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ARTICLE

Cortinarius hesleri from eastern North America and related species from Europe and western North America

Joseph F. Ammirati, Karen W. Hughes, Kare Liimatainen, Tuula Niskanen, and P. Brandon Matheny

Abstract: The following four species of *Cortinarius* are presented: *Cortinarius californicus* and *Cortinarius hesleri* from North America and *Cortinarius cinnabarinus* and *Cortinarius coccineus* from Europe. *Cortinarius cinnabarinus* and *C. coccineus* form a clade with *C. bulliardii*, whereas *C. californicus* and *C. hesleri* form a clade with *C. colymbadinus*. An epitype is selected for *C. cinnabarinus*, and ***Cortinarius hesleri*** is described as a new species from eastern North America.

Key words: Telamonia, *Dermocybe*, *Cinnabarini*, Basidiomycota, Agaricales.

Résumé : Les auteurs présentent les quatre espèces suivantes de *Cortinarius:* les *Cortinarius californicus* et *Cortinarius hesleri* de l'Amérique du Nord et le *Cortinarius cinnabarinus* ainsi que le *Cortinarius coccineus* d'Europe. Le *Cortinarius cinnabarinus* et le C. *coccineus* forment un clade avec le *C. bulliardii*, alors que le *C. californicus* et le *C. hesleri* forment un clade avec le *C. colymbadinus.* Les auteurs choisissent un épitype pour le *C. cinnabarinus*, et décrivent le ***Cortinarius hesleri*** comme nouvelle espèce pour l'est de l'Amérique du Nord. [Traduit par la Rédaction]

Mots-clés : Telamonia, *Dermocybe*, *Cinnabarini*, Basidiomycota, Agaricales.

Introduction

Cortinarius cinnabarinus, *Cortinarius coccineus*, *Cortinarius hesleri*, and *Cortinarius californicus* are rather attractive orange to orange red species of subgenus *Telamonia*. *Cortinarius cinnabarinus* and *C. coccineus* occur in hardwood forests of Europe, *C. hesleri* is found in mixed forests of hardwoods and conifers in eastern North America, and *C. californicus* is a species of mixed and coniferous forests in western North America (Smith 1939; Moser 1974; Keller and Ammirati 1983; Ammirati and Smith 1984; Høiland 1983, Bidaud et al. 1994). The basidiomata of these species contain a variety of anthraquinone and anthraquinoid pigments that in combination provide the coloration of individual species (Keller and Ammirati 1983; Gill and Steglich 1987). Because of similarity in pigmentation, *C. cinnabarinus* and *C. californicus* were frequently associated with species of *Dermocybe* (Moser 1974; Høiland 1983; Moser 1983; Ammirati and Smith 1984), although Keller and Ammirati (1983) suggested that differences in pigment composition could be used to distinguish the *Cinnabarinae* from the *Sanguineae sensu stricto*. Liu et al. (1997), using ITS nuclear ribosomal DNA (rDNA) sequences of material from the *C. californicus* group, showed that they are in *Telamonia* rather than *Dermocybe*. Høiland and Holst-Jensen (2000), Garnica et al. (2005), and Harrower et al. (2011) further support this initial finding. Here we publish the descriptions and preliminary phylogenetic positions of four species, *C. californicus*, *C. cinnabarinus*, *C. coccineus*, and *C. hesleri* (Fig. 1). In addition, an epitype is selected for *C. cinnabarinus* Fr. and *C. hesleri* is described as a new species from eastern North America.

Materials and methods

Morphological studies

Microscopic descriptions were made from sections of dried material mounted in 3% KOH or fresh material mounted in water or 3% KOH. Basidiospores also were mounted in Melzer's reagent to determine the dextrinoid reaction. Macrochemical color reactions were made with 3% KOH. Color notations are from Ridgway (1912). The description of fresh basidiomata and microscopic features are based on an evaluation of multiple collections except for *C. coccineus*, which is only known from the type collection. Basidiospore measurements and Q values are based on 20 spores from each of the collections listed as Specimens Examined. In all instances, basidiospore samples came from deposits on the stipe and (or) veil surface. Materials that provide a better understanding of each taxon are listed under Additional Specimens Examined.

Molecular analyses

Collections used for ITS sequencing and GenBank sequences are given in Table 1. DNA extractions, PCR, and sequencing followed techniques in Hughes et al. (2007) and Niskanen et al. (2009). The ITS1-5.8S-ITS2 nuclear ribosomal DNA (ITS) was amplified using primers ITS1F or ITS5 and ITS4B or ITS4 (White et al. 1990; Gardes and Bruns 1993). The amplification protocol was as follows: 4 min at 94 °C, 1 cycle; 1 min at 94 °C, 1 min at 52 °C, 1 min at 72 °C, 35 cycles; 3 min at 72 °C, 1 cycle; hold at 4 °C. Primers and unincorporated nucleotides were removed from the PCR product by digestion with ExoSAP-IT (Amersham Biosciences, Piscataway, New Jersey, USA), following manufacturer's directions. Sequencing was performed using the ABI Big Dye Terminator Cycle Sequencing Kit version 3.1. Sequencing primers were ITS4 and ITS5. Depending on the quality of the sequence, both forward and reverse primers were sometimes used to form an overlapping contiguous sequence. The sequencing reaction was cleaned with a Sephadex G-50 column to remove dyes and sequenced using an automated ABI 3100 DNA sequencer.

