



# *Cortinarius* subgenus *Leprocybe*, unexpected diversity and significant differences in species compositions between western and eastern North America

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## Key words

Agaricales  
barcodes  
*Cortinariaceae*  
ectomycorrhiza  
Europe  
ITS  
North America

**Abstract** The focus of this paper is the North American species of *Cortinarius* in subg. *Leprocybe*. Eighteen species, including twelve new ones, and two tentative (aff.) species, are delimited based on morphological and molecular data (DNA ITS-LSU sequences). Existing type specimens of species in subg. *Leprocybe* were also studied, and neo- or epitypes designated for *C. cotoneus*, *C. melanotus*, *C. phrygianus* and *C. venetus* to stabilize the nomenclature. In addition, to improve the infrasubgeneric classification of *Leprocybe* three new sections are proposed: sect. *Fuscotomentosi*, sect. *Melanoti* and sect. *Squamiveneti*. This study adds substantial information to the knowledge of subg. *Leprocybe* in North America against a background of European species. To date only two species, *C. phrygianus* and *C. squamivenetus* have been reported from both continents.

**Citation:** Ammirati J, Liimatainen K, Bojantchev D, et al. 2021. *Cortinarius* subgenus *Leprocybe*, unexpected diversity and significant differences in species compositions between western and eastern North America. *Persoonia* 46: 216–239. <https://doi.org/10.3767/persoonia.2021.46.08>. Effectively published online: 27 May 2021 [Received: 6 May 2020; Accepted: 1 December 2020].

## INTRODUCTION

*Cortinarius* is an extremely large and taxonomically complex genus that traditionally has been subdivided into subgenera primarily on the basis of morphological characteristics. These included the subgenera *Cortinarius*, *Telamonia*, *Myxadium*, *Phlegmacium* and *Leprocybe* with *Dermocybe* treated as either a genus or subgenus (Høiland 1983, Moser 1983). With the introduction of molecular data these subgenera have been shown to be more or less artificial and polyphyletic (Peintner et al. 2004, Garnica et al. 2005, 2016, Høiland 2008, Niskanen 2008, Liimatainen et al. 2014, Stensrud et al. 2014). Recently, some new subgenera have been suggested based on phylogenetic evidence, including *Callistei*, *Camphorati*, *Illumini* and *Orellani* (Gasparini 2004), but these taxa are not adopted by all researchers (Soop et al. 2019).

Subgenus *Leprocybe* (Moser 1969, 1970) is based on the type species *Cortinarius cotoneus*. It and closely related species contain leprocybin and have UV yellow fluorescent basidiomata (Gill & Steglich 1987). Brandrud et al. (1998) classified *C. cotoneus* and relatives in subg. *Cortinarius* sect. *Leprocybe*, while Niskanen et al. (2008) placed these taxa in subg. *Cortinarius* sect.

*Veneti*. The four loci phylogenetic analysis by Soop et al. (2019) showed that *C. cotoneus* and all its relatives in the Northern Hemisphere, e.g., *C. venetus*, form a monophyletic group with high support and treated the entity as sect. *Leprocybe*. In the same analysis two other leprocyboid groups, sect. *Veronicae* and sect. *Persplendidi*, from the Southern Hemisphere were found as sister clades to sect. *Leprocybe*, but only the relationship with sect. *Veronicae* was well supported.

Historically only a few species of *Leprocybe* were published from North America, *Cortinarius clandestinus*, *C. flavifolius*, *C. lutescens* and *C. rubroclavus*. Additional species, for example, *C. annulatus* and *C. croceicolour* (both = *C. tofaceus*) and *C. luteus* (= *C. limonius*), were considered related to the above species based on the stature, morphology and/or colouration (Kauffman 1932). In addition, some European names were applied to North American species, for example, *C. melanotus*, *C. venetus* var. *montanus* and *C. cotoneus*, but in most cases incorrectly so. Previous to this study there has been no concerted effort to report on subg. *Leprocybe* in North America. Ammirati et al. (2012) described *Cortinarius parkeri* from western North America and *C. aureopigmentatus* from Central America (Ammirati et al. 2007).

The results of this study show considerable diversity in subg. *Leprocybe* across North America. We report 18 species, including 12 new ones and two tentative (aff.) species. Only two European species have been reported from North America, *C. phrygianus* and *C. squamivenetus*. To recognize the diversity in subg. *Leprocybe* we propose three new sections based on morphological, ecological and molecular data, in addition to the two existing sections *Leprocybe* and *Veneti*. Four of the sections, *Fuscotomentosi*, *Leprocybe*, *Squamiveneti* and *Veneti* include species from both North America and Europe, while

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**Table 1** Specimens included in the molecular study. The sequences generated in this study are marked in **bold**.

Species	Voucher	Herb.	Locality	GenBank accession number
<i>C. apius</i> (holotype)	3460	CMMF	Canada, QC	<b>MW009182</b>
<i>C. atkinsiae</i> (holotype)	RMA7, 071879	TENN	USA, TN	MG663233
<i>C. atosquamosus</i> (holotype)	TN12-278, 7068349	H	USA, CA	<b>MW009183</b>
	SDA357	WTU	USA, WA	<b>MW009184</b>
	SDA421	WTU	USA, WA	<b>MW009185</b>
	JFA10385	WTU	USA, WA	<b>MW009186</b>
	JFA10040	WTU	USA, WA	<b>MW009236</b>
<i>C. borealis</i> (holotype)	5412	PC	France	<b>MW009187</b>
<i>C. brunneofibrillosus</i> (holotype)	JFA13654, 073591	WTU	USA, WA	<b>MW009188</b>
	DBB28271	WTU	USA, CA	<b>MT853253</b>
	06MWB111910	WTU	USA, CA	<b>MW009189</b>
	06MWB112013	WTU	USA, WA	<b>MW009190</b>
	JFA13664	WTU	USA, WA	<b>MW009191</b>
	11MWB111813	WTU	USA, WA	<b>MW009192</b>
	13MWB111813	WTU	USA, WA	<b>MW009193</b>
	15MWB111813	WTU	USA, WA	<b>MW009194</b>
	09MWB111610	WTU	USA, WA	<b>MW009195</b>
	01MWB110310	WTU	USA, WA	<b>MW009196</b>
	02MWB111308	WTU	USA, WA	<b>MW009197</b>
	05MWB111910	WTU	USA, WA	<b>MW009198</b>
<i>C. cepistipes</i> (holotype)	452176	G	France	<b>MW009199</b>
<i>C. clandestinus</i> (holotype)	19-10-1915	MICH	USA, WA	<b>MW009200</b>
	JFA10285	WTU	USA, WA	<b>MW009201</b>
	JFA8986	WTU	USA, WA	<b>MW009202</b>
	JFA13263	WTU	USA, WA	<b>MW009203</b>
	TN11-454	H	USA, WA	<b>MW009204</b>
	JMB42	WTU	USA, WA	<b>MW009205</b>
	1995-165a	IB	USA, WA	<b>MW009206</b>
	DBB21905	WTU	Canada, BC	<b>MT853251</b>
	SDA396	WTU	USA, WA	<b>MW009207</b>
	BD326	MIN	USA, MN	<b>MW009209</b>
	HRL0186	WTU	Canada, QC	<b>MW009210</b>
<i>C. clandestinus</i> (non-fibrillose scaly form)	BD325	MIN	USA, MN	<b>MW009208</b>
	CLC2233	MONT	USA, MT	<b>MW009211</b>
	DBB15293	WTU	USA, CA	<b>MT853248</b>
	DBB15563	WTU	USA, CA	<b>MT853249</b>
	JFA9011	WTU	USA, CO	<b>MW009212</b>
	JFA9286	WTU	USA, ID	<b>MW009213</b>
	ADP090515-1	WTU	USA, WA	<b>MW009214</b>
	19970069	IB	USA, WY	<b>MW009215</b>
<i>C. cotoneus</i> (neotype)	CFP1032, F44846	S	Sweden	<b>MW009216</b>
<i>C. aff. cotoneus</i>	DBB50175	WTU	USA, CA	<b>MT853255</b>
<i>C. flavifolius</i> (epitype)	EH 230, 068695	TENN	USA, TN	<b>MW009217</b>
	TN14-227	H	USA, FL	<b>MW009218</b>
	RH72	ISC	USA, IA	<b>MW009219</b>
	3226	CMMF	Canada, QC	<b>MW009220</b>
<i>C. fuscoflavidus</i> (holotype)	JFA11644, 41324	WTU	USA, OR	<b>MW009221</b>
	TN09-158	H	USA, WA	<b>MW009222</b>
	DBB41055	WTU	USA, CA	<b>MW009223</b>
<i>C. fuscotomentosus</i> (holotype)	DBB00566, 073590	WTU	USA, CA	<b>MT853246</b>
	DBB26988	UC	USA, CA	<b>MT853252</b>
	DBB13228	UC	USA, CA	<b>MT853247</b>
	DBB40695	UC	USA, CA	<b>MT853254</b>
<i>C. hughesiae</i> (holotype)	JFA13086, 75725	TENN	USA	<b>MW009224</b>
	EH235, F-068689	TENN	USA, TN	<b>MW009225</b>
	TLB11, F-074722	TENN	USA, TN	MF686506
<i>C. leproleptopus</i> (holotype)	84, 109	PC	France	<b>MW009226</b>
<i>C. loringii</i> (holotype)	SCL6030, 67669	WTU	USA, OR	<b>MW009227</b>
<i>C. lutescens</i> (holotype)	NYSf1781	NYS	USA, NY	<b>MW009228</b>
	TN07-232, 7000893	H	Canada, NL	<b>MW009229</b>
<i>C. melanotus</i> (epitype)	CFP1101, F44883	S	France	<b>MW009230</b>
<i>C. olivaceosquamosus</i> (holotype)	TN10-105, 7068353	H	Canada, NL	<b>MW009231</b>
	TN11-118	H	USA, AK	<b>MW009232</b>
	3539	CMMF	Canada, QC	<b>MW009233</b>
<i>C. phrygianus</i> (neotype)	CFP774, F44888	S	Sweden	<b>MW009234</b>
	YL4300	CMMF	Canada, QC	<b>MW009235</b>
<i>C. pseudovenetus</i> (holotype)	RH3412	PC	France	<b>MW009237</b>
<i>C. rubroclavus</i> (holotype)	256	MICH	USA, IA	<b>MW009238</b>
<i>C. squamivenetoideus</i> (holotype)	TN11-005, 7068355	H	USA, AK	<b>MW009239</b>
<i>C. squamivenetus</i>	4032	CMMF	Canada, QC	MQCOR862
<i>C. cf. squamivenetus</i>	4072	CMMF	Canada, QC	MQCOR864
<i>C. subcotoneus</i> (holotype)	2143	PC	France	<b>MW009240</b>
<i>C. subleproleptopus</i> (holotype)	TN12-344, 7068356	H	USA, CA	<b>MW009241</b>
	DBBNS3	WTU	USA, CA	<b>MT853256</b>
<i>C. submelanotus</i> (holotype)	5454	PC	France	<b>MW009242</b>
<i>C. veneto-occidentalis</i> (holotype)	TN11-051, 7068357	H	USA, AK	<b>MW009243</b>
	TN11-106	H	USA, AK	<b>MW009244</b>
	TN11-258	H	USA, AK	<b>MW009245</b>
	TN11-053	H	USA, AK	<b>MW009246</b>
	TN11-262	H	Canada, AB	<b>MW009247</b>
	TN11-281	H	Canada, AB	<b>MW009248</b>
<i>C. aff. veneto-occidentalis</i>	JFA10341	WTU	USA, WY	<b>MW009249</b>
<i>C. venetus</i> (neotype)	CFP112, F44498	S	Sweden	<b>MW009250</b>
	CFP523	S	Sweden	<b>MW009251</b>
<i>C. venetus</i> var. <i>viridis</i> (holotype)	245	PC	France	<b>MW009252</b>
<i>C. xantholamellatus</i> (holotype)	5410	PC	France	<b>MW009253</b>
<i>C. zonatus</i> (holotype)	2005-20	PC	France	<b>MW009254</b>

*Melanoti* so far only from Europe. Existing type specimens of subg. *Leproclybe* were studied, and neo- or epitypes designated for early European names to stabilize the nomenclature. A morphogenetic update on the nine *Leproclybe* species restricted to Europe: *C. cotoneus*, *C. jimenezianus*, *C. leproleptopus*, *C. melanotus*, *C. pescolanensis*, *C. selinolensis*, *C. subcotoneus*, *C. venetus* and *C. viridans* is proposed in the companion paper (Bidaud et al. 2021).

## MATERIALS AND METHODS

### Morphological

Macroscopic descriptions are from notes and photographs of fresh basidiomata. Exsiccatae colour was recorded using a full spectrum (Ott–lite) lamp. UV fluorescence of fresh basidiomata and exsiccatae was recorded with a 366 nm UV lamp. Microscopic characteristics are from air-dried specimens (exsiccatae) revived in 3 % KOH. Dextrinoid basidiospore reactions were made from small pieces of lamellae placed in Melzer's reagent. Basidiospore measurements are preferentially from spores deposited in stipe apex, veil or pileus surface, and in cases when not available, from lamellae.

### Molecular

GenBank numbers are given for sequences of the nuc rDNA internal transcriber spacer (ITS1-5.8S-ITS2 = ITS) from 81 specimens, including 30 type specimens, produced in this study (Table 1). DNA was extracted from dried material (pieces of lamellae) with the NucleoSpin Plant kit (Macherey-Nagel, Düren, Germany). For some specimens Phire Plant Direct PCR kit (ThermoFisher Scientific, MA, USA) was used for DNA extraction and PCR was done according to manufacturer's protocol. Primers ITS 1F and ITS 4 (White et al. 1990, Gardes & Bruns 1993) were used to amplify ITS regions and the same primer pairs were used in direct sequencing. Polymerase chain reaction amplification and sequencing followed Liimatainen et al. (2014).

### Data analyses

Sequences were assembled and edited with Sequencher 4.1 (Gene Codes, Ann Arbor, Mich., USA). For phylogenetic analysis, ours as well as published ITS sequences of *Cortinarius* subg. *Leproclybe* were included. In addition, all the published LSU sequences from *Leproclybe* were added. *Leproclybe* was shown to be monophyletic with a bootstrap support value of 100 % in Soop et al. (2019). Subgenus *Cortinarius* was chosen as out-group. The ITS and LSU alignment of 95 sequences was produced with the program MAFFT v. 7.0 (Katoh & Standley 2013) under default settings. The phylogenetically informative indels in the ITS region were coded as characters using FastGap v. 1.2 program (Borchsenius 2009). The alignment including ITS, LSU and the binary data was manually adjusted in SeaView (Galtier et al. 1996). The alignment is composed of 1724 nucleotides (ITS 672, LSU 987, and binary 65) and is available at TreeBASE under 26834 (<http://www.treebase.org/treebase-web/home.html>). A phylogenetic tree was generated using maximum likelihood (ML) analyses with 1000 bootstrap replicates under the GTRGAMMA model for nucleotide partitions (ITS+LSU) and the default setting for binary (indel) data in RAxML 8 (Stamatakis 2014).

Genetic differences within and between species were calculated for paired sequences by dividing the number of indels and/or substitutions found in the ITS1+5.8S+ITS2 regions by the length of the shortest sequence in the pair.

