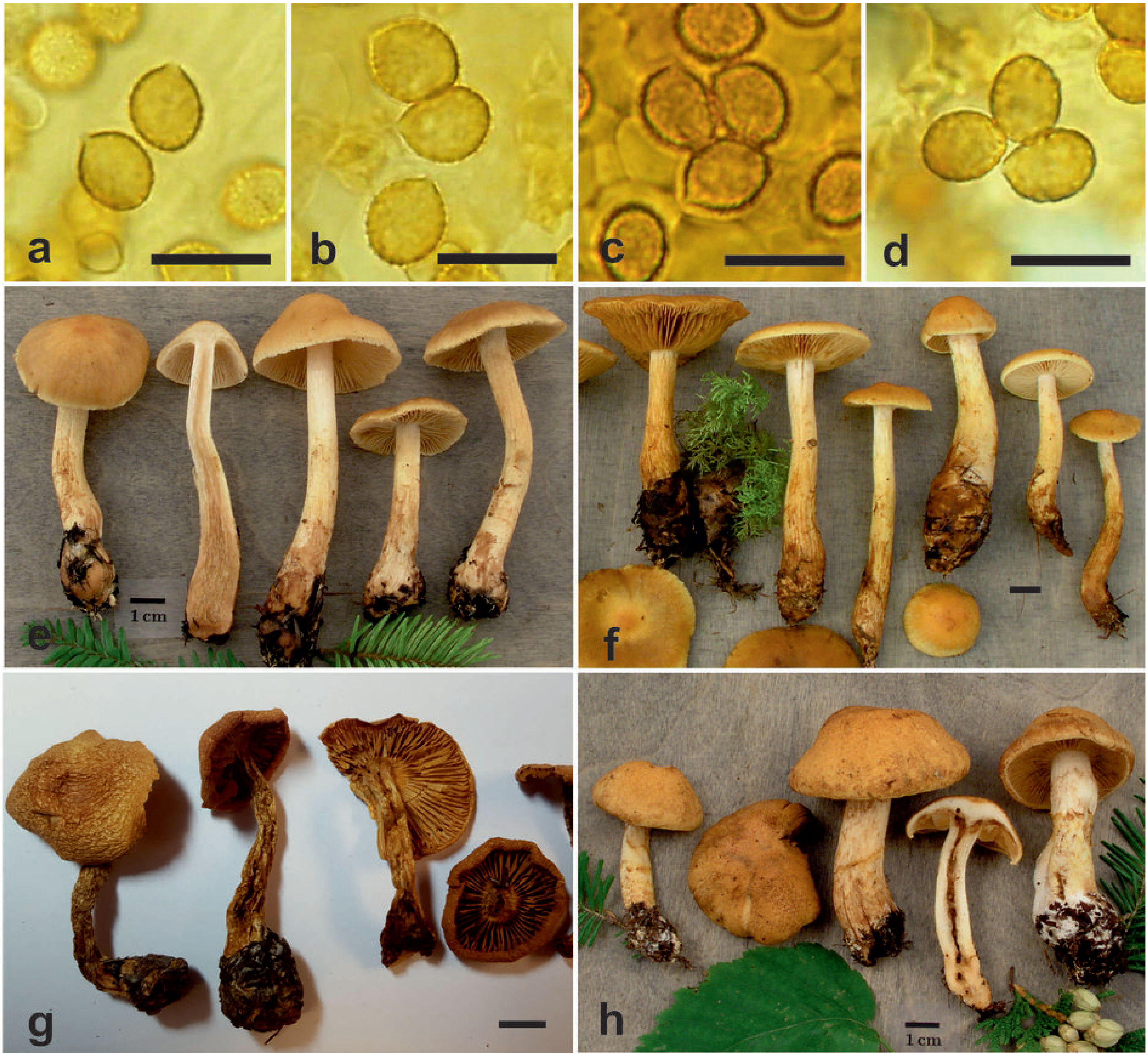
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