Data analyses

Sequence alignments were performed manually using the seqlab program in Genetics Computer Group (2000). Preliminary

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Table 1. Collections included in the ITS sequence analysis.

Herbarium No.	Field/ collection No.	Name	GenBank No.	Geographical origin	Original designation
TN04-557 (H)		*C. uraceus*[b]	HMO17844	Finland	
JFA13069 h1&h2[a]		*C. heslerii*	JQ974380 JQ974381	US, TN, GSMNP	*C. cinnabarinus*
AHS81565 (MICH) Holotype		*C. heslerii*	JQ974489	US, Michigan	
61122 (TENN) c1-c5[a]	TFB12560	*C. heslerii*	JQ974382- JQ974386	US, TN, GSMNP	*C. cinnabarinus*
61793 (TENN)	CLO4589	*C. heslerii*	JQ974387	US, NC, GSMNP	*Dermocybe californicus*
66242 (TENN)	SAT-11-17702	*C. heslerii*	JQ974388	US, TN, GSMNP	
Is506 (WTU)	CU56023	*C. californicus*[c] Liu	U56023	US, California	
10327 (MICH) Holotype	AHS8957	*C. californicus*	JX114946	US, California	
F19593 (UBC)	2081121-006	*C. californicus*	HQ604737	Not given in record	*C. cinnabarinus*
F17259 (UBC)	OC187	*C. californicus*	GQ159845	Not given in record	
F19590 (UBC)	2081113-008	*C. californicus*	HQ604736	Not given in record	
	OC39	*C. californicus*	FJ039679	Canada, BC	
	OC28	*C. californicus*	FJ039678	Canada, BC	
F17152 (UBC)	OC80	*C. californicus*	GQ159895	Not given in record	*C. idahoensis*
F17199 (UBC)	OC127	*C. californicus*	GQ159788	Canada, BC	*C.* cf. *cinnabarinus*
CFP587 (S) Neotype		*C. brunneus*[d]	DQ117927	Sweden: Ang, Sabra	
IB19990511		*C. laniger*[e]	AF325592	Not given in record	
IK85–1517 (H)		*C. cinnabarinus*	JX114943	Finland	
CFP379 (S) Epitype		*C. cinnabarinus*	JX114944	Sweden	
UDB000161	T29	*C. cinnabarinus*	UDB000161	Norway	
MCVE voucher 764		*C. bulliardi*	JF907860	Italy	
IB19920363		*C. bulliardi*[g]	AF389154	Not given in record	
F41127 (S)	CFP499	*C. bulliardi*	JX114942	Sweden	
435745 (GK) Holotype	MP3568	*C. coccineus*	JX114945	France	
CFP584 (S) NEOTYPE		*C. armillatus*[d]	DQ114744	Sweden: Ang, Sabra	
IB19960060		*C. traganus*[g]	AF325598	Not given in record	
TUB011887		*C. malachius*[f]	AY669681	Not given in record	
AHS17461 (MICH) HOLOTYPE		*C. boulderensis*[h]	DQ499466	US, Washington	
IB19980189		*C. saturninus*[i]	AY083189	Not given in record	
MCVE voucher 853		*C. colymbadinus*	JF907865	Italy	
CFP1130 (S)		*C. colymbadinus*	JX127302	Sweden	
No voucher		Environmental sample[j]	FJ553926	Canada, BC	Boletales
No voucher		Environmental sample[j]	FJ553195	Canada, BC	Cortinarius
No voucher		Environmental sample[j]	FJ554334	Canada, BC	Cortinarius
No voucher		Environmental sample[j]	FJ553431	Canada, BC	Cortinarius
No voucher		Environmental sample[j]	FJ554058	Canada, BC	Agaricales
No voucher		Environmental sample[j]	FJ553786	Canada, BC	Cortinarius
No voucher		Environmental sample[j]	FJ554394	Canada, BC	Cortinarius
No voucher		Environmental sample[j]	FJ554284	Canada, BC	Cortinarius
No voucher		Environmental sample[j]	FJ553807	Canada, BC	Cortinarius

[a]"h" refers to haplotypes determined from uncloned sequences. "c" refers to cloned sequences.
[b]Niskanen et al. 2011.
[c]Liu et al. 1997.
[d]Kytövuori et al. 2005.
[e]Peintner et al. 2001.
[f]Garnica et al. 2005.
[g]Peintner et al. 2004.
[h]Niskanen et al. 2006.
[i]Peintner et al. 2003.
[j]Hartmann et al. 2009.