## RESULTS

### Molecular data

The phylogenetic tree resulting from our analysis is shown in Fig. 1. Within *Leproclybe* four clades received BS > 90 % support; /Fuscotomentosi (BS 93 %), /Leproclybe (BS 100 %), /Squamiveneti (BS 100 %) and /Veneti (BS 96 %) and they are recognized as sections below. In addition, /Melanoti that is shown to include *C. jimenezianus*, *C. melanotus* and *C. viridans* and is well-supported in the phylogenetic analysis by Bidaud et al. (2021) is also described as a new section. The sections are delimited based on being the largest monophyletic unit in the phylogenetic tree that is supported by morphological characters and morphological differences from the adjacent group(s). The remaining monotypic groups are currently treated under 'Incertae sedis'.

When comparing the morphological and ITS diversity of the entire Northern Hemispheric *Leproclybe* lineage to the recent studies of other sections of *Cortinarius* (e.g., sect. *Arguti*, Cripps et al. 2015; sect. *Armillati*, Niskanen et al. 2011; sect. *Bicoloures*, Liimatainen et al. 2017; sect. *Disjungendi*, Liimatainen et al. 2015; sect. *Sanguinei*, Niskanen et al. 2013; sect. *Riederi*, Brandrud et al. 2018) it is obvious that the Northern Hemispheric *Leproclybe* is more diverse than any of the sections that have gone through a molecular revision. Therefore, we divide the Northern Hemispheric *Leproclybe* into several sections in contrast to Soop et al. (2019) that considered it as one section. We believe that it is also practical to recognize groups within the Northern Hemispheric lineage to facilitate communication now that more species are known and more will very likely to be found when, e.g., data from Asia is added.

Based on the analysis and morphological data the Northern Hemispheric *Leproclybe* includes 28 species and two undescribed ones, *C. aff. veneto-occidentalis* and *C. aff. cotoneus* which require further study. In addition, morphologically and phenotypically distinct collections within *C. clandestinus* were designated as a non-fibrillose scaly form but not assigned an official taxonomic rank pending further study.

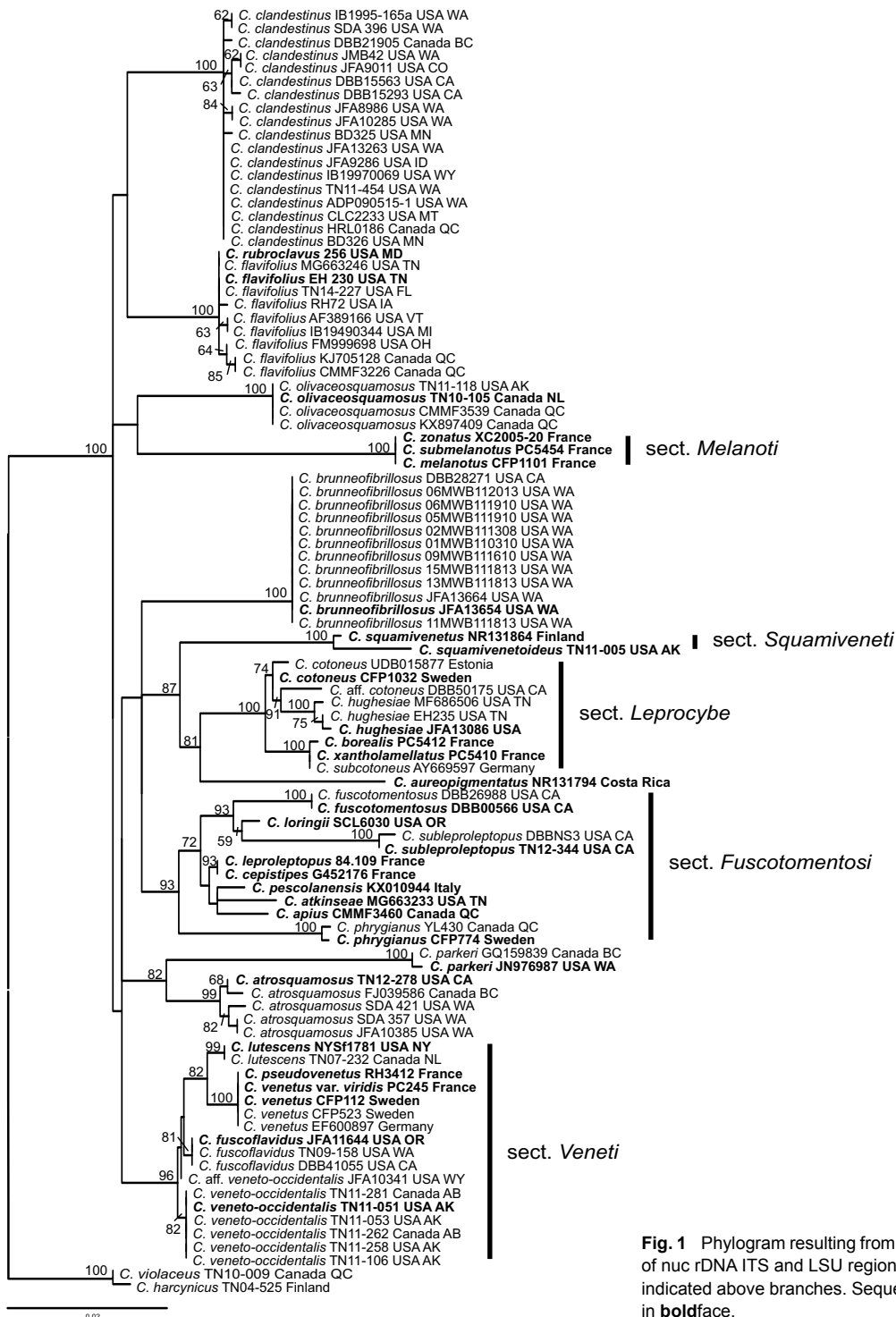
All species recognized in this study formed a monophyletic clade. Most of them with greater than 90 % bootstrap support (BS) value, exceptions are *C. cotoneus* and the *C. veneto-occidentalis* complex. The intraspecific variation in the ITS region is < 0.5 %, with the exception of *C. clandestinus*, with 1 %, *C. atosquamosus* with 0.7 %, and *C. hughesiae* with 0.5 % variation, and also a greater morphological variation within species. Only four species pairs have interspecific variation of < 1.5 %; *C. apius* and *C. leproleptopus* (1.3 %), *C. cotoneus* and *C. hughesiae* (0.8 %), *C. lutescens* and *C. venetus* (1.0 %) and *C. veneto-occidentalis* and *C. fuscoflavidus* (0.5 %). Therefore, some of these groups are not well resolved in our phylogenetic analyses and also are morphologically somewhat difficult to distinguish from one another. Nine species are known only from Europe and 16 only from North America. So far only two species, *C. phrygianus* and *C. squamivenetus*, are known from both North America and Europe. Additionally, one species, *C. aureopigmentatus* is known only from Costa Rica.

### Taxonomy and nomenclature

***Cortinarius* subg. *Leproclybe*** M.M. Moser, Z. Pilzk. 35: 223. 1969, p.p., the Northern Hemispheric lineage

*Type species. Cortinarius cotoneus* Fr.

Description — *Basidiomata* with yellow, yellow green, yellow brown, brown, olive brown or blackish brown to blackish olive colours, often discolouring orange or reddish brown in age;



**Fig. 1** Phylogram resulting from the maximum likelihood (RAxML) analysis of nuc rDNA ITS and LSU regions. Bootstrap values greater than 50 % are indicated above branches. Sequences originating from type specimens are in boldface.

*pileus* surface innately fibrillose, fibrillose, fibrillose tomentose or fibrillose scaly to squamulose; *basidiospores* subglobose to broadly ellipsoid or ellipsoid, distinctly verrucose; *contextual hyphae* commonly with yellow refractive particles; *clamp connections* present. UV. Basidiomata in some part bright yellow and containing leprocybin.

**Habitat & Distribution** — In conifer, mixed conifer-broadleaf and broadleaf forests, occurring on acidic or basic soils. Forming ectomycorrhizas with members of the *Pinaceae*, *Betulaceae*, *Fagaceae*, sometimes in forests with members of the *Salicaceae* and *Ericaceae*. Producing basidiomata in the spring, summer, autumn and/or winter seasons depending on elevation, latitude, geographical location and climate.

Currently including — sect. *Fuscotomentosi*, sect. *Leprocybe*, sect. *Melanoti*, sect. *Squamiveneti*, sect. *Veneti*.

**Notes** — The limits of subg. *Leprocybe* are not yet fully known and there is no consensus on the number or the limits of the subgenera in *Cortinarius* based on molecular data. The description above only includes the Northern Hemispheric species that formed a well-supported monophyletic group in the four loci phylogenetic analysis by Soop et al. (2019). Their results, however, also suggested that the Southern Hemispheric sect. *Veronicae* could be included in the subgenus (BS 100 %) and perhaps also another Southern Hemispheric sect. *Persplendidi* (BS < 50 %) but the final delimitation of the subgenus is beyond the scope of our paper.



**Fig. 2** Basidiomata. a. *Cortinarius hughesiae* JFA13086 (holotype); b. *C. aff. cotoneus* DBB50175; c. *C. flavifolius* HRL0925 2; d. *C. olivaceosquamosus* YL CMMF003539; e. *C. parkeri* ADP090511-2; f. *C. apius* CMMF003460 (holotype); g. *C. atkinsiae* RMA7 (holotype); h. *C. fuscotomentosus* DBB26988. — Photos by: a. J. Ammirati; b, h. D. Bojantchev; c. R. Lebeuf; d, f. Y. Lamoureux; e. A.D. Parker; g. R.I. Sweney.

***Cortinarius* sect. *Leprocybe* M.M. Moser 1969**

Type. *Cortinarius cotoneus* Fr.

Description — Basidiomata medium- to large-sized. Pileus fibrillose, fibrillose-scaly or minutely squamulose, yellow, brownish to brownish olive, non-hygrophanous. Stipe clavate to bulbous. Veil olive to brown. Basidiospores  $L \times W_m > 7.7 \times 6.2 \mu\text{m}$ .

Habitat & Distribution — Known from Eastern North America and Europe, primarily in deciduous forests with *Corylus*, *Fagus*, *Quercus* and *Tilia* but also in mixed woods of *Quercus*, *Pinus* and *Tsuga*.

Currently including — *C. cotoneus*, *C. aff. cotoneus*, *C. hughesiae* and *C. subcotoneus*, and based on Bidaud et al. (2021) also *C. selinolens*.

Notes — This section is best characterized by the olive to brown universal veil, relatively large basidiomata and  $\pm$  large basidiospores. Other species with dark universal veils are *C. phrygianus* and *C. clandestinus* or in sect. *Melanoti*. Species in this clade have considerable yellowish, yellowish green or yellowish brown intercellular and intracellular pigment associated with the contextual hyphae. Below are two species related to *C. cotoneus*, *C. hughesiae* from eastern North America and *C. aff. cotoneus* from California. *Cortinarius cotoneus* and *C. hughesiae* have an interspecific variation of 0.8 %, and *C. hughesiae* has an intraspecific variation 0.5 %.

***Cortinarius cotoneus* Fr., Epicr. Syst. Mycol. (Upsaliae): 289. 1838 '1836–1838'**

Type. SWEDEN, Gotland, Vallstena sn, Alvena lindångar, broad-leaved deciduous forest, calcareous soil (*Corylus*, *Quercus*, *Tilia*), 1 Oct. 1990, coll. Brandrud et al., CFP1032, F44846 (S, neotypus *hic designatus*). MycoBank MBT 393873; ITS barcode GenBank MW009216.

***Cortinarius hughesiae* Ammirati, Matheny, Liimat. & Niskanen, sp. nov. — MycoBank MB 837381; Fig. 2a, 3e**

*Etymology.* Named for Professor Karen Hughes, plant and fungal geneticist, University of Tennessee.

*Typus.* USA, Great Smokey Mountain National Park, Cades Cove, Primitive Baptist Church, mixed woods, 13 Sept. 2004, coll. P.B. Matheny (holotype TENN 075725); ITS barcode GenBank MW009224.

Diagnosis — With *Quercus* and in mixed broadleaf-conifer forests; eastern North America; medium sized basidiomata, dominated by brown to yellow colours; basidiospores  $L \times W_m 8.2 \times 6.2 \mu\text{m}$ , significantly smaller than European *C. cotoneus*. Forming a clade with *C. cotoneus* and *C. aff. cotoneus*, and with 5 differences from *C. cotoneus* in the ITS region, a similarity of 99.2 %.

*Pileus* 40–50 mm diam, at first obtusely conic umbonate then obtusely convex, margin incurved to decurved, surface dry, margin  $\pm$  rimose, margin appressed fibrillose to finely fibrillose scaly, disc  $\pm$  tomentose or matted fibrillose, disc and margin pale chamois buff, grayish yellow, olive brown or medium brown, in age disc dark brown, margin becoming yellowish brown or brassy brown. *Lamellae* adnexed, dull yellow brown, in age dark rusty brown or dark brown, edges slightly paler,  $\pm$  uneven. *Stipe* to 65 mm long, 7–13 mm thick above, clavate, tapered at base, to 17 mm thick, straw yellow, pale yellowish, yellowish white, with some slight ochraceous to yellow tones,  $\pm$  covered with zones of brownish to brownish olive veil, basal mycelium dull whitish, buff white. *Context* of pileus solid, firm, dull whitish to pallid buff or grayish yellow, in stipe straw yellow, pale yellowish to yellowish white or watery yellowish olive brown, in base discoloured dark brown. *Odour* of context raphanoid to mild, *taste* raphanoid to acidic. *Exsiccatae.* Pileus dark brown to medium brown, lamellae rich brown to rust brown, stipe faintly yellowish, darker brown or grayish, base dull light yellowish

cream to brownish, context dull light cream colour or brownish in older stipe. *UV.* Fresh basidiomata pileus surface negative, lamellae, stipe and context rich, bright yellow or lamellae and flesh yellow, pileus and stipe brown; *exsiccatae* pileus context light dull yellow, lamellae  $\pm$  bright yellow, pileus surface negative, stipe negative or in places bright yellow.

*Basidiospores*  $7.4\text{--}8.5\text{--}(9.3) \times 6.3\text{--}7.0\text{--}(7.4) \mu\text{m}$ ,  $L \times W_m 8.2 \times 6.2$ ,  $Q 1.1\text{--}1.3$ ,  $Q_m 1.2$ , subglobose, very coarsely verrucose, moderately to slightly more dextrinoid. *Basidia* 4-spored,  $37\text{--}40 \times 8\text{--}9 \mu\text{m}$ , clavate, colourless or with yellow to yellow brown contents, walls sometimes darkly pigmented. *Pileipellis:* epicutis  $\pm$  well developed, hyphae  $\pm$  radially arranged, interwoven on margin, interwoven to entangled on disc, mostly  $4\text{--}22 \mu\text{m}$  wide,  $\pm$  cylindrical, broadly cylindrical or enlarged, colourless to yellowish brown or filled with yellow brown contents, walls  $\pm$  refractive,  $\pm$  thickened, yellowish to colourless, smooth or encrusted; hypocutis not well developed, hyphae interwoven, radially arranged,  $7\text{--}30 \mu\text{m}$  wide, cylindrical to broadly cylindrical or enlarged, yellowish to colourless, wall refractive, colourless to yellowish, smooth.

Habitat & Distribution — So far known only from North America, Great Smokey Mountain National Park, Tennessee, *Quercus* or mixed woods of *Quercus*, *Fagus*, *Pinus* and/or *Tsuga*.

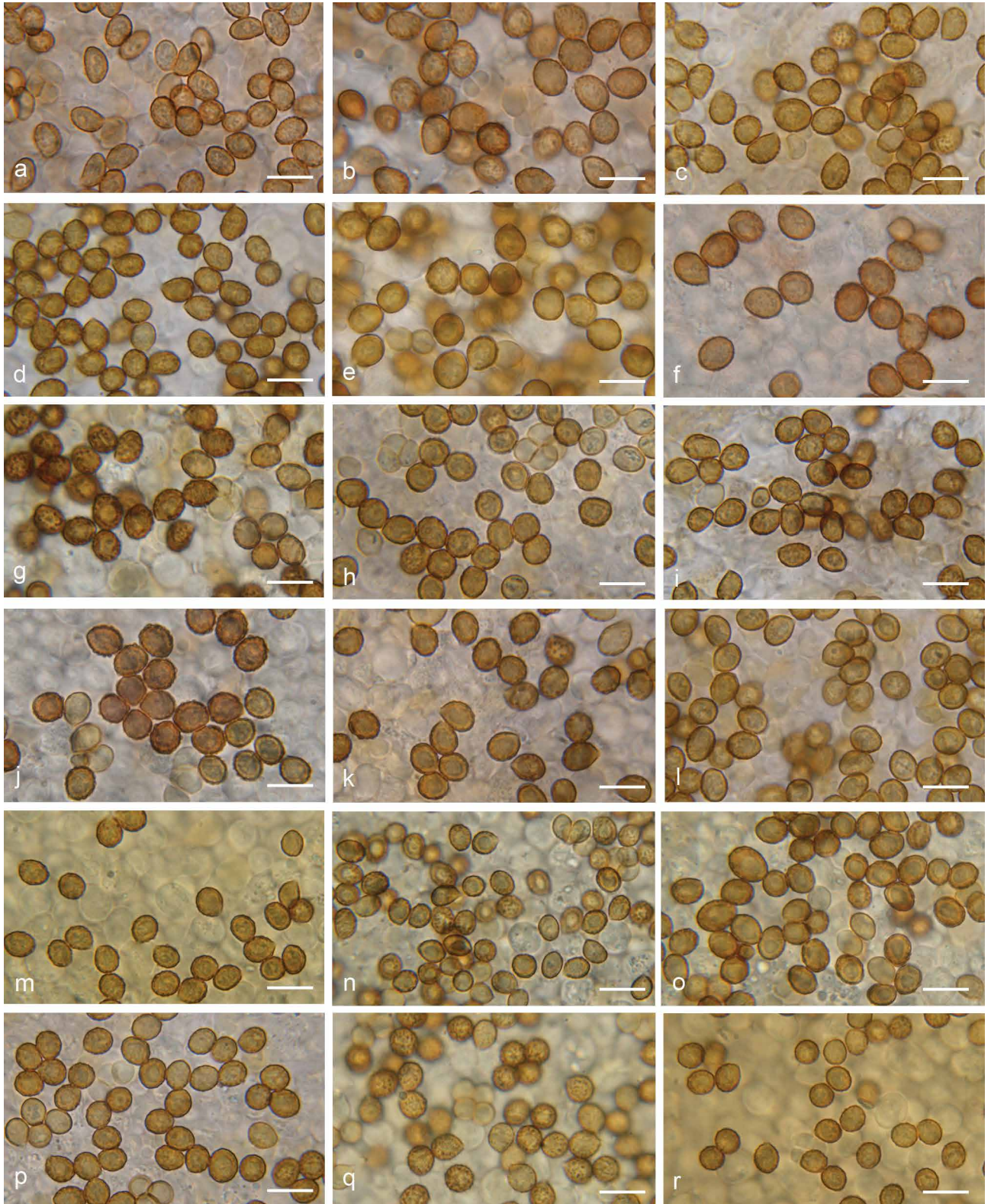
*Additional specimens examined.* USA, Tennessee, Sevier County, Pittman Center, mixed woods, 30 Aug. 2013, coll. E. Harrower EH235 (TENN-F-068689), GenBank MW009225; Union County, Big Ridge State Park, *Fagus*, *Pinus virginiana*, 12 Oct. 2015, coll. T.L. Bailey, TLB11 (TENN-F-074722), GenBank MF686506.

Notes — *Cortinarius hughesiae* occurs with *Quercus* or in mixed conifer-broadleaf forests that include *Quercus* and/or *Fagus*. It produces medium sized basidiomata, the pileus is appressed fibrillose, fibrillose scaly to tomentose and brown to yellow with some olivaceous tones, the lamellae are yellowish, and the stipe clavate and yellowish to yellowish white with brownish veil zones. The basidiospores are subglobose, very coarsely verrucose, and significantly smaller in size ( $L \times W_m 8.2 \times 6.2 \mu\text{m}$ ) than collections of *C. cotoneus* from Europe ( $L \times W_m 9.2 \times 7.7 \mu\text{m}$ ) and *C. aff. cotoneus* California ( $L \times W_m 8.6 \times 7.4 \mu\text{m}$ ). The basidia and hyphae of *exsiccatae* are distinctly yellow to yellow brown pigmented in KOH. Sequenced collections of *C. hughesiae* show 0.5 % intraspecific variation from samples within a small geographical region.

***Cortinarius aff. cotoneus* — Fig. 2b, 3f**

*Pileus* 60–100 mm diam, convex to plano-convex, margin involute, frequently upturned at age, moderately fibrillose to tomentose, more so towards the margin, olive-brown to yellow-brown. *Stipe* 60–110 mm long, 20–35 mm thick, cylindrical to subclavate, pale olivaceous yellow, veil olive to olive brown, partially covering the lower stipe, occasionally leaving a distinct girdle. *Lamellae* sinuate, moderately crowded, 6–12 mm broad, mustard yellow, turning rusty brown, edges even. *Context* pale olivaceous. *Odour* distinctly raphanoid. *Taste* not recorded. *Exsiccatae.* Pileus surface dark brown to reddish brown, lamellae olive brown, context dull cream to light brown, stipe surface gray brown to olivaceous brown, basal mycelium brownish cream. *UV.* Fresh basidiomata yellow; *exsiccatae* pileus surface negative, lamellae and context orange yellow to yellow, stipe light brown to  $\pm$  orange yellow or yellow.

*Basidiospores*  $(7.6\text{--})8.0\text{--}9.0\text{--}(9.3) \times (6.8\text{--})7.2\text{--}7.5\text{--}(7.8) \mu\text{m}$  ( $L \times W_m 8.6 \times 7.4 \mu\text{m}$ ),  $Q 1.1\text{--}1.25$ ,  $Q_m 1.17$ , subglobose to broadly ellipsoid, moderately to more coarsely verrucose, slightly to moderately dextrinoid. *Basidia* 4-spored, clavate,  $40\text{--}48 \times 8.9\text{--}9.6 \mu\text{m}$ , colourless or with yellowish granules. *Pileipellis:* epicutis hyphae  $\pm$  radially arranged to ascending, interwoven to



**Fig. 3** Basidiospores. a. *Cortinarius atosquamosus* TN12-278 (holotype); b. *C. bunneofibrillosus* 11mwb111813; c. *C. clandestinus* Kauffman (holotype); d. *C. clandestinus* (non-fibrillose scaly form) CLC2233; e. *C. hughesiae* JFA13086 (holotype); f. *C. aff. cotoneus* DBB50175; g. *C. flavifolius* EH230 (epitype); h. *C. olivaceosquamosus* CMMF003539 (holotype); i. *C. parkeri* ADP000502-1 (holotype); j. *C. apius* CMMF003460 (holotype); k. *C. atkinsiae* RMA7 (holotype); l. *C. fuscotomentosus* DBB00566 (holotype); m. *C. loringii* SCL6030 (holotype); n. *C. phrygianus* YL4300; o. *C. subleproleptopus* TN12-344 (holotype); p. *C. squamivenetoideus* TN11-005 (holotype); q. *C. veneto-occidentalis* TN11-051 (holotype); r. *C. fuscoflavidus* JFA11644 (holotype). — Photos by J. Ammirati. — Scale bar = 10  $\mu$ m.

entangled, hyphae (3.7–)6–15 µm wide, cylindrical, colourless to yellowish or brownish, wall refractive, ± thickened, colourless to yellowish, smooth to encrusted; hypocutis slightly developed, hyphae radially arranged, interwoven, cylindrical, broadly cylindrical or enlarged, 7.4–22 µm wide, yellowish to yellowish brown, walls ± refractive, colourless to yellowish, ± thickened, smooth to slightly encrusted.

**Habitat & Distribution** — Mixed conifer-broadleaf forest with *Quercus agrifolia*, *Pseudotsuga* and *Sequoia*, known only from coastal California.

**Specimen examined.** USA, California, San Mateo County, Huddart Park, *Quercus agrifolia*, *Sequoia*, *Pseudotsuga*, 1 Apr. 2012, coll. D. Bojantchev, DBB50175 (Pers. Herb., WTU), GenBank MT853255.

**Notes** — *Cortinarius* aff. *cotoneus* sequence data places it very close (a similarity of 99 %) to *C. cotoneus* from Europe and *C. hughesiae* from eastern North America. Basidiospore measurement are significantly larger (8–9 × 7.2–7.5 µm) than collections of *C. hughesiae* (7.4–8.5 × 6.3–7 µm) but are similar to those of European material (8–9.5 × 7–8 µm). The habitat, which includes *Quercus agrifolia*, is similar to that of other species in this group of taxa. The April collection date is of interest. Additional collections are needed to further evaluate the position of this collection. In general, *C. aff. cotoneus* fits the concept of *C. cotoneus* of Europe, except perhaps for its less distinctly clavate bulbous stipe base.

***Cortinarius* sect. *Fuscotomentosi*** Niskanen, Liimat. & Ammirati, sect. nov. — MycoBank MB 837382

**Etymology.** Named for the type species of the section.

**Type.** *Cortinarius fuscotomentosus* Bojantchev, Liimat. & Niskanen.

**Description** — Basidiomata medium- to large sized. Pileus fibrillose, fibrillose tomentose, fibrillose scaly to appressed squamulose, yellow, olive yellow, brownish yellow, olive brown to brown, not hygrophanous. Stipe cylindrical to clavate. Veil white, yellow, yellow olive, olive brown or blackish brown. Basidiospores  $L \times W_m \leq 7.6 \times 6 \mu\text{m}$ .

**Habitat & Distribution** — Known from Western and Eastern North America and Europe, in conifer and broadleaf forests.

Currently including — *C. apius*, *C. atkinsiae*, *C. fuscotomentosus*, *C. leproleptopus*, *C. loringii*, *C. pescolanensis*, *C. phrygianus* and *C. subleproleptopus*.

**Notes** — This is the most species-rich section of subg. *Leprocybe* showing diversification in both Eastern and Western North America and Europe. It includes species that are often associated with broadleaf forests. There is considerable morphological variation within the section, species tend to have a non-hygrophanous pileus. To distinguish these species from one another the most useful combination of characters is the colour of the universal veil, basidiospore size, and distribution and ecology. The overall colouration of the basidiomata and the structure of the pileus surface are also useful features for identification.

***Cortinarius apius*** Y. Lamoureux, Liimat. & Niskanen, sp. nov. — MycoBank MB 837383; Fig. 2f, 3j

**Etymology.** Named for the strong, distinct, fruity-herbaceous odour.

**Typus.** CANADA, Quebec, Sainte-Julienne (Chemin McGill), *Quercus rubra*, *Fagus grandifolia*, *Acer saccharum*, *Populus grandidentata*, *Ostrya virginiana*, 18 Aug. 2000, coll. Y. Lamoureux (holotype CMMF 003460), (isotype WTU); ITS barcode GenBank MW009182 generated from the isotype.

**Diagnosis** — Found in broadleaf forests; eastern North America; medium sized basidiomata, clavate to bulbous stipe; odour fruity herbaceous; basidiospores rather small,  $L \times W_m 7.6 \times 6 \mu\text{m}$ , ± subglobose to broadly ellipsoid; eight differences in ITS from *C. leproleptopus*, a similarity of 98.7 %.

**Pileus** 30–70 mm diam, globose to broadly convex, dark brown olive to yellow olive, remaining dark brown on disc, tomentose to appressed squamulose with fibrillose margin. **Lamellae** adnexed, rather narrow, close, at first yellow olive, soon yellow-saffron from the spores, edges lighter in colour, irregular. **Stipe** 50–70 mm long, 10–15 mm thick above, up to 25 mm thick at base, clavate, fibrillose, yellowish olive to pale yellowish, somewhat whitish in age, veil leaving a yellow olive annular zone on the stipe, basal mycelium yellow olive. **Context** of pileus fragile-brittle, thick in center, thinner towards margin, when young marbled with dark watery olive-brownish spots and olive-yellow streaks, becoming uniformly yellowish or whitish when dry, context of stipe similar in colour, solid then ± stuffed. **Odour** of lamellae fruity-herbaceous, similar to *Flammula alnicola*. **Taste** not recorded. **Exsiccatae.** Pileus rich brown, slightly reddish, context pale brown or slightly reddish, lamellae rich cinnamon brown, no stipe in packet. **UV.** Exsiccatae pileus surface reddish orange with slight brown in places, lamellae and context of basidiomata yellow, no stipe in packet.

**Basidiospores** 6.7–8 × 6–6.3 µm,  $L \times W_m 7.6 \times 6 \mu\text{m}$ , Q 1.1–1.4,  $Q_m 1.3$ , ± subglobose, coarsely verrucose, moderately dextrinoid. **Basidia** 4-spored, 30–33 × 8–9 µm, clavate, colourless or yellowish. **Pileipellis:** epicutis well developed, hyphae interwoven, radially arranged, with some ascending fascicles, 5–13 µm wide, ± cylindrical, reddish, pinkish, colourless or with yellowish contents, walls refractive, colourless to yellowish, ± thickened, smooth or slightly encrusted; hypocutis poorly developed, hyphae interwoven, radially arranged, 6–15 µm wide, cylindrical, colourless or pinkish, walls colourless, refractive, smooth.

**Habitat & Distribution** — Mixed broadleaf forests, *Quercus rubra*, mixed with *Fagus grandifolia*, and scattered *Acer saccharum*, *Populus grandidentata* and *Ostrya virginiana*. Known only from southern Quebec.

**Specimens examined.** None except holotype.

**Notes** — Well characterized by the olive yellow colouration, fibrillose to appressed squamulose pileus, an annulate veil zone on stipe, aromatic odour and association with broadleaf forests. See also comments under *C. atkinsiae*.

***Cortinarius atkinsiae*** Matheny, Ammirati, Liimat. & Niskanen, sp. nov. — MycoBank MB 837384; Fig. 2g, 3k

**Etymology.** Named for the collector R.M. Atkins, University of Tennessee.

**Typus.** USA, Tennessee, Campbell County, Norris Dam State Park, Andrews Ridge Trail, coll. R.M. Atkins, field photo, R.I. Swenie, 18 Sept. 2017 (holotype TENN 071879); ITS barcode GenBank MG663233.