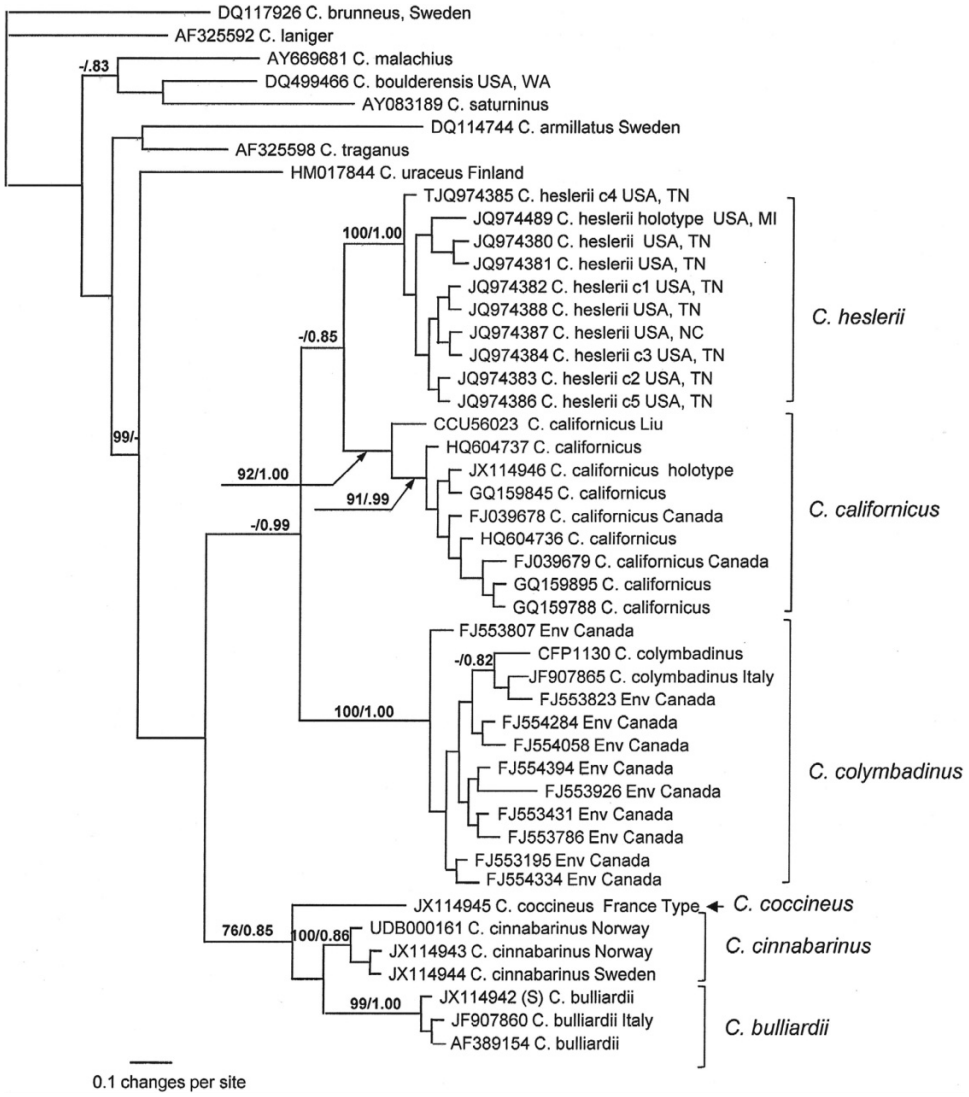
analyses of unrooted trees were performed to select appropriate taxa for an outgroup. Both Maximum Parsimony and Bayesian analyses were performed. Parsimony was performed using PAUP* (Swofford 2002). Characters were unordered and weighted equally; starting trees were obtained via stepwise addition with addition sequence = furthest; the number of trees held at each step during stepwise addition = 1; the branch-swapping algorithm was a tree-bisection-reconnection (TBR). Since gaps were small (1–2 base pairs (bp)), no gap coding was attempted and gaps were treated as a fifth base. One-thousand bootstrap replicates were performed. Model Test was used to estimate the appropriate model of evolution for Bayesian analysis (Posada and Crandall 1998). The model selected by Model Test was the Hasegawa–Kishina–Yano model (Hasegawa et al. 1985) with a proportion of invariant sites and a gamma distribution (HKY + G + I). Bayesian analysis was performed using Mr. Bayes (Huelsenbeck and Ronquist 2005; Ronquist and Huelsenbeck 2003) with the following settings; nst = 2, basefreq = estimate. The MCMC search was run with four chains for 500 000 generations with sampling every 100 generations. The first 1000 trees were discarded based on preliminary analyses showing that likelihood values had reached stability with the first 1000 trees. Posterior probabilities were estimated by sampling trees generated after likelihood values diverged. For Bayesian analysis, all bases were included in the analysis.

Results

Molecular studies

The overall topology of trees produced by Bayesian and Parsimony analyses was similar. Bayesian and Parsimony analyses produced the same well-supported clades; *C. hesleri*, *C. californicus*, *C. colymbadinus*, and related environmental samples, and *C. cinnabarinus* and *C. bulliardii*. *Cortinarius cinnabarinus* and *C. bulliardii* formed a monophyletic group

Fig. 1. Phylogenetic tree of *Cortinarius* species based on the ribosomal ITS region. Bootstrap and posterior probabilities are listed to the left of the supported node. Consistency index (CI) = 0.6845; Homoplasy index (HI) = 0.3155. 598 total characters, 425 characters were constant, 78 were parsimony uninformative, and 95 parsimony informative. Tree length was 317 steps. Gaps were treated as a fifth base. The Bayesian model of evolution was TVM + I + G selected by Modeltest 3.7.



in both analyses, as did *C. californicus* and *C. hesleri*. Deeper nodes in both Parsimony and Bayesian analysis were poorly supported. This is in part due to incomplete sampling of taxa related to these species. To resolve this problem additional field studies as well as further molecular evaluation will be required. A clade from western Canada composed of environmental sequences was affiliated with *C. colymbadinus* from Europe. This species is also known from collections made in western North America (T. Niskanen and K. Liimatainen, unpublished data). In Parsimony analysis, *C. coccineus* was basal to *C. bulliardii*, whereas in Bayesian analysis, *C. coccineus* was basal to a clade containing both *C. bulliardii* and *C. cinnabarinus* but without strong support in either case. Whereas *C. uraceus* was basal to the *C. hesleri*/*C. californicus*/*C. cinnabarinus*/*C. bulliardii* group in both Parsimony and Bayesian analyses, support for this node was poor in Bayesian analysis.

Only one of the available collections of *C. hesleri* from Michigan could be sequenced and differs from the southern Appalachian collections by a single transition. TENN61122 is heterozygous for two 1-base indels and was cloned to obtain a clean sequence. Additional bp variability was seen in other collections of *C. hesleri* but overall, variability within collections of *C. hesleri* was low (less than 0.5% bp divergence). *Cortinarius californicus* collections were more variable (2.19% bp divergence) indicating that this species requires further investigation. The three *C. cinnabarinus* collections, in contrast, differed by 0.004% in sequence bp divergence.

Taxonomic studies

Cortinarius californicus A. H. Sm., Contrib. Univ. Mich. Herb. 2:37–38. Plate XII. 1939.

Figs. 2, 3, 7.

Pileus 30–85 mm broad, obtusely conic, becoming broadly umbonate, with a decurved margin, glabrous, hygrophanous, evenly reddish brown (Hay's Russet) when moist, fading to brown (Cinnamon Rufous), margin appressed against the stipe and faintly silky at first; flesh watery, moderately thick on the disk, concolorous with the surface of both moist and faded pilei; odor and taste not distinctive; lamellae brownish orange (Mars Orange) when young, brownish red (Burnt Sienna) in age, adnate, becoming slightly adnexed, narrow to moderately broad, subdistant, edges slightly serrulate or fimbriate. Stipe 8–15

Figs. 2–3. *Cortinarius californicus* basidiomata (photos by A. & O. Ceska, OC25, x 1).

Figs. 4–6. *Cortinarius hesleri* basidiomata (photos by S. Trudell (Fig. 5, SAT11–177-02, x 1/2) & M. Kuo (Fig. 4, MK07110401, x 2, Fig. 5, MK06300710, x 1).

(–20) cm long, 5–15 mm thick, equal, sometimes the base slightly enlarged or sometimes narrowed, becoming hollow, at first sparsely fibrillose below with orange fibrils from remains of the cortina, dull orange overall (paler than the lamellae); mycelium orange red.

Exsiccatae: Stipe surface shiny, brownish orange buff with some reddish tints or more brownish to vinaceous; lamellae rich deep brown, but in some younger ones reddish where the lamellae meet the stipe; pileus surface brownish with a vinaceous cast in places, in older specimens blackish centrally.

Microscopic description: Basidiospores 7.7–9.6 (–10.2) μm × 4.8–5.5 (–7) μm, Q 1.4–1.9, ellipsoid to broadly ellipsoid or narrowly amygdaloid to amygdaloid, coarsely verruculose, moderately to strongly dextrinoid. Pileipellis duplex, epicutis of interwoven, more or less cylindrical hyphae 3–10 μm wide, some encrusted, colorless to yellowish or containing yellow brown pigments; hypocutis of cylindrical to enlarged hyphae 8–23.4 μm wide, some short cells present, some encrusted, colorless to yellowish or containing yellow brown pigment; sections of pileus including pileus trama purplish in 3% KOH.

Habitat: Mixed forests of fir and pine and mixtures of *Pseudotsuga*, *Thuja*, *Arbutus*, *Quercus garryana*, and *Acer*.

Specimens examined: USA. California. Del Norte County: Jedediah Smith Redwoods State Park, Is506, 26–11–1956; Oregon. Lane County: California-Oregon line on Highway W–199, AHS8957 (Holotype), MICH, 20–10–1937. Canada. Vancouver Island. Observatory Hill, Sannich, F16457 (OC28) UBC, 24–11–2007, F16458 (OC39) UBC, 29–11–2007, F17259 (OC187), UBC, 13–12–2005; Royal Roads, Colwood, F17152 (OC80), UBC, 1–1–2003; Heals Rifle Range, DND, F17199 (OC127), UBC, 5–12–2003.

Additional specimens examined: USA. California. Siskiyou County. Siskiyou National Forest, AHS8316, MICH, 1–11–1937. Oregon. Lane County. Blue River, AHS8081, MICH, 22–10–1937; Belknap Springs, AHS8132, MICH, 23–10–1937.

Observations: The original description of *Cortinarius californicus* is based mainly on AHS8081 with a very small amount of additional information from AHS 8132 and AHS8957 (the designated holotype). Basidiospore measurements (7–9 μm × 4–4.5 μm) were made by Alex Smith from AHS8081. Based on the collection locations and ecology, all of the collections of *C. californicus* cited by Smith (1939) likely represent the species.

Morphological, microscopical, ecological and molecular sequence data clearly show that *C. californicus* is distinctive from *C. hesleri* and *C. cinnabarinus*. Based on current information they are also separated biogeographically. The sequence of the type collection of *C. californicus* has been compared to GenBank sequences with the result that six collections from western British Columbia, Canada, represent this species. Oluna and Adolph Ceska, in their studies of the mycota of Vancouver Island, photographed and wrote notes on several collections of *C. californicus* (OC28,

Fig. 7. *Cortinarius californicus* basidiospores mounted in 3% KOH.