**Diagnosis** — In broadleaf forests of eastern North America; medium sized basidiomata, stipe clavate; basidiospore size ( $L \times W_m 7.3 \times 5.6 \mu\text{m}$ ), shape and ornamentation similar to *C. apius*, but differing from it by more yellow colouration and lack of fruity herbaceous odour (odour of exsiccatae extremely pungent); nine differences in ITS from *C. leproleptopus*, a similarity of 98.5 %.

**Pileus** 39–68 mm diam, convex, margin incurved, smooth, not viscid, yellow to brownish yellow, with very thin, fine, brown fibrils and fibrillose scales. **Lamellae** adnate, broad, close to subdistant, yellow then brownish yellow, edges even. **Stipe** 52–105 mm long, up to 20 mm thick, clavate, brown fibrillose, veil thin, whitish with some yellowish tints, forming a fibrillose zone, veil fibrils sometimes attached to pileus margin. **Context** light yellow, not staining, spongy, firm. **Odour** of context raphanoid. **Taste** of context mild. **Exsiccatae.** Pileus surface light brown to dark brown centrally, shiny, with small fibrillose scales, stipe brownish to pale creamy white or yellowish in places, basal mycelium pale yellow, lamellae light- to dark brown, coated with basidiospores, context creamy to slightly



yellowish pallid or brownish where injured (larvae tunnels). Odour strong pungent. *UV*. Fresh context yellow; exsiccatae pileus surface rich brown, stipe brown except for yellow apex and basal mycelium, lamellae brown to light yellow, context bright pale yellow.

*Basidiospores* (6.3–)6.7–7.6(–8) × 5.2–6 μm, L × W<sub>m</sub> 7.3 × 5.6 μm, Q 1.2–1.4, Q<sub>m</sub> 1.3, broadly ellipsoid to subglobose, coarsely verrucose, slightly dextrinoid. *Basidia* 30–34 × 7.4–9 μm, clavate, 4- rarely 2-spored, colourless, yellowish, or with yellow contents, some with grayish walls. *Pileipellis*: epicutis well developed, hyphae radially arranged, interwoven or forming entangled fascicles, 4–16 μm wide, cylindrical to broadly cylindrical or enlarged, yellowish to brownish yellow or colourless, some with brownish yellow contents, walls ± thickened, refractive, colourless to yellowish, smooth or slightly encrusted; hypocutis well developed, hyphae radially arranged, ± interwoven, cylindrical, broadly cylindrical or more enlarged, 7–23 μm wide, colourless to yellowish, some with yellowish contents, walls ± thickened, refractive, yellowish.

**Habitat & Distribution** — Broadleaf forest of *Fagus*, *Quercus* and *Carya*, Tennessee.

*Specimens examined*. None beyond the holotype.

**Notes** — *Cortinarius atkinsiae* is known only from one collection in Tennessee. It is related to *C. apius*, a species known from Quebec in broadleaf forests. These species share morphological and ecological similarities with *Cortinarius pescolanensis* and all have ± coarsely verrucose basidiospores.

***Cortinarius fuscotomentosus*** Bojantchev, Liimat. & Niskanen, *sp. nov.* — MycoBank MB 837385; Fig. 2h, 3l

*Etymology*. From Latin: 'fuscus' black and 'tomentum' woolly hairs.

*Typus*. USA, California, Yuba County, New Bullard's Bar Reservoir, *Notholithocarpus*, *Pinus ponderosa*, 18 Nov. 2007, coll. D.B. Bojantchev (holotype WTU 073590), (isotype UC); ITS barcode GenBank MT853246.

**Diagnosis** — Occurring with *Notholithocarpus*, sometimes mixed with *Quercus*, *Pseudotsuga*, *Pinus*, California; medium to larger basidiomata, dominated by olive colours; basidiospores small, L × W<sub>m</sub> 6.7 × 5.3 μm, subglobose; twelve differences in ITS from *C. loringii*, a similarity of 98.1 %.

**Pileus** 40–100 mm diam, convex to plano-convex, margin involute then frequently upturned at age, prominently fibrillose tomentose to ± fibrillose scaly over the entire surface, margin dark olive, olive gray to olive brown, darker brown to black on the disc. **Lamellae** moderately crowded, sinuate, pale yellow to pale olive at first, olive at maturity, becoming rusty brown from spores, edges even. **Stipe** 40–120 mm long, 20–35 mm thick, cylindrical to subclavate, white then brownish, often with prominent white rhizomorphs, veil olive to olive brown, partially covering the lower stipe, occasionally leaving a distinct zone. **Context** pale olivaceous. **Odour** of basidiomata context distinctly raphanoid. **Taste** not recorded. **Exsiccatae**. Pileus surface grayish olive to blackish olive, lamellae rusty brown from spores, stipe light cream colour to slightly brownish, context cream colour to pale brownish. **UV**. Fresh distinctly yellow; exsiccatae pileus surface dark, context light yellow, stipe yellowish with some darker areas, lamellae rust brown coated with spores.

*Basidiospores* (5.8–)6.0–7.0(–7.3) × (4.8–)5.0–5.5(–5.8) μm, L × W<sub>m</sub> 6.7 × 5.3 μm, Q 1.2–1.32, Q<sub>m</sub> 1.26, mostly subglobose, slightly- to moderately verrucose, slightly dextrinoid. *Basidia* 4-spored, 24–34 × 6–9 μm, cylindrical clavate, colourless to grayish or with yellowish pigment, often with refractive granules. *Pileipellis*: epicutis well developed, hyphae interwoven to entangled, forming clusters or ascending loose fascicles or more radially arranged, 6–23 μm wide, cylindrical to broadly cylindrical or ± enlarged, commonly blackish to grayish, or

sometimes yellow to yellow green or colourless, sometimes with dark cytoplasmic granules, walls refractive, ± thickened, colourless to yellowish, smooth or slightly encrusted; hypocutis poorly developed, hyphae ± radially arranged, ± interwoven, 6–21 μm wide, cylindrical to broadly cylindrical or more enlarged, colourless or with grayish to yellowish contents, walls colourless, ± refractive, smooth.

**Habitat & Distribution** — Autumnal species in the coastal forests and Sierra Nevada foothills of California. All collections found where tanoak (*Notholithocarpus densiflorus*) occurs, potentially its primary host.

*Additional specimens examined*. USA, California, Humboldt County, HW 199, west of Hoppa, mixed broadleaf forest, *Pseudotsuga*, 21 Nov. 1981, coll. D. Largent, JFA8575 (WTU); San Mateo County, Huddart Park, *Notholithocarpus densiflorus*, *Quercus agrifolia*, *Pseudotsuga*, 9 Jan. 2009, coll. D. Bojantchev, DBB13228 (Pers. Herb.), GenBank MT853247; loc. cit., 4 Dec. 2010, DBB40695 (Pers. Herb.), GenBank MT853254; Sonoma County, Salt Point State Park, 0.5 mi North of Hwy 1, *Notholithocarpus densiflorus*, *Pinus muricata*, *Pseudotsuga*, 23 Nov. 2007, coll. D.B. Bojantchev, DBB26988 (UC, Pers. Herb.), GenBank MT853252.

**Notes** — *Cortinarius fuscotomentosus* is characterized by a dark olive to brown or blackish fibrillose tomentose pileus and olivaceous coloured lamellae and veil. It has small, ± subglobose basidiospores, which it shares with closely related *C. loringii* and *C. subleproleptopus*. They all occur in the same general geographical region of western North America in forests with *Fagaceae*.

***Cortinarius loringii*** Ammirati, Liimat. & Niskanen, *sp. nov.* — MycoBank MB 837386; Fig. 3m, 4a

*Etymology*. Named for Scot Loring.

*Typus*. USA, Oregon, Douglas County, Irwin Rocks, *Pseudotsuga*, mixed woods *Quercus* spp., 16 Nov. 2010, coll. S. Loring (holotype WTU 67669); ITS barcode GenBank MW009227.

**Diagnosis** — In mixed forest, *Quercus*, *Pseudotsuga*; basidiomata medium sized, dominated by brownish colours, stipe cylindrical to subclavate. Odour fragrant; basidiospores small, L × W<sub>m</sub> 6.5 × 5.3 μm; nine differences in ITS from *C. leproleptopus*, a similarity of 98.5 %.

**Pileus** 30–80 mm diam, rounded convex to plano-convex, ± umbonate, margin incurve to decurved then plane, surface ± finely fibrillose scaly, disc and inner margin rich brown to blackish brown, outer margin lighter brown to tan. **Lamellae** adnate to slightly adnexed, close to crowded, light coloured, yellow then yellow brown. **Stipe** 80–115 mm long, cylindrical to subclavate, 8–15 mm thick above, 11–19 mm thick below, whitish, bruising brown, veil white leaving a slight creamy zone above, otherwise only some brownish fibrils on stipe surface. **Context** pileus white, in stipe stuffed to hollow, whitish bruising brown; **odour** sweet (fragrant). **Taste** not recorded. **Exsiccatae**. Pleasant celery odour, pileus disc olive black to dark olive, margin light olive black to grayish olive, lamellae creamy to brownish, stipe creamy yellowish, context creamy to brownish or blackish. **UV**. Exsiccate pileus surface negative, lamellae light yellow, stipe and context yellow.

*Basidiospores* 5.8–6.8 × 5–5.9 μm, L × W<sub>m</sub> 6.5 × 5.3 μm, Q 1.2–1.34, Q<sub>m</sub> 1.23, mostly subglobose, some broadly ellipsoid, moderately to coarsely verrucose, ± moderately dextrinoid. *Basidia* 4-spored (rarely 2-spored), clavate to narrowly clavate, 30–33.5 × 7.4–8.1 μm, colourless to yellowish, walls becoming grayish thickened. *Pileipellis*: epicutis well developed, hyphae on disc ascending or in fascicles, on margin ascending fascicles or more radially arranged, interwoven, 5.5–17 μm wide, cylindrical to broadly cylindrical, blackish, yellow brown, orange yellow brown or colourless, containing black particles, walls ± thickened, refractive, colourless to yellowish, smooth or slightly encrusted; hypocutis slightly- to moderately developed,



**Fig. 4** Basidiomata. a. *Cortinarius loringii* SCL6030 (holotype); b. *C. phrygianus* YL4300; c. *C. subleproleptopus* NS3; d. *C. squamivenetoideus* CMMF004032; e. *C. lutescens* CMMF001219; f. *C. veneto-occidentalis* TN11-051 (holotype); g. *C. fuscoflavidus* DBB41055; h. *C. aff. veneto-occidentalis* SDA 382. — Photos by: a. P.B. Matheny; b, d–e. Y. Lamoureux; c, g. D. Bojantchev; f. K. Liimatainen; h. S.D. Adams.

sometimes appearing cellular, hyphae interwoven, radially arranged or entangled, 5.9–23 µm wide, cylindrical to enlarged, yellowish, yellowish orange, yellowish brown or colourless, walls refractive, colourless to yellowish, ± thickened, smooth or slightly encrusted.

Habitat & Distribution — Mixed woods, *Quercus* spp. and *Pseudotsuga*, southwestern Oregon.

*Specimens examined.* None beyond the holotype.

Notes — *Cortinarius loringii* is characterized by small, subglobose basidiospores, a brown fibrillose scaly pileus, ± slender habit and a fragrant odour. The whitish context bruises brown. The pigmentation of the epicutis hyphae (exsiccatae in KOH) is similar to *C. clandestinus*, and the exsiccatae themselves resemble the latter as well. Additional observation will be needed to fully determine its ecology and distribution.

***Cortinarius phrygianus* (Fr.) Fr., Hymenomyc. Eur.: 365. 1874**  
— IF 152271; Fig. 3n, 4b

*Type.* SWEDEN, Darlana, Rättvik sn, Enån, coniferous forest, *Pinus*, 14 Sept. 1988, coll. Brandrud et al., CFP774, F44888 (S, *neotypus hic designatus*). MycoBank MBT 393872; ITS barcode GenBank MW009234.

= *Cortinarius sublanatus* var. *phrygianus* Fr., *Epicr. Syst. Mycol.*: 283. 1838.

Forming a weakly supported lineage with uncertain position. *Incertae sedis!*

*Pileus* 30–60 mm diam, hemispherical to campanulate then plano-convex, sometimes broadly umbonate, coarsely fibrillose to scaly, dark olivaceous gray when young, then olivaceous yellow, reddish yellow to reddish brown with blackish brown scales. *Lamellae* crowded, pale ochraceous with tinge of olive. *Stipe* 40–80 mm long, 5–12 mm thick, clavate, whitish when young then turning slightly yellowish brown from the base upward, veil blackish brown to olivaceous gray forming distinct girdles or scales on the stipe. *Context* whitish or with olivaceous yellow tinged watery streaks in the stipe apex, becoming darker yellow brown from the base upward. *Odour* of basidiomata indistinct, raphanoid or peppery. *Taste* not recorded. *Exsiccatae.* Pileus surface medium brown to grayish or blackish, lamellae rich yellow brown, context pale yellowish cream to yellowish white stipe pale brownish to grayish (veil), base brown to yellowish. *UV.* Exsiccatae context yellow, lamellae pale yellowish, pileus and stipe surfaces essentially negative.

*Basidiospores* 5.3–6.5(–7.0) × 4.4–5.2 µm, L × W<sub>m</sub> 6.2 × 4.7 µm, Q 1.2–1.5, Q<sub>m</sub> 1.36, broadly ellipsoid to subglobose, moderately to ± coarsely verrucose, slightly- to moderately dextrinoid. *Basidia* 4-spored, 26–30 × 6.7–8 µm, clavate, colourless or yellowish to grayish yellow pigmented, with refractive droplets and/or granules, some with thickened gray walls. *Pileipellis:* epicutis well developed, hyphae entangle to interwoven or ascending, sometimes forming fascicles, or more radially arranged, cylindrical to broadly cylindrical, 5–15 µm wide, colourless or with orange yellow, grayish or black pigment, walls ± thick, refractive, colourless or yellowish; hypocutis poorly developed, hyphae interwoven, ± radially arranged, cylindrical to ± enlarged, 6–20 µm wide, colourless or yellow, yellow orange and red orange to brown orange pigmented, some with granules, walls often refractive, ± thickened, smooth or slightly encrusted.

Habitat & Distribution — Known from central and northern Europe and eastern North America. Rather rare, occurring in conifer and mixed conifer-broadleaf forests, typically where *Pinus* is present.

*Additional specimens examined.* CANADA, Quebec, Saint-Côme (Chemin des Vennes), *Pinus banksiana*, *Betula papyrifera* nearby, 23 Sept. 2014, coll. Y. Lamoureux, YL4300, CMMF020725, GenBank MW009235. — FINLAND,

Parainen, Lemlaxön, Fallsbogen, heath forest, *Pinus sylvestris*, among mosses, 1 Oct. 1990, coll. J. Vauras, 5385F (TURA). — SWEDEN, Dalarna, Rättvik, Enån, 14 Sept. 1988, CFP774, F44888 (S), GenBank MW009234.