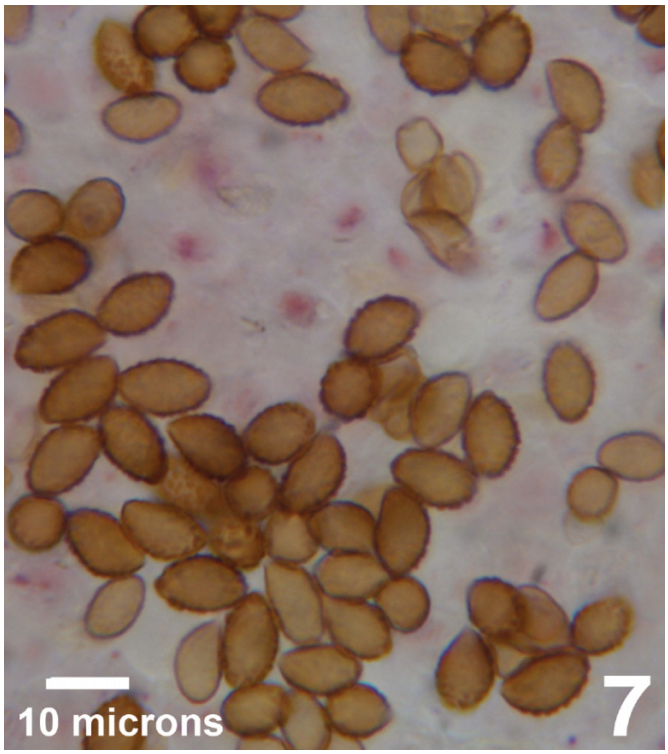
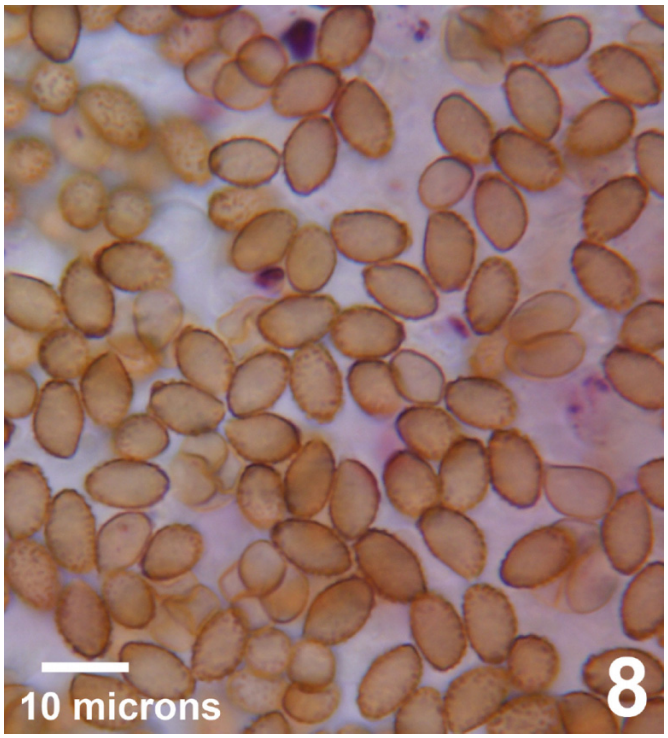


Fig. 8. Cortinarius cinnabarinus basidiospores mounted in 3% KOH.



OC39, OC80, OC127), which have been very helpful in expanding the knowledge of the species.

The collection made by Bill Issac (Is506) and sequenced by Liu et al. (1997) was for some decades considered representative of *Cortinarius californicus*. However, there are no notes on the fresh material and no information on habitat of this collection. The *exsiccatae* have light orange buff and vinaceous colors on the stipe surface, and the base is more pinkish buff, the lamellae are bright rusty brown, and the pileus surface vinaceous to vinaceous brown or blackish vinaceous. The basidiospores are amygdaloid to broadly amygdaloid, coarsely ornamented, moderately to strongly dextrinoid and 8.1–10 μm × 5.1–5.8 μm (Q 1.5–1.9); similar to the spores of *C. californicus*. In this study Is506 (U56023) falls outside the clade containing the type collection of *C. californicus* (0.009% sequence divergence from collection F15193 (HQ604737)).

So far as known the *C. californicus* complex occurs in coastal and inland forests of the Pacific Northwest from northern California into British Columbia and also occurs on the east side of the Cascades in eastern Washington to the Idaho border. It can be locally common in some years but often difficult to find in other years. We are currently evaluating collections from various locations and habitats and plan to publish further on this group in the near future.

Cortinarius cinnabarinus Fr., Epicr. syst. mycol. (Upsaliae): 287. 1838.
Fig. 8.

Type: Sweden: Västergötland: V Tunhem sn, Prästgården, in dry oak-hazel forest, 23 Sep 1985, Lindström et al. CFP379 (S epitype). Epitypus hic designatus.

Pileus 30–60 mm diam, hemispherical then convex, rarely with a low umbo, glabrous, hygrophanous, drying concentrically, color dark cinnabar to brown red, paler orange red to yellowish red when dry. Lamellae moderately crowded, cinnabar red to brown red, the red tinge persistent, edges paler. Stipe 30–70 mm long, cylindrical, slightly clavate at base (10–15 mm thick), brown red to orange red, basal mycelium felt-like, vermillion, veil saturated red to orange red, sparse and fibrillose. Context brown red, pale brownish with red tinge when dry, becoming deep purplish red with KOH. Odor faint, radish-like.