Notes — The material from Quebec is the first documented report of this species from North America. The photo of the material represents the species well as do the characteristically small basidiospores. There is no description of the material from Quebec so the description here is based on CFP774.

In Brandrud et al. (2012) the name *C. arenatus* was used for the species. The protologue of *C. arenatus* includes a reference to Bulliard's plate (tab. 586 f. 1). The basidiomata illustrated in the figure most resemble those of *C. pholideus*. Thus we do not follow the interpretation of Brandrud et al. and continue the use of the name *C. phrygianus* for the species.

***Cortinarius subleproleptopus* Liimat., Niskanen & Bojantchev, sp. nov.** — MycoBank MB 837387; Fig. 3o, 4c

*Etymology.* Similarity to *C. leproleptopus*.

*Typus.* USA, California, Monterey County, Fort Ord, live oak (*Quercus*) woods, 15 Dec. 2012, coll. Z. Mikalonis, T. Niskanen (holotype H 7068356), (isotype K); ITS barcode GenBank MW009241.

*Diagnosis* — Associated with *Quercus* in coastal California forests; basidiomata medium sized, dominated by yellowish to yellowish brown colours; veil forming a sock-like covering on the lower stipe; 14 differences in ITS from *C. leproleptopus*, a similarity of 97.8 %.

*Pileus* 40–60 mm diam, at first hemispherical, later low convex to plane, somewhat hygrophanous, fibrillose, pale brownish yellow becoming more brownish in age. *Lamellae* adnexed, somewhat crowded, yellowish brown. *Stipe* 50–70 mm long, 8–10 mm thick above, base 8–11 mm thick, cylindrical to somewhat clavate, very pale brownish yellow; veil pale yellow, forming a sock-like sheet on the lower part of the stipe. *Context* very pale yellow brown, almost whitish when dry. *Odour* and *taste* not recorded. *Exsiccatae.* Pileus surface medium brown on margin with some dark to blackish areas, disc blackish, lamellae light medium brown, flesh of pileus pale. *UV.* Exsiccatae pileus surface negative, dark brown, lamellae bright yellow, pileus flesh pale yellow.

*Basidiospores* 7.0–7.5(–7.8) × 5.2–5.9(–6.3) µm, L × W<sub>m</sub> 7.2 × 5.6 µm, Q 1.24–1.35, Q<sub>m</sub> 1.28, subglobose to broadly ellipsoid, moderately to ± coarsely verrucose, slightly to moderately dextrinoid. *Basidia* 4-spored, 27–35 × 7–8 µm, clavate to narrowly clavate, containing yellow pigment, colourless or grayish with darkened wall, often with refractive particles. *Pileipellis:* epicutis well developed, hyphae radially oriented, ± interwoven or towards disc forming entangled mounds, 4–20 µm wide, cylindrical, broadly cylindrical or more enlarged, colourless, grayish or with yellow pigment, walls refractive, ± thickened, colourless, yellowish or darkened, smooth or slightly encrusted; hypocutis poorly developed, hyphae radially oriented, ± interwoven, 4–20 µm wide, cylindrical to broadly cylindrical or enlarged, colourless or with yellow contents, walls refractive, colourless to yellowish.

Habitat & Distribution — In live *Quercus* forests. Known only from California.

*Additional specimen examined.* USA, California, Riverside County, Cleveland National Forest, Potrero El Cariso 'Big Woods', under *Quercus* spp., 10 Feb. 2010, coll. D. Bojantchev, Noah Siegel NS3 (pers. herb.), WTU, GenBank MT853256.

Notes — *Cortinarius subleproleptopus* shares a distribution with *C. fuscotomentosus* and *C. loringii* in mixed forest with *Quercus* in southwestern Oregon and north western California. They are morphologically different from one another but have in common relatively small basidiospores.

***Cortinarius* sect. *Melanoti*** Niskanen, Liimat. & Ammirati, *sect. nov.* — MycoBank MB 837388

*Etymology.* Named for the type species of the section.

*Type.* *Cortinarius melanotus* Kalchbr.

**Description** — Basidiomata medium-sized. Pileus tomentose to finely dark scaly, olivaceous brown to olivaceous green, non-hygrophanous. Stipe cylindrical or slightly clavate. Universal veil blackish brown. Basidiospores  $L \times W_m$   $7.3 \times 5.7 \mu\text{m}$ .

**Habitat & Distribution** — Known from Europe, in conifer forests (*Abies*, *Pinus*) on calcareous soil.

Currently including — *C. melanotus* and based on Bidaud et al. (2021) also *C. jimenezianus* and *C. viridans*.

**Notes** — The combination of dark pileus, blackish brown universal veil and basidiospores  $L \times W_m$   $7.3 \times 5.7 \mu\text{m}$ , distinguish this section from all other members of the subgenus.

***Cortinarius melanotus*** Kalchbr., in Fries, *Hymenomyc. Eur. (Upsaliae)*: 365. 1874 — IF 219634

*Types.* Kalchbrenner 1874, illustration in a manuscript later published in Kalchbrenner, *Icones selectae Hymenomycetum Hungariae III*, Budapest: tab. 27, f. 2, 1875 (*holotypus*). — FRANCE, Ain, Brenod, Jalinaud, in *Abies* forest on calcareous ground, 7 Oct. 1991, *Lindström et al.* CFP1101, F44883 (S, *epitypus hic designatus*). MycoBank MBT 393870; ITS barcode GenBank MW009230.

= *Cortinarius submelanotus* Bidaud, in Bidaud, Moëgne-Loccoz, Carteret, Reumaux & Eyssartier, *Atlas des Cortinaires (Meyzieu)* 15: 1032. 2005.

= *Cortinarius zonatus* Reumaux, in Bidaud, Moëgne-Loccoz, Carteret, Reumaux & Eyssartier, *Atlas des Cortinaires (Meyzieu)* 15: 1033. 2005.

***Cortinarius* sect. *Squamiveneti*** Niskanen, Liimat. & Ammirati, *sect. nov.* — MycoBank MB 837389

*Etymology.* Named after the type species of the section.

*Type.* *Cortinarius squamivenetus* Kytöv., Liimat. & Niskanen.

**Description** — Basidiomata small- to medium-sized. Pileus with rather small, dark scales, yellow, olive yellow, pale olivaceous brown or pale yellow brown, somewhat hygrophanous. Stipe cylindrical to somewhat clavate. Universal veil yellow or sparse and pale yellow brown. Basidiospores  $L \times W_m$   $6.6 \times 5.6 \mu\text{m}$ .

**Habitat & Distribution** — Known from boreal eastern North America and Europe, in coniferous forests on calcareous ground.

Currently including — *C. squamivenetoideus* and *C. squamivenetus*.

**Notes** — The combination of small spores, a pileus with small, dark scales, yellow to yellow brown veil and a habitat with coniferous trees separate these species from most of the other *Leprocybe*. The somewhat similar *C. phrygianus* has even smaller spores ( $L \times W_m$   $6.2 \times 4.7 \mu\text{m}$ ).

***Cortinarius squamivenetoideus*** Niskanen, Liimat. & Ammirati, *sp. nov.* — MycoBank MB 837390; Fig. 3p, 4d

*Etymology.* Similarity to *C. squamivenetus*.

*Type.* USA, Alaska, Fairbanks, Chena Lakes and Trails, mossy *Picea* dominated forest with some *Betula* and *Populus* on rich ground, 5 Aug. 2011, coll. K. Liimatainen, T. Niskanen (holotype H 7068355), (isotype K); ITS barcode GenBank MW009239.

**Diagnosis** — In conifer dominated forests, sometimes mixed with *Betula* and *Populus*; basidiomata medium sized; similar in morphology and microscopic features to its sister taxon *C. squamivenetus* but differing from it in the ITS region by 10 differences, a similarity of 98.4 %.

**Pileus** 30–50 mm diam, at first hemispherical, later low convex to plane, somewhat hygrophanous, yellow to olive-yellow but

covered with dark scales, center almost blackish brown. *Lamel-lae* adnexed, medium spaced to somewhat crowded, yellowish brown, edge yellow. *Stipe* 70–110 mm long, 6–9 mm thick above, base 7–10 mm thick, cylindrical to somewhat clavate, pale brownish yellow, veil yellow, forming zones and incomplete girdles on the stipe. Context pale olivaceous yellowish brown. *Odour* strongly raphanoid. *Taste* not recorded. *Exsiccatae.* Pileus medium brown to gray brown with some darker areas, lamellae deep medium brown, flesh of pileus pale, no stipe. *UV.* Exsiccatae pileus surface negative, only lamellae and flesh of pileus slightly yellow, no stipe.

*Basidiospores*  $6.3\text{--}7.4\text{--}7.8 \times 5.2\text{--}5.9\text{--}6.3 \mu\text{m}$ ,  $L \times W_m$   $6.9 \times 5.7 \mu\text{m}$ ,  $Q$  1.13–1.29,  $Q_m$  1.23,  $\pm$  subglobose, moderately to coarsely verrucose, slightly to moderately dextrinoid. *Basidia* 4-spored,  $30\text{--}34 \times 7.4\text{--}8.9 \mu\text{m}$ , clavate, colourless, with yellow pigment or grayish with darkened walls, often with refractive particles. *Pileipellis*: epicutis  $\pm$  well developed, often somewhat collapsed, hyphae radially arranged and interwoven or forming  $\pm$  loose ascending fascicles, 4–12  $\mu\text{m}$  wide, cylindrical to broadly cylindrical, end cells rounded to tapered, colourless to grayish or with yellow to green yellow pigment, walls  $\pm$  thickened, refractive, colourless to yellowish, smooth; hypocutis poorly developed, hyphae radially arranged, interwoven, 4–14  $\mu\text{m}$  wide, cylindrical to broadly cylindrical, colourless, wall refractive,  $\pm$  thickened, colourless, smooth.

**Habitat & Distribution** — *Cortinarius squamivenetoideus* occurs in boreal coniferous forests, *Abies*, *Picea*, or mixed forest *Picea*, *Betula*, *Populus*, on rich to calcareous ground. Known from Alaska.

*Specimens examined.* None beyond the holotype.

**Notes** — *Cortinarius squamivenetoideus* and *C. squamivenetus* are similar in size and colouration, share relatively small basidiospores and occur in boreal conifer dominated forests. See additional comments under *C. squamivenetus*.

***Cortinarius squamivenetus*** Kytöv., Liimat. & Niskanen, in Liimatainen, *Index Fungorum* 196bis: 2. 2014 — IF 550843

**Pileus** 30–90 mm diam, rounded-campanulate, convex, then low convex with a low umbo to plane, often wavy-irregular, dry, yellow brown to olivaceous brown, covered by black appressed fibrillose scales, sometimes entirely black on buttons or completely ochraceous yellow if totally covered by veil, paler and fibrillose toward margin. *Lamel-lae* adnexed, crowded to subdistant, medium ochre yellow to olivaceous yellow then olivaceous brown. *Stipe* 50–130 mm long, 5–15 mm thick at above, 10–20(–30) mm at base, cylindrical, clavate to rounded bulbous at base, yellowish to olivaceous yellow, dry, whitish at apex, *veil* ochraceous to medium brownish yellow, often leaving a distinct annular zone and fibrils or patches on stipe, basal mycelium pale yellow-ocher. *Context* of pileus and stipe thick but soft, marbled in wet weather, pale yellow, pale olivaceous or yellowish brown, paler faded. *Odour* almost none in lamellae, rarely weakly fruity or raphanoid, in context distinctly raphanoid. *Taste* not recorded. *Exsiccatae.* Not observed. *UV.* Yellow.

*Basidiospores*  $5.9\text{--}7.0\text{--}7.5 \times 5\text{--}6.1 \mu\text{m}$ ,  $L \times W_m$   $6.4 \times 5.5 \mu\text{m}$ ,  $Q = 1.08\text{--}1.22$ ,  $Q_m$  1.16, subglobose, moderately, sharply verrucose, moderately to fairly strongly dextrinoid. *Basidia* 4-spored. *Pileipellis*: epicutis hyphae with blackish pigment; hypocutis poorly developed.

**Habitat & Distribution** — In conifer dominated boreal forests, *Abies balsamea*, *Picea mariana* and *Thuja occidentalis*. South-eastern Canada, known also from Finland.

*Additional specimens examined.* CANADA, Quebec, Saint-Côme (Parc de la Chute-à-Bull), 24 Aug. 2006, coll. Y. Lamoureux, CMMF004032 (MQCOR862); loc. cit., 25 Aug. 2007, coll. Y. Lamoureux, CMMF004072 (MQCOR864).

Notes — The two collections of *C. squamivenetus* presented here are similar morphologically to European material. Sequence of MQCOR862 is the same as the type of *C. squamivenetus*, and there are two alleles in almost all the sites which differ from the type and MQCOR864 (cf. *C. squamivenetus*). Nonetheless, there are eight differences in the ITS region between the type and MQCOR864 which makes position of latter specimen uncertain. There are ten differences in ITS from *C. squamivenetoideus*, a similarity of 98.4 %.

**Cortinarius sect. Veneti** Bellanger, Niskanen, Ammirati & Liimat., *sect. nov.* — MycoBank MB 837402

= *Cortinarius* sect. *Veneti* Konrad & Maubl. invalid (Art. 38.1)

*Type. Cortinarius venetus* (Fr.) Fr. 1838.

Description — Basidiomata rather small- to medium-sized. Pileus generally olive yellow to yellowish brown or olive brown, but also dark olive brown to blackish brown, innately fibrillose, tomentose or with  $\pm$  small, fibrillose scales,  $\pm$  hygrophanous. Stipe cylindrical to somewhat clavate. Veil olive yellow to greenish yellow. Basidiospores relatively small,  $L \times W_m$  7.2  $\times$  5.8  $\mu\text{m}$ .

Habitat & Distribution — Known from western and eastern North America and Europe. In a variety of coniferous and mixed forests.

Currently including — *C. fuscoflavidus*, *C. lutescens*, *C. veneto-occidentalis*, *C. aff. veneto-occidentalis* and *C. venetus*.

Notes — Konrad & Maublanc (1937) divided the genus *Cortinarius* in 6 subgenera, each of them further divided in several sections. In subgenus IV-*Dermocybe*, they introduced *A-Ochroleuci*, *B-Cinnamomei*, *C-Anomali* and *D-Veneti* (p. 170, type species *C. venetus*). The rank was not explicit in this case, in contrast to other subgenera like *Phlegmacium* for instance. Moreover, the authors did not provide any diagnosis for these groups/sections, despite this became compulsory two years before (Cambridge rules of the International Code of Botanical Nomenclature, 1935). In the literature, (e.g., *Cortinarius* Flora Photographica, Brandrud et al. 1994), the year of publication for sect. *Veneti* is erroneously indicated as 1930, resulting from a confusion between vol. VI and fasc. 6 of the *Icones Selectae Fungorum* (J. Melot, pers. comm.). As a result, none of the sections published in the French monograph after 1935 are valid and thus the section name *Veneti* is validated here, although in much narrower boundaries than those initially proposed by Konrad & Maublanc.

Members of the section are characterized by a  $\pm$  hygrophanous pileus with a minutely scaly or innately fibrillose pileus, olive yellow to greenish yellow universal veil and small- to medium-sized basidiomata. No other section in the subgenus has the same combination of characters. In North America the *C. veneto-occidentalis* clade shows considerable variation in morphology and ITS sequence divergence, consequently *C. fuscoflavidus* and *C. aff. veneto-occidentalis* are recognized here. More sampling is also necessary to determine the distribution and ecological parameters of these taxa.