Exsiccatae: Stipe surface pale orange buff with orange and vinaceous areas, basal area more intensely orange to orange red; lamellae are rich brown with an olivaceous sheen, in places orange, for example the lamella edges; pileus surface orange buff, dull reddish orange to brownish, some areas blackish.

Microscopic description: Basidiospores 7.5–8.5 (–9.2) × 4.8–5.5 μm, Q 1.5–1.7, amygdaloid, strongly verrucose, with low warts, strongly dextrinoid. Pileipellis duplex, epicutis of interwoven cylindrical hyphae 3–8 (–10) μm wide, containing orange yellow to orange red vacuolar, granular or cytoplasmic pigment, hypocutis well developed, of cylindrical to enlarged hyphae 15–30 μm wide, with thick, pigmented walls.

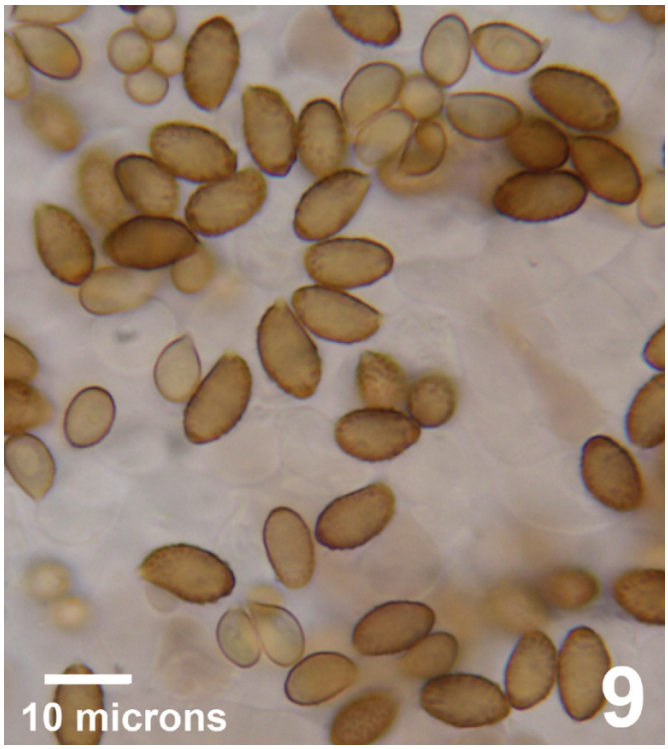
Habitat: In dry oak-hazel forest, hardwood, grass-herb forest of *Quercus*, *Ulmus*, *Carpinus*, *Tilia*, *Betula* and *Alnus glutinosa* and beech woods.

Specimens examined: Finland. Varsinais-Suomi, Turku, Commune, Ilkka Kytövuori 851517, 6/10/1985 (H). Sweden. Västergötland, V Tunhem sn, Prästgården, *Cortinarius* Projektet Fb nr. 0044, Blidnr. 379, 23/9/1985 (S), designated Epitype.

Additional specimens examined: Sweden. Småland, *Dullaberget*, *Femsjö*, *JFA12471 (WTU)*, *9/13/1998*; Blekinge, Förkärla parish, Tromtö, Museo Botanico Upsaliense Distributi, Seth Lundell 2697, 30/9/1946 (MICH).

Observations: The name *Cortinarius cinnabarinus* was used for *C. hesleri* in eastern North America for decades (McIlvaine and Macadam 1902; Kauffman 1918). Based on the present study of morphological and molecular data, the former species does not occur in eastern North America; instead *C. hesleri* (see below),

Fig. 9. *Cortinarius coccineus* basidiospores mounted in 3% KOH.



which is very similar in appearance to *C. cinnabarinus*, is the hardwood and mixed woods associated species found throughout this region.

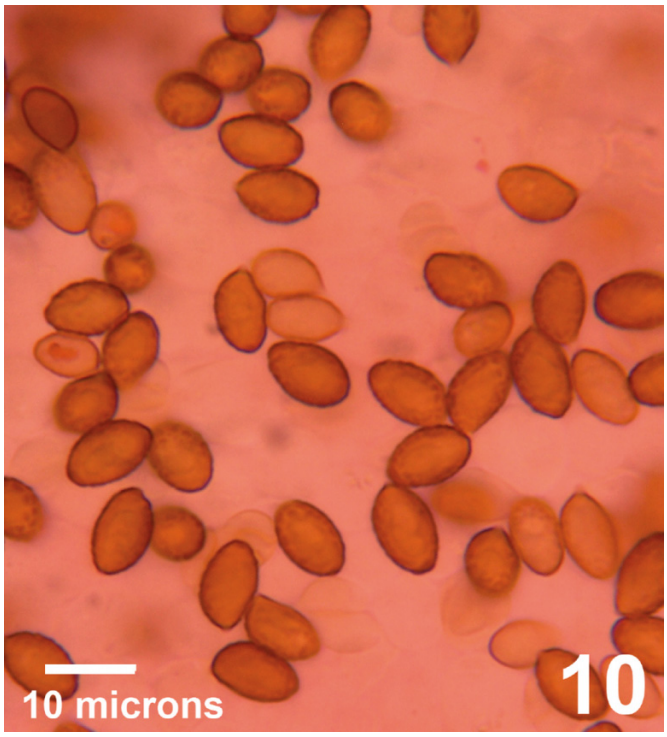
In Europe *C. cinnabarinus* is widespread but not common, occurring from northern Europe into the Mediterranean (Brandrud et al. 1994; Consiglio et al. 2003). *Cortinarius coccineus,* described from oak forests in France (see below), is similar in appearance to *C. cinnabarinus.* The two species are sympatric at a broad geographical scale, however, little has been reported on the ecology of *C. coccineus*. For a color illustration of *C. cinnabarinus* see Brandrud et al. 1994. Because this is a commonly used name but with no type collection we designated an epitype to stabilize the application of the name and allow for the addition of molecular data to define the species.

Cortinarius coccineus Reumaux, in Bidaud, Moënne-Loccoz, Reumaux & Henry, *Atlas des Cortinaires* (Meyzieu) **6**: 189 (1994)
Fig. 9.

Pileus 10–30 mm diam, obtusely convex to plano-convex, sometimes slightly umbonate, margin easily split, strongly enrolled at first, relatively smooth, not hygrophanous, vivid red as in *Hygrocybe coccinea*. Lamellae subconcolorous with pileus surface, becoming somewhat orange, somewhat close, adnate. Stipe fusoid, hollow, base acutely attenuated, strongly orange red, above somewhat lighter colored in places, veil fire red, base becoming blackish when handled. Context concolorous with pileus, strongly orange in stipe medulla. NaOH black on the pileus surface and context. Dried specimens fuschia purple with KOH. Odor faint or lacking.

Exsiccatae: Specimens are very small; stipe surface reddish brown to vinaceous, some with orange tones at apex and midstipe, basal area with some orange buff mycelium; lamellae dull reddish to dark brown or blackish, edges sometimes orange; pileus surface reddish brown to vinaceous brown, some areas blackish, in places orange.

Fig. 10. *Cortinarius hesleri* basidiospores mounted in 3% KOH.



Basidiospores 7.3–8.5 μm × 4.6–5.8 μm, moderately to coarsely ornamented, more or less ovoid, ellipsoid, broadly ellipsoid or subamygdaloid to amygdaloid, dextrinoid reaction variable, slightly to moderately or strongly dextrinoid (in general mature basidiospores give the strongest reaction with Melzer's reagent). Pileipellis duplex, epicutis hyphae cylindrical, 6–12 μm wide, containing rose red vacuolar pigment, hypocutis subcellular, hyphae cylindrical to enlarged, 15–25 μm wide, containing red vacuolar pigment.

Habitat: Under Quercus, calcareous soils.

Specimens examined: France. Forêt de Sénart (Ill-de-France), coll. M. Pelerin, 3568, 04.10.1993, herbarium number 435745 (holotype) (GK).

Additional specimens examined: None.

Observations: Based on the type description *Cortinarius coccineus* is a relatively small species as compared to *C. cinnabarinus.* It is a vivid red species similar in appearance to *Hygrocybe coccinea*, with a fusoid-tapered stipe and somewhat smaller basidiospores than *C. cinnabarinus*. There are no specimens except for the type collection (pers. comm., 4 May 2012, Pierre-Arthur Moreau "I have asked André Bidaud and Patrick Reumaux about it. They both only know the species by its type collection".)This species is in need of a thorough description of fresh specimens as well as further ecological notes. For a color illustration of *C. coccineus* see Bidaud et al. 1994.

Cortinarius hesleri Ammirati, Niskanen, Liimat. & Matheny, sp. nov.
Figs. 4, 5, 6, 10.

Etymology: Named for Dr. L. R. Hesler, noted mycologist, former Professor, and Chairman of the Botany Department and Dean of the School of Liberal Arts, University of Tennessee, Knoxville.

MycoBank Number: MB800437

Pileus 30–90 mm, conicus vel plano-convexus, plus minusve hygrophanus, brunneolus cinnabarinus vel brunneolus aurantiacus. Lamellae confertae,

brunneolae cinnabarinae vel rubroauranticae. Stipes 20–100 mm, apice stipitis 5–12(15) mm, cinnabarinus, rubroaurantiacus vel pallide aurantiacus. Sporae (7.5–) 8–10.2 (–11) × 4.8–6.0 (–6.6) μm, ellipsoideae vel amygdaloidae, grosse verrucosae. In silvis cum Quercus. Holotypus AHS 81565 (MICH), 8/19/1972, *prope* Gorman Lake, Washtenaw County, Michigan, USA.

Pileus 30–90 mm diam, conic becoming conic-campanulate then convex to plano-convex to plane, margin inrolled when young then decurved, becoming almost straight, surface innately fibrillose to glabrous, streaked at times, not scaly, not striate, moist when fresh, hygrophanous to subhygrophanous, color brownish red (Brazil Red), cinnabar red, brownish red (Brunt Sienna), brownish orange (Mars Orange) or reddish orange to brownish orange (Orange Rufous to Xanthine Orange) or more orange to orange buff, usually paler on the margin. Lamellae adnexed to adnate or decurrent by a tooth, close, broad to moderately broad, color brownish red (Brazil Red), cinnabar red, brownish orange to reddish orange (Mars Orange to Orange Rufous), usually becoming brownish orange in age, edges uneven. Stipe 20–100 mm long, 5–12 (–15) mm thick, more or less equal or slightly enlarged downward, terete to slightly flattened, coated with cinnabar red to reddish orange or brownish orange (Orange Rufous) to orange fibrils below, beneath the fibrils usually paler colored, in some places brownish to orange buff, upper portion pale, otherwise tinted with pileus colors or light orange (more or less Orange Buff), base watery, darkening on handling, often reddish brown or brownish red (Brazil Red). Context in pileus thin, more or less concolorous with the surface, in stipe stuffed to hollow, more or less concolorous with surface, often darker, brownish red (Brazil Red) in base. Odor raphanoid to slightly fragrant or indistinctive; taste raphanoid, slightly bitter (then fading) or indistinctive.