**Cortinarius fuscoflavidus** Niskanen, Liimat., Bojantchev & Ammirati, *sp. nov.* — MycoBank MB 837391; Fig. 3r, 4g

*Etymology.* Named for the dark blackish to yellowish colouration.

*Typus.* USA, Oregon, Wasco County, Bear Springs Campground, mixed conifers, 27 Oct. 1995, coll. E. Horak (holotype WTU 41324), (isotype K); ITS barcode GenBank MW009221.

Diagnosis — In montane and coastal conifer and mixed conifer broadleaf forests; pileus surface densely fibrillose scaly, and dark blackish brown in colour; basidiospores  $L \times W_m$  6.8  $\times$  5.4  $\mu\text{m}$ . Sister species to *C. veneto-occidentalis* with three differences in ITS, a similarity of 99.5 %.

*Pileus* 20–60 mm diam, obtusely conic umbonate to obtusely convex,  $\pm$  subumbonate, margin  $\pm$  incurved to decurved, densely covered with small fibrillose scales, especially on disc, scales  $\pm$  upturned on disc and inner margin, edge fibrillose, at times with a thin yellow olive sheen, dark blackish brown with edge dull olive yellow. *Lamellae* adnexed,  $\pm$  distant, sometimes intervenose, dark brown becoming rich brown, edges  $\pm$  yellowish buff. *Stipe* 23–68 mm long, 5–11 mm thick above, base clavate tapered, 8–13 mm thick, above silky fibrillose, whitish to pale yellowish, below whitish to pale yellowish in between veil covering, developing olive brown to brown colours below, basal mycelium yellowish buff with some white mycelium in soil, rhizomorphs dingy yellowish buff, veil light yellow, thin in places, leaving small patches and slight strands on stipe surface. *Context* in pileus concolourous or gray olive to dingy yellow, in stipe hollow, cortex cream colour to yellow above, below olive brown to olive yellow or darker olive brown in base. *Odour* of lamellae and/or context slight fungoid. *Taste* of context somewhat bitter, fungoid. *Exsiccatae.* Pileus surface dark gray olive brown to gray olive, pileus and stipe context dull pale grayish white to pale gray, stipe surface pale dull yellowish white to grayish brown, lamellae light grayish brown to brown. *UV.* Fresh basidiomata context, lamellae and stipe bright yellow, pileus surface brown with some yellow; exsiccatae pileus surface negative, context, lamellae and some areas of stipe light to bright yellow.

*Basidiospores* 6.3–7(–7.4)  $\times$  (4.9–)5.2–5.6(–5.9)  $\mu\text{m}$ ,  $L \times W_m$  6.8  $\times$  5.4  $\mu\text{m}$ ,  $Q$  1.17–1.37,  $Q_m$  1.25,  $\pm$  subglobose, rarely broadly ellipsoid, moderately to coarsely verrucose, slightly to moderately dextrinoid. *Basidia* 4-spored, 30–33.5  $\times$  6.7–7.4  $\mu\text{m}$ , narrowly clavate to clavate, colourless or containing yellowish to colourless granules. *Pileipellis:* epicutis well developed, hyphae radially arranged, interwoven or in  $\pm$  ascending fascicles, (4.5–)7.4–23  $\mu\text{m}$  wide, cylindrical to broadly cylindrical, colourless to yellowish brown or containing dark yellow brown, orange or reddish pigment, wall smooth or encrusted, yellowish refractive; hypocutis poorly developed, hyphae interwoven to ascending, 11–25  $\mu\text{m}$  wide, broadly cylindrical to enlarged, dull yellowish to pale yellow brown, some with dull yellowish granules, walls somewhat yellowish refractive, smooth to encrusted.

Habitat & Distribution — Mixed conifer and conifer broadleaf forests, British Columbia, California, Oregon and Washington. October to December.

*Additional specimens examined.* CANADA, British Columbia, Ectomycorrhizal study, UNITE no. UDB032444. – USA, California, Mendocino County, Jackson State Forest, mixed woods, 6 Dec. 1969, HDT24431 (SFSU); Sonoma County, Salt Point State Park, 0.25 mi South of Hwy 1, *Notholithocarpus densiflorus*, *Pinus muricata*, *Pseudotsuga menziesii*, 18 Dec. 2010, coll. D. Bojantchev, DBB41055 (WTU, Pers. Herb.), GenBank MW009223; Oregon, Wasco County, Ectomycorrhizal study, GenBank DQ365640; voucher: OSC 80195, GenBank EU669233; Washington, Olympic National Park, Deer Park, mixed conifer forest, 27 Oct. 2009, coll. K. Liimatainen, T. Niskanen 09-158 (H), GenBank MW009222.

Notes — *Cortinarius fuscoflavidus* has a dark coloured, fibrillose scaly pileus, and epicutis hyphae that are generally more pigmented than those of *C. veneto-occidentalis*. The basidiospores also are smaller in size in comparison to *C. veneto-occidentalis*. The basidiomata (including the exsiccatae) are similar in appearance to *C. atrosquamosus*. The distribution and differing forest habitats of this species is notable.

**Cortinarius lutescens** Peck, Ann. Rep. N.Y. State Mus. 42: 118. 1889 — IF 218338; Fig. 4e

*Pileus* 25–75 mm diam, broadly convex to nearly plane, unpolished, margin innately fibrillose, disc and inner margin minutely squamulose, colour yellowish, yellowish green and yellowish brown, with brown, dark brown or blackish brown colours on disc when mature, in age sometimes marked with

reddish brown spot. *Lamellae* rather broad, close to subdistant, adnexed, light brownish yellow becoming more brownish with yellowish tones mature. *Stipe* 25–40 mm long, 4–6.5 mm thick, equal, firm, silky fibrillose, whitish to pale, especially above, to yellowish or olive yellow to brownish yellow below, *veil* pale yellow, leaving some zones and/or patches on stipe surface, basal mycelium in litter white. *Context* whitish in pileus and portions of upper stipe, in lower stipe yellowish to dingy yellow or olive yellow. *Odour* and *taste* not recorded. *Exsiccatae*. Pileus light brown to dark brown, lamellae light brown to light gray brown, stipe light gray brown with pale base, flesh pale. *UV*. *Exsiccatae* lamellae, flesh and stipe base yellow, otherwise negative.

*Basidiospores* (6.3–)6.7–7.4(–8.1) × (5.4–)5.6–5.9(–6.3) μm, L × W<sub>m</sub> 7.2 × 5.7 μm, Q 1.2–1.5, Q<sub>m</sub> 1.3, subglobose or broadly ellipsoid, moderately to coarsely verrucose, slightly- to ± moderately dextrinoid. *Basidia* 4-spored, 31–33 × 7.5–8.1 μm, clavate, colourless, some with yellow pigment, occasionally with dark, thickened walls. *Pileipellis*: epicutis poorly to more strongly developed, hyphae often forming a distinct yellow compacted layer, radially arranged, interwoven, or sometimes forming entangled fascicles, 3–19 μm wide, cylindrical to broadly cylindrical or more enlarged, colourless to yellow, walls colourless to yellow, ± thickened, smooth or encrusted; hypocutis poorly developed, hyphae radially oriented, interwoven, 5–26 μm wide, cylindrical to broadly cylindrical or more enlarged, colourless to yellowish, walls colourless or yellowish, refractive, somewhat thickened, smooth or slightly encrusted.

**Habitat & Distribution** — In mesic to damp coniferous forest (*Abies balsamea*, *Picea*) with *Betula*, calcareous soil and mixed woods. Known from New York and Newfoundland.

*Additional specimens examined*. CANADA, Newfoundland, West coast, Gros Morne National Park, south side of Bonne Bay East Arm, Lomond River hiking trail, 19 Sept. 2007, coll. K. Liimatainen, T. Niskanen, TN07-232 (H7000893), GenBank MW009229; Quebec, Chertsey (Lanaudière-Nord), *Abies-Picea*, with *Betula*, 9 Sept. 1993, coll. Y. Lamoureux, YL2025 (CMMF002025); Magog (Estrie), *Tsuga-Abies* forest with *Betula*, 13 Sept. 1990, coll. Y. Lamoureux, CMMF001219. — USA, New York, Essex County, North Alba, Sept., mossy ground in woods, coll. C.H. Peck, NYSf1781.2, NYSf1781.1 (holotype), GenBank MW009228.

**Notes** — The macroscopic description of *C. lutescens* is based on Peck's original observations, with additional notes from TN07-232 and two collections from Quebec. Its morphology and basidiospores are similar to *C. venetus* and it has 6 differences in ITS from *C. venetus*, a similarity of 99 %.

***Cortinarius veneto-occidentalis*** Niskanen, Liimat. & Ammirati, *sp. nov.* — MycoBank MB 837395; Fig. 3q, 4f

*Etymology*. Western *C. venetus*.

*Typus*. USA, Alaska, Fairbanks, Ballaine Lake Trails, *Picea* dominated forest with *Betula* and *Populus*, rich soil, 14 Aug. 2011, K. Liimatainen, T. Niskanen (holotype H 7068357), (isotype K); ITS barcode GenBank MW009243.

**Diagnosis** — Alaska and western Canada; boreal conifer forests; small to medium sized basidiomata dominated by yellowish, olive yellow and yellowish brown colours; microscopically similar to *C. venetus*; differing by eight differences in ITS from *C. lutescens* (a similarity of 98.7 %) and three differences from *C. fuscoflavidus* (99.5 %).

*Pileus* 25–55 mm diam, first hemispherical, later low convex to plane, somewhat hygrophanous, fibrillose tomentose to minutely fibrillose scaly, disc dark yellowish brown, towards the margin pale olive-brown to olive-yellow. *Lamellae* adnexed, somewhat crowded, when young olive yellow, later yellowish brown, edge concolourous. *Stipe* 40–80 mm long, 6–12 mm thick above, base 7–13 mm, cylindrical to clavate, pale greenish yellow fibrillose, later brownish yellow, brown at the base, *veil* pale greenish yellow, sparse, forming some incomplete zones on the stipe. *Context* in pileus dark yellowish brown, in the upper

part of the stipe pale yellowish brown to olive yellow, dark yellowish brown towards the base. *Odour* of lamellae indistinct. *Taste* not recorded. *Exsiccatae*. Pileus light brown to dark gray brown, lamellae medium brown, stipe light brown to grayish brown or yellowish, base more yellowish, context pale yellowish to pale brown. *UV*. Basidiomata context, lamellae, stipe and some areas of pileus bright yellow; *exsiccatae* lamellae, stipe and flesh yellow, with some duller areas on stipe and context, pileus brownish with some yellow areas.

*Basidiospores* (6.3–)6.7–7.8(–8.1) × 5.6–6.3(–7) μm, L × W<sub>m</sub> 7.3 × 6 μm, Q 1.1–1.4, Q<sub>m</sub> 1.2, subglobose or broadly ellipsoid, moderately to coarsely verrucose, ± moderately dextrinoid. *Basidia* 4-spored, clavate, 28–33 × 8–9 μm, colourless or grayish with darkened walls, some with yellow contents, commonly with refractive granules. *Pileipellis*: epicutis well developed, hyphae on disc forming entangled to interwoven mounds, on margin radially arranged, interwoven with some ascending loose fascicles, 4–22 μm wide, cylindrical, broadly cylindrical or enlarged, colourless, yellowish or orange yellow, some containing yellow pigment, walls refractive, ± thickened, yellowish colourless or darkened, smooth or encrusted; hypocutis poorly developed, on disc interwoven to entangled, on margin radially arranged, interwoven, 4.5–22.0 μm wide, cylindrical to broadly cylindrical or enlarged, colourless to yellow or orange yellow, some with yellow pigment, walls refractive, colourless to yellowish, smooth.

**Habitat & Distribution** — August and September, boreal conifer and mixed forests, *Picea*, *Pinus*, *Betula* and *Populus*. Known from Alaska and Alberta, Canada.

*Additional specimens examined*. CANADA, Alberta, Hinton, S. of centre, road to Percotte Creek, 1.5 km from the crossing, near creek, mixed forest *Picea*, *Populus* some *Pinus*, rich soil, 1 Sept. 2011, coll. K. Liimatainen, T. Niskanen 11-262 (H), GenBank MW009247; Hinton S/SW, from road 40 to Cold Creek Road, Cold Creek, older mixed forest of *Populus*, *Picea*, 2 Sept. 2011, coll. K. Liimatainen, T. Niskanen, 11-281 (H), GenBank MW009248. — USA, Alaska, Fairbanks, Ballaine Lake Trails, *Picea* dominated forest with *Betula* and *Populus*, rich soil, 14 Aug. 2011, K. Liimatainen, T. Niskanen, TN11-051 (H), GenBank MW009243; loc. cit. K. Liimatainen, T. Niskanen, TN11-053 (H), GenBank MW009246; Wedgewood Resort Trails, *Picea* dominated forest, some *Betula* and *Populus*, 16 Aug. 2011, coll. K. Liimatainen, T. Niskanen 11-106 (H), GenBank MW009244; loc. cit., 25 Aug. 2011, coll. K. Liimatainen, T. Niskanen 11-258 (H), GenBank MW009245.

**Notes** — *Cortinarius veneto-occidentalis* typical has a fibrillose to fibrillose tomentose to minutely squamulose pileus surface that is dark yellowish brown centrally and pale olive-brown to olive-yellow on the margin. It so far is known only from boreal forests. *Cortinarius veneto-occidentalis* s.lat. is widespread and common in western North America. It is related to *C. venetus* on the basis of sequence data, and has a similar morphology and ecology. Also, see *C. fuscoflavidus*, which has a darker pileus surface and corresponding darkly pigmented epicutis hyphae, and *C. aff. veneto-occidentalis* which is somewhat divergent from typical *C. veneto-occidentalis* and tends to have darker olivaceous pileus surface.

***Cortinarius aff. veneto-occidentalis*** — Fig. 4h

*Pileus* 32–62 mm diam, obtuse to obtusely umbonate, then plano-convex to plane or uplifted, usually umbonate to subumbonate, disc sometimes slight depressed to flattened, margin slightly incurved to decurved becoming plane to somewhat uplifted to irregular undulate, surface dry, ± matted fibrillose tomentose on disc, margin more radially fibrillose tomentose, disc yellowish olive with slight tint of brown in places, margin slightly lighter in colour or more yellowish, outer margin with watery olive streaks, disc and inner margin becoming more brownish to olive brown, then overall more brownish in age, eventually developing stronger brown, orange brown and red brown colours, broken areas stain orange brown, colours be-

come somewhat faded in very old pilei. *Lamellae* dull yellow buff to olive yellow, gradually brownish with olive undertone then more brownish, developing reddish stains, edges even to uneven, at first paler than concolourous, sinuate to emarginated with slight decurrent line. *Stipe* 42–55 mm long, 5–18 mm thick, clavate to clavate bulbous, apex shiny, silky fibrillose, pale olive buff, basal mycelium dull yellowish buff to more olive, surface developing reddish stains in age, lower one-half to two-thirds of stipe covered by a  $\pm$  persistent yellowish *veil*. *Context* of pileus solid, firm becoming fragile, at first whitish buff, becoming ochraceous buff with slight orange cinnamon stains, in stipe solid, stuffed, in age tunneled by larvae, cortex dull yellow buff or olive buff becoming brownish, in base pale brownish, developing reddish discolourations in age. *Odour* and *taste* of flesh  $\pm$  raphanoid. *Exsiccatae*. Pileus dark gray brown, grayish brown, light brown or pale olive yellow, lamellae brown to rust brown, context light buff, whitish buff, pale olive buff to brownish buff, stipe pale yellowish, grayish white, yellowish buff or brownish, basal mycelium yellowish white, yellowish, brownish or reddish brown. *UV*. Fresh basidiomata pileus surface and veil on stipe negative, otherwise bright, rich yellow; exsiccatae flesh and lamellae pale to light yellow, otherwise negative.

*Basidiospores* (6.7–)7–8.1(–8.5–9.6)  $\times$  5.6–6.7(–7–7.8)  $\mu\text{m}$ ,  $L \times W_m$  7.5  $\times$  6.1  $\mu\text{m}$ ,  $Q$  (1.1–)1.2–1.3(–1.4),  $Q_m$  1.26, subglobose, less commonly broadly ellipsoid,  $\pm$  coarsely verrucose, slightly- to somewhat moderately dextrinoid. *Basidia* mostly 4-spored (some 2- or 3-spored), broadly clavate to narrowly clavate, mostly 26–32  $\times$  7.4–8  $\mu\text{m}$ , colourless with colourless granules or filled with yellowish to yellowish brown pigment, wall somewhat thickened mature. *Pileipellis*: epicutis slightly to moderately developed, hyphae  $\pm$  radially arranged, interwoven to entangled, mostly 3–11  $\mu\text{m}$  wide, cylindrical to broadly cylindrical, colourless, yellowish or yellowish brown, occasionally with yellowish, orangish or reddish orange pigment, walls  $\pm$  refractive, colourless to yellowish, smooth or encrusted; hypocutis moderately developed, not forming a well-defined layer, hyphae  $\pm$  radially arranged, interwoven, mostly 4.5–20  $\mu\text{m}$  wide, cylindrical to broadly cylindrical or more enlarged, colourless or yellowish to yellowish brown, walls  $\pm$  refractive, smooth to encrusted.

*Habitat & Distribution* — In mixed conifer subalpine forests, of *Picea*, *Abies* and *Pinus*, Rocky Mountains, Siskiyou Mountain, August to October.

*Additional specimens examined*. USA, California, Siskiyou County, Carter Meadows, *Abies*, *Alnus*, 2 Oct. 1983, coll. J. Lennox, J. Ammirati, 10-2-83-7 (WTU); Colorado, Pitkin County, Frypan River, below Savage Lakes, *Picea*, 20 Aug. 1978, coll. J. Ammirati, JFA8148 (WTU); Oregon, Douglas County, Roseburg District, BLM, 23 Nov. 1998, coll. J. Trappe, OSC80195, GenBank EU669233; Washington, King County, Denny Creek, *Abies*, *Tsuga*, *Pseudotsuga*, 15 Oct. 2018, coll. S.D. Adams, SDA 382 (WTU); Wyoming, Teton County, Flagstaff Road, coll. J. Ammirati, 1 Sept. 1991, JFA10341 (WTU), GenBank MW009249; Fourmile Meadow, *Picea*, 3 Sept. 1991, coll. M. Moser, JFA10364 (WTU).

*Notes* — Morphologically very similar to typical material of *C. veneto-occidentalis* but strongly olivaceous coloured, especially on the pileus disc. Intermediate in ITS sequence between it and *C. fuscoflavidus*. A number of collections with similar colouration and basidiospores are included for reference. The basidiomata of *C. veneto-occidentalis* with darkly pigmented pileus surfaces are very similar in appearance and somewhat difficult to separate from one another.

***Cortinarius venetus* (Fr.) Fr., Epicr. Syst. Mycol. (Upsaliae): 291. 1838 '1836–1838'**

*Basionym*. *Agaricus raphanoides*  $\beta$  *venetus* Fr. 1821.

Sanctioning citation: Fr., Syst. Mycol. 1: 230. 1821.

= *Cortinarius pseudovenetus* Rob. Henry, Bull. Trimestriell. Soc. Mycol. France 77 (2): 116. 1961.

= *Cortinarius venetus* var. *viridis* Moëgne-Locc., in Bidaud, Moëgne-Loccoz, Carteret, Reumaux & Eyssartier, Atlas des Cortinaires (Meyzieu) 15: 1033. 2005. — Type: Sweden, Uppland, Uppsala-näs sn, Dalkarlskäret, coniferous forest (*Pinus*, *Picea*), 18 Aug. 1986, Lindström et al. CFP112, F44498 (S, *neotypus hic designatus*), IF 143469, MycoBank MBT 393869; ITS barcode GenBank MW009250.

### *Incertae sedis*

***Cortinarius atosquamosus* Niskanen, Liimat., Peintner, Kuhn.-Fink. & Ammirati, sp. nov.** — MycoBank MB 837396; Fig. 3a, 5a–c

*Etymology*. Named for the dark squamulose pileus surface.

*Typus*. USA, California, Mendocino County, Mendocino, *Notholithocarpus*, *Pseudotsuga*, 8 Dec. 2012, coll. K. Liimatainen, T. Niskanen (holotype H 7068349), (isotype K); ITS barcode GenBank MW009183.

*Diagnosis* — In conifer and conifer-broadleaf forests of western North America. Basidiomata medium sized; pileus black, dark brown to olive brown; lamellae olive yellow to olive brown; veil thin, pale, with yellow to olive or brown tints; basidiospores  $L \times W_m$  7.3  $\times$  5.4  $\mu\text{m}$ , moderately to more coarsely verrucose, subglobose, broadly ellipsoid and ellipsoid. Forming a strongly supported monotypic lineage with relatively high (0.7 %) intraspecific variation.

*Pileus* 30–60 mm diam, at first hemispherical then low convex to plane, margin  $\pm$  incurved, surface velvety scaly,  $\pm$  fibrillose scaly or squamulose, black, dark brown to olive brown. *Lamellae* adnexed, somewhat crowded, olive yellow to olive brown. *Stipe* 35–65(–104) mm long, 4–10 mm thick above, base 7–12 mm thick, cylindrical to somewhat clavate, surface at first covered with white fibrils, later becoming very pale brownish yellow. *Veil* white developing yellow to brown or olive brown tints, thin, sometimes forming thin, sock-like sheath on the lower part of the stipe. *Context* in pileus dark brown, in stipe pale yellow brown. *Odour* of lamellae and context raphanoid. *Taste* raphanoid. *Exsiccatae*. Pileus surface black to olive black, lamellae dull dark brown, stipe and context grayish to blackish or olivaceous with some pale areas, basal mycelium pale to off white. *UV*. Fresh basidiomata bright yellow overall, but pileus and stipe with some brown areas; exsiccatae pileus surface negative, lamellae pale greenish yellow to pale yellow, stipe surface yellow, pale orange or negative, stipe base bright yellow, context yellow or negative.

*Basidiospores* 5.9–7.8(–8.3)  $\times$  (4.4–)5.2–5.9(–6.3)  $\mu\text{m}$ ,  $L \times W_m$  7.3  $\times$  5.4  $\mu\text{m}$ ,  $Q$  1.2–1.63,  $Q_m$  1.4, subglobose, broadly ellipsoid or ellipsoid, moderately to more coarsely verrucose, non-dextrinoid to slightly dextrinoid. *Basidia* 4-spored, 27–39  $\times$  7.0–7.5  $\mu\text{m}$ , clavate to narrowly clavate, colourless, pale yellow or pale grayish yellow. *Pileipellis*: epicutis well developed, hyphae interwoven, radially arranged or ascending, often forming fascicles, especially on disc, 5–20  $\mu\text{m}$  wide, cylindrical, broadly cylindrical or enlarged, olivaceous to yellowish olive then pale yellowish or pale orange-yellow to colourless, some with orange-yellow contents, walls  $\pm$  thickened, colourless to yellowish, refractive, smooth or encrusted; hypocutis poorly developed, hyphae  $\pm$  radially arranged, interwoven on margin, interwoven to entangled on disc, 6–21  $\mu\text{m}$  wide, cylindrical to broadly cylindrical or enlarged, colourless, slightly olive or yellowish, wall colourless to yellowish, refractive, smooth or encrusted.

*Habitat & Distribution* — Primarily occurring in conifer forest, but also in mixed conifer-broadleaf forests, *Pseudotsuga* and *Notholithocarpus*, *Pseudotsuga*, *Tsuga* and *Betula*, coastal to subalpine, reported from northern California to British Columbia.

*Additional specimens examined*. CANADA, British Columbia, McCabe Trail, Smithers, mixed conifers, Sept. 2006, coll. M. Kranabetter, F16365, SMI A38 (UBC), GenBank FJ039586. — USA, Oregon, Benton County, Woods



**Fig. 5** Basidiomata. a. *Cortinarius atosquamosus* TN-12-278 (holotype); b. *C. aff. atosquamosus* SDA 421; c. *C. aff. atosquamosus* JFA10385; d. *C. brunneofibrillosus* 11MWB111813; e. *C. clandestinus* DBB21905 (western); f. *C. clandestinus* ADP151006-1 (western); g. *C. clandestinus* BD325 (eastern); h. *C. clandestinus* (non-fibrillose scalyform) CLC 3340. — Photos by: a. K. Liimatainen; b–c. S.D. Adams; d. M. Beug; e. D. Bojantchev; f. A.D. Parker; g. B. Dentinger; h. C. Cripps.



Creek Road, trail to Mary's Peak, *Tsuga, Pseudotsuga*, 13 Nov. 1995, coll. *J. Ammirati*, JFA11754 (WTU); Washington, Chelan County, Rainy Pass, trail to Lake Ann, *Abies, Picea*, 29 Aug. 1989, coll. *M.M. Moser, J. Ammirati*, JFA10003 (WTU), (= IBF19890363); Jefferson County, Buckhorn Wilderness Area, *Abies, Tsuga, Pseudotsuga*, 11 Oct. 1995, coll. *J. Ammirati*, JFA11545 (WTU); King County, Redmond Watershed Preserve (Watermain Woods), mixed conifer/alder forest, 17 Nov. 1984, coll. class foray, JFA9104 (WTU); Tonga Ridge, *Abies, Tsuga*, 8 Oct. 2018, coll. *S.D. Adams*, SDA357 (WTU), GenBank MW009184; King-Kittitas County Line, Stampede Pass, mixed conifers, 3 Oct. 1981, coll. *J. Ammirati*, JFA8508 (WTU); Island County, Langley, *Pseudotsuga, Tsuga*, 9 Nov. 1993, coll. *S. Redhead, G. Barron*, JFA11157 (WTU); Mason County, High Steel Bridge, Olympic National Forest, *Pseudotsuga, Tsuga, Abies*, 3 Nov. 2018, coll. *S.D. Adams*, SDA421 (WTU), GenBank MW009185; loc. cit. Deer Lake trail, Canyon Creek area, *Pseudotsuga, Tsuga*, 4 Oct. 1995, coll. *J. Ammirati*, JFA11511 (WTU); Mason Lake, *Pseudotsuga*, 17 Nov. 1979, coll. *J. Ammirati*, JFA8453 (WTU); Mount Rainier National Park, Cougar Rock Campground, *Tsuga, Pseudotsuga, Abies, Pinus*, 18 Oct. 1995, coll. *J. Ammirati*, JFA11590 (WTU); Skagit County, Easy Pass Trailhead, 6 Sept. 1989, mixed conifers, *Abies lasiocarpa, Pseudotsuga, Picea engelmannii*, coll. *J. Ammirati*, JFA10040 (WTU), (IBF19890434), GenBank MW009236; loc. cit., 29 Sept. 1991, coll. *J. Ammirati*, JFA10385 (WTU), GenBank MW009186; Whatcom County, Lucie Road, *Pseudotsuga, Tsuga, Betula*, 30 Oct. 2010, coll. *J. Ammirati*, JFA13611 (WTU).

Notes — *Cortinarius atrosquamosus* is widespread, overlaps in distribution with *C. clandestinus*, and their habit of growth and colouration are somewhat similar except that the veil in *C. clandestinus* is more distinctly yellow to greenish yellow or olivaceous. The exsiccatae can be separated on the basis of the pileus epicutis hyphae; when mounted in KOH they are yellow to orange-yellow or olivaceous in *C. atrosquamosus*, and black to grayish in *C. clandestinus*. *Cortinarius atrosquamosus* also has significantly smaller basidiospores than *C. clandestinus*. Spore shape is somewhat variable in *C. atrosquamosus*, and is usually a combination of ellipsoid, broadly ellipsoid and subglobose spores, but some collections, e.g., JFA10040, have a larger proportion of ellipsoid spores. The exsiccatae are somewhat variable in colour, typically the pileus is blackish with olivaceous tones and the stipe is tinted olivaceous gray, but in other collections the pileus and stipe have less olive colour. Some fresh collections, mainly those from subalpine conifer forests tend to have darker brown to blackish brown pileus colouration (e.g., less olive colouration than the holotype, compare Fig. 5a, b, c), which to some degree correlates with exsiccatae colour. Intraspecific variation in ITS sequences is relatively high (0.7 %) in *C. atrosquamosus*. For example, SDA357, JFA10385 (Fig. 5c) and JFA10040 differ from the type of *C. atrosquamosus* by 2 base pairs while SDA421 (Fig. 5b) differs from the type of *C. atrosquamosus* and from SDA357, JFA10385 and JFA10040 by 3 base pairs. However, so far this variation does not appear to be consistent with any set of morphological or ecological characteristics and requires further study in the future.

***Cortinarius brunneofibrillosus*** Ammirati, Beug, Niskanen, Liimat. & Bojantchev, *sp. nov.* — MycoBank MB 837397; Fig. 3b, 5d

*Etymology.* The name refers to the brown fibrillose pileus surface.

*Typus.* USA, Washington, Klickitat County, Balch Farm, *Quercus garryana*, scattered *Pinus ponderosa*, 13 Nov. 2010, coll. *J. Ammirati, M. Beug* (holotype WTU 073591), (isotype K); ITS barcode GenBank MW009188.

*Diagnosis* — In *Quercus* and mixed *Quercus* conifer woodlands of western North America; basidiomata medium to larger in size; pileus surface fibrillose, fibrillose tomentose and fibrillose scaly; colouration dull olivaceous to yellowish brown, with reddish brown discolourations; odour often of marjoram; basidiospores  $L \times W_m$   $8 \times 6.4$   $\mu\text{m}$ , subglobose to broadly ellipsoid, moderately to coarsely verrucose. Forming a strongly supported monotypic lineage with some intraspecific variation.

*Pileus* 68–75(–132) mm diam, obtuse to broadly obtuse, umbonate, margin slightly incurved to decurved then straight, irregular

or upturned, surface dry to moist, fibrillose, fibrillose tomentose and fibrillose scaly, ground colour light buff, chamois or dull yellowish buff, sometimes hardly visible beneath fibrillose covering, overall colour olive brown to olive with blackish tones on disc, developing dull reddish brown to dark red-brown or watery red brown colours, then the olive brown fibrils sometimes less obvious. *Lamellae* adnexed, close to subdistant,  $\pm$  thick, edges uneven, colour yellowish to brownish yellow, rather brightly coloured at first, then more brownish, in age dark rust brown. *Stipe* 60–111(–118) mm long, above 15–18(–28) mm thick, tapered to base (base sometimes slightly enlarged), general colour of stipe whitish to faintly yellowish buff or pale yellowish above veil zone, longitudinally fibrillose with apex shiny and fibrillose, in age discolouring yellowish to brownish or reddish brown, veil yellowish and thinly sheathing below, ending in a narrow zone near mid-stipe. *Context* of pileus solid, firm, whitish, pallid, pale yellowish buff, brownish white or watery brown to brownish yellow above stipe apex, context of stipe buff white to pallid or yellowish buff with dull watery brown streaks, cortex sometimes more yellowish, in base darker yellow, sordid or dull brownish, context darkening on exposure or in age, brown to reddish brown in stipe. *Odour* of lamellae and/or flesh marjoram like or raphanoid; *taste* of context mild to slightly bitter. *Exsiccatae*. Pileus surface blackish to gray brown, with a slight purplish cast, lamellae dull rust brown, edges sometimes blackish, stipe dull creamy white or brownish, base reddish brown, context dull creamy white to brownish. *UV*. Fresh basidiomata pileus, lamellae and stipe bright yellow to yellow brown or light to pale yellow, context bright yellow to yellow brown; exsiccatae pileus brown, lamellae pale greenish gray, stipe surface light yellow, context pale coloured but not yellow.

*Basidiospores*  $7.4$ – $8.5$ (– $9.3$ )  $\times$   $5.9$ – $6.7$   $\mu\text{m}$ ,  $L \times W_m$   $8 \times 6.4$   $\mu\text{m}$ ,  $Q$   $1.2$ – $1.4$ ,  $Q_m$   $1.3$ , subglobose to broadly ellipsoid, moderately to coarsely verrucose, moderately dextrinoid. *Basidia* 4-spored,  $33$ – $44 \times 7.4$ – $8.0$   $\mu\text{m}$ , clavate to narrowly clavate, colourless, yellowish or grayish becoming olive yellow brown. *Pileipellis*: epicutis hyphae interwoven to entangled,  $5$ – $12$   $\mu\text{m}$  wide, cylindrical to somewhat broadly cylindrical, with gray or brown contents or colourless, walls thickened, refractive, yellowish, smooth or slightly encrusted; hypocutis poorly developed, hyphae  $\pm$  radially arranged, interwoven,  $9$ – $20$   $\mu\text{m}$  wide, broadly cylindrical to enlarged, colourless to yellowish, walls somewhat thickened, refractive, colourless or yellowish, smooth.

*Habitat & Distribution* — Known only from western North America. In oak woodland *Quercus garryana*, *Q. agrifolia* or mixed woods *Q. garryana*, *Abies grandis* and *Pseudotsuga* or *Q. garryana* and *Pinus ponderosa*.

*Additional specimens examined.* USA, California, San Mateo County, Huddart Park, *Quercus agrifolia*, 24 Nov. 2009, coll. *D. Bojantchev*, DBB28271 (WTU, Pers. Herb.), GenBank MT853253; Shasta County, Castella, mixed woods, *Quercus, Pseudotsuga, Pinus*, 29 Nov. 2009, coll. *J. Ammirati*, JFA13388 (WTU); Washington, Klickitat County, Balch Farm, *Q. garryana*, scattered *Pinus ponderosa*, 13 Nov. 2010, coll. *J. Ammirati, M. Beug*, JFA13654 (holotype) (WTU), GenBank MW009188; loc. cit., *Q. garryana*, 20 Nov. 2013, coll. *M. Beug*, 06MWB112013 (WTU), GenBank MW009190; Beug Farm, *Q. garryana*, 20 Nov. 2010, coll. *J. Ammirati, M. Beug*, JFA13664 (WTU), GenBank MW009191; Lower Staats Road, *Q. garryana*, 18 Nov. 2013, coll. *M. Beug*, 11MWB111813 (WTU), GenBank MW009192; loc. cit., coll. *M. Beug*, 13MWB111813 (WTU), GenBank MW009193; loc. cit., 18 Nov. 2013, coll. *M. Beug*, 15MWB111813 (WTU), GenBank MW009194; above Old Lindseth Road, *Q. garryana*, 16 Nov. 2010, coll. *M. Beug*, 09MWB111610 (WTU), GenBank MW009195; Rattle Snake Creek Natural Area, *Q. garryana*, 3 Nov. 2010, coll. *M. Beug*, 01MWB110310 (WTU), GenBank MW009196; Spring Creek Road, *Q. garryana, Pseudotsuga, Abies grandis*, 12 Nov. 2008, coll. *M. Beug*, 02MWB111308 (WTU), GenBank MW009197; intersection of Staats and Rattlesnake Roads, *Q. garryana*, coll. *M. Beug*, 05MWB111910 (WTU), GenBank MW009198; loc. cit., coll. *M. Beug*, 06MWB111910 (WTU), GenBank MW009189.

Notes — This species can be rather common and is consistently associated with *Quercus*. The colouration of the fresh basidiomata, including the reddish brown discoloration in age, make this an easy species to identify in the field. With a sister relationship to *C. clandestinus* from which it is morphologically distinctive.

***Cortinarius clandestinus*** Kauffman, N. Amer. Fl. (New York) 10 (5): 324. 1932 — IF 261040; Fig. 3c, 5e–g

Forming a strongly supported monotypic lineage with intraspecific variation around 1 % and sister to *C. flavifolius* from which it is morphologically distinctive.

**Pileus** 43–100 mm diam, campanulate-convex to convex umbo then plane, becoming depressed around slight umbo, margin incurved to decurved, when young with an olivaceous yellow silky veil, surface dry, densely covered with dark olive brown, blackish olive or black fibrillose scales overall or disc densely fibrillose scaly and margin less densely fibrillose scaly, the edge with similarly coloured fibrillose streaks, ground colour on margin yellowish buff, yellowish, olivaceous yellow, edge grayish olive buff in places. **Lamellae** adnexed to adnate, close to subdistant, pallid to brownish chamois, yellow or yellow brown with olivaceous tinge, becoming rich medium brown to rusty brown mature, edges pale, somewhat irregular to uneven. **Stipe** 40–100 mm long, apex (5–)7–18 mm thick, equal or tapered to base, or base sometimes clavate to bulbous, pallid yellowish buff, pale yellow, yellowish white or pale yellow to light yellow, basal mycelium yellowish white to pale sulfur yellow, discolouring rust brown to reddish brown in age; **veil** yellow, light greenish yellow, pale olivaceous or dark olivaceous, sheathing the lower surface or forming zones and fibrils. **Context** of pileus solid, in stipe stuffed to hollow, firm, buff, pale yellow or yellowish olive throughout, some areas becoming rust brown, orange buff, orange brown or reddish brown, in base tinted dingy or grayish olive. **Odour** pleasant, raw potatoes, parsley, or raphanoid; **taste** of context raphanoid. **Exsiccatae**. Pileus blackish to blackish olive or brown or pale gray olive, lamellae bright rusty cinnamon, stipe variable in colour, pale whitish, yellowish white, olive to grayish, blackish or orange brown, basal mycelium whitish, context pale whitish to somewhat brownish. **UV**. Fresh basidiomata lamellae and stipe cortex brilliant yellow, pileus surface, veil zones and interior of stipe and pileus negative; exsiccatae lamellae very bright yellow, stipe surface and cortex yellow to orange yellow, context pale whitish or yellow in stipe base, pileus surface and veil zones negative.

**Basidiospores** (6.3–)6.7–8.3(–8.9–9.6) × 5.2–6.3(6.6–7.4) µm, L × W<sub>m</sub> 7.5 × 5.8 µm, Q 1.25–1.45, Q<sub>m</sub> 1.3, broadly ellipsoid to subglobose, moderately to coarsely verrucose, ± moderately dextrinoid. **Basidia** 4-spored, 27–37 × 7.5–8.5 µm, clavate to cylindrical clavate, colourless, yellowish, darkly pigmented, some with refractive granules. **Pileipellis**: epicutis well developed, hyphae interwoven, radially arranged in places, but mainly in ascending fascicles, 4–15(–22) µm wide, cylindrical, broadly cylindrical or somewhat enlarged, blackish, grayish, olive gray, olive, yellowish or colourless, some with blackish refractive granules, walls ± thickened, refractive, colourless to yellowish or grayish, smooth or encrusted; hypocutis somewhat developed, hyphae ± radially arranged, interwoven to strongly interwoven on disc, 5.2–24 µm wide, cylindrical, broadly cylindrical or enlarged, colourless, yellowish or with orange to orange red pigment, walls refractive, ± thickened, colourless or yellowish, smooth.

**Habitat & Distribution** — From lowland to subalpine and boreal conifer forests, occurring with *Pseudotsuga*, *Tsuga*, *Abies*, *Picea* and/or *Pinus*, in boreal forests also in mixed forests of conifers with *Populus*, *Betula* and *Alnus*. From California to

British Columbia east into the Rocky Mountains, also occurring in the Great Lakes region and south eastern Canada. Producing basidiomata from spring through the fall season, depending on location and elevation. In eastern North America, only known from the spring season. In the spring and summer the typical form co-occurs with the non-fibrillose scaly form.

**Specimens examined**. CANADA, British Columbia, Vancouver Island, Squamish, Alice Lake Provincial Park, *Picea sitchensis*, *P. engelmannii*, 20 Oct. 2009, coll. D. Bojantchev, DBB21905 (WTU, Pers. Herb.), GenBank MT853251; East Sooke Park, *Pinus*, *Pseudotsuga*, 12 Apr. 2008, coll. O. Ceska, OC6, F16361 (UBC); Mt Washington, mixed conifers, 13 Sept. 2001, coll. O. Ceska, OC47, F17119 (UBC); loc. cit., mixed forest, 2 July 2002, coll. O. Ceska, OC55, F17127 (UBC); Sheep Creek Road, south of Salmo, conifer forest, *Tsuga*, 9 June 2013, coll. A.D. Parker, ADP-130609-1 (WTU); Quebec, Saint-Émile-de-Suffolk, mixed forests, coll. A. Paul, R. Lebeuf, 30 May 2009, HRL0186 (WTU, Pers. Herb.), GenBank MW009210; loc. cit., coll. R. Lebeuf, 29 May 2011, HRL0678 (WTU, Pers. Herb.). — USA, California, Sierra County, Camp Leonard, conifer forest, 22 Sept. 1975, coll. H.D. Thiers, HDT34911 (SFSU); Siskiyou County, Carter Meadows, mixed conifers, 2 Oct. 1983, coll. J. Lennox, JFA 10-2-83-1 (WTU); Idaho, Idaho County, Upper Hazard Lake, mixed conifers, 28 June 1965, coll. O.K. Miller, OKM3184 (VPI); Fall Creek, mixed conifers, 4 Sept. 1964, coll. H.D. Thiers, HDT11651 (SFSU); loc. cit., 6 Sept. 1964, coll. H.D. Thiers, HDT11699 (SFSU); Michigan, Cheboygan County, Reese's Bog, mixed woods, *Pinus*, 4 June 1970, coll. J. Ammirati, JFA4077 (MICH); Otsego County, Pigeon River, mixed conifer-broadleaf forest, 15 May 1982, coll. C. Ovrebo, CO1400 (MICH); Minnesota, Lake County, Duluth, Lester Park, *Abies*, *Pinus*, *Picea*, *Populus*, *Betula*, *Alnus*, 29 May 2005, coll. B. Dentinger, BD326 (MIN), GenBank MW009209; Montana, Gallatin County, Hyalite Canyon, *Picea*, *Pinus contorta*, 25 Sept. 2017, coll. C.L. Cripps, CLC3624 (MONT); Park County, New World District, *Pinus*, *Picea*, *Abies*, 11 July 2005, coll. C. Cripps, CLC2114 (MONT); loc. cit., *Pinus albicaulis*, CLC2115 (MONT); loc. cit., *Pinus albicaulis*, 12 July 2006, CLC2123 (MONT); Oregon, Deschutes County, Elk Lake, Mt Bachelor, conifer forest, 27 June 1984, coll. J. Ammirati, JFA8964 (WTU); Washington, Chelan County, Smith Brook Road, about 2 mi from HW 2, *Tsuga*, *Abies*, 27 June 1991, coll. J. Ammirati, JFA10284, JFA10285 (WTU), GenBank MW009201; King County, Mason Lake trailhead, 1 May 2004, *Tsuga*, *Pseudotsuga*, coll. J.M. Birkebak, JMB165 (WTU); Stamped Pass, mixed conifers, 2 June 1984, coll. G. Picionne, JFA8986 (WTU), GenBank MW009202; Snoqualmie Pass, *Pseudotsuga*, 10 June 2003, coll. J. Birkebak, JMB42 (WTU), GenBank MW009205; Kittitas County, Table Mountain, subalpine, *Picea*, *Pinus*, *Abies*, *Tsuga*, 11 Sept. 2008, coll. J. Ammirati, JFA13261, JFA13263, GenBank MW009203 (WTU); loc. cit., 9 Oct. 2011, coll. J. Ammirati, K. Liimatainen, TN11-454 (H), GenBank MW009204; Circle 8 Ranch, mixed conifers, 17 May 2003, coll. foray member, S. Trudell, SAT03-137-02 (WTU); Mason County, Lake Cushman, mixed conifers, 19 Oct. 1915, coll. C.H. Kauffman (holotype) (MICH), GenBank MW009200 (ITS1 only); Snohomish County, Barlow Pass, *Tsuga*, *Abies*, 22 Sept. 1995, coll. M. Moser, IB1995-165a (IBF), GenBank MW009206; Olympic National Park, Deer Lake, *Tsuga*, *Abies*, 12 Oct. 1995, coll. J. Ammirati, JFA11560 (WTU); Pend Oreille County, Sullivan Creek road, *Tsuga*, *Thuja*, *Abies*, 1 June 2009, coll. A.D. Parker, ADP090601-1 (WTU); Pierce County, Buck Creek, HW 410, *Tsuga*, *Pseudotsuga*, 27 Oct. 2000, coll. B. Matheny, JFA12864 (WTU); Skagit County, Easy Pass Trailhead, *Abies*, *Picea*, 3 Sept. 1989, coll. M.M. Moser, JFA10026 (WTU), IBF19890407 (IBF); Skamania County, Lake Takhlakh, *Abies*, *Pinus*, *Picea*, *Tsuga*, 24 June 2001, coll. J. Ammirati, JFA12890 (WTU); Whatcom County, Silver Fir Camp, *Tsuga*, *Abies*, 8 Nov. 1987, coll. J. Ammirati, JFA9665 (WTU).

Notes — Typical *C. clandestinus* is one of the most common and widely distributed species in western North America, reproducing throughout the growing season depending on location and elevation. In eastern North America it is less frequent and known only from the spring season. Basidiospore size and shape are rather consistent, but some collections (e.g., JMB165) have a higher proportion of larger spores, 8.9 µm or more in length. The dark fibrillose scales often completely cover the surface of the pileus, however, in a number of collections, especially when the pilei are expanded, the fibrillose scales become ± spaced and dispersed over the pileus