Exsiccatae: Surface of stipe shiny brown with some vinaceous and orange tones, basal mycelium orange to light orange buff; lamellae rusty brown with some orange tones, and in places orange, for example, near pileus edge; pileus surface rich dull light orange to orange buff with some brownish tones, some areas darker vinaceous brown.

Microscopic description: Basidiospores (7.5–) 8–10.2 (–11) × 4.8–6.0 (–6.6) μm, amygdaloid or somewhat ellipsoid, (sometimes short and broad), coarsely ornamented, moderately dextrinoid. Pileipellis duplex, epicutis of radially arranged, somewhat interwoven, cylindrical hyphae, 5–10 μm wide, colorless to pinkish, some containing pale reddish pigment or reddish purple granules, not encrusted, hypocutis of radially arranged, interwoven, cylindrical to enlarged hyphae, 10–25 μm wide, colorless to pinkish, some containing pale reddish pigment or reddish purple granules, not encrusted; sections of pileus purple in 3% KOH.

Habit and habitat: Gregarious to subcaespitose; in mixed woods, *Quercus* with *Pinus* and *Quercus* and *Carya*.

Specimens examined: USA: Michigan. Oakland County: Proud Lake, MSG883 (MICH), 30/7/1970. Washtenaw County: Gorman Lake, AHS81565 (Holotype) (MICH), 8/19/1972. North Carolina. Swain County: Indian Creek Trail, CLO4589 (TENN061793), 07/19/2006. Tennessee. Blount County: Cades Cove, JFA13069 (TENN), 9/9/2004. Sevier County: Greenbrier Field Station, Pittman Center, SAT–11–177–02, (TENN066242), 06/26/2011. Virginia. Montgomery County: between Radford and Christianburg, GB604 (WTU), o7/6/ 1983.

Additional specimens examined: USA: Illinois. Clark County: Lincoln Trail State Park, MK06140203 (MK), 6/14/2002. Coles County: Fox Ridge State Park, MK07110401 (MK), 7/11/2004, MK05300702 (MK), 5/30/2007, MK06300710 (MK), 6/30/2007, MK07110803 (MK), 7/11/2008. Michigan. Livingston County: Highland Lake, AHS86257 (MICH), 9/7/1975. Washtenaw County: Lake Winnawana, AHS86041 (MICH), 31–8–1975; Waterloo Recreation Area, FH2427 (MICH), 31/8/1972. North Carolina. Great Smokey Mountain National Park. Indian Creek, LRH12257 (TENN), 7/30, 1939; Deep Creek, LRH35202, 8/7/1969. Tennessee. Anderson County: Norris, LRH25697 (TENN), 7/26/1963. Blount County: Cades Cove, LRH23767 (TENN), 6/28/1960. Claiborne County: near Arthur LRH24799 (TENN), 6/10, 1962. Great Smokey Mountain National Park. Clingman's Dome, LRH23398 (TENN), 9/13/1959; Indian Gap, LRH18020 (TENN), 8/30/1947.

Observations: *Cortinarius hesleri* was identified as *C. cinnabarinus* in the early part of the 20th Century, and was not recognized as a separate species until the early to mid-1980s (Keller and Ammirati 1983; Ammirati and Smith 1984). Its habit of growth, and association with *Quercus* and other hardwoods, together with its stature and coloration, make it remarkably similar to *C. cinnabarinus*. The basidiospores tend to be consistently larger in *C. hesleri* than in the latter species but are similar in shape and ornamentation. Molecular studies clearly show that *C. hesleri* is a distinct species, more closely related to *C. californicus* than to *C. cinnabarinus. Cortinarius hesleri* occurs across most of eastern North America in hardwood or mixed forests from May to September. It is known from Florida west to Texas and north to New York and Michigan (Ammirati 1972) but likely is widespread in the eastern and southern portion of North America. *Cortinarius praecox* was used as a herbarium name prior to the adoption of the name *C. hesleri*.

Conclusions

The genetic relationships and biogeographical patterns of the species treated here add significant information to our understanding of speciation in the genus *Cortinarius*. The relationship between *C. hesleri* and the *C. californicus* complex suggests an early separation between these two species in North America, likely owing to mountain building events in the western part of North America (Mix et al. 2011); the former species residing with *Quercus* in mixed forest of eastern North America and the latter associated with mixed forest with conifers in western North America. The *C. californicus* complex requires further study to determine relationships among populations in the Pacific Northwest and those in northern California. Collections of a similar appearing species from Costa Rica suggests an even more complex pattern of speciation and biogeography, as seen in the *C. arcuatorum* complex (Garnica et al. 2011). *Cortinarius cinnabarinus* is widespread in Europe in hardwood forests, whereas its close relative *C. coccineus*, a hardwood associated species known only from the type locality, has an unknown distribution pattern in Europe.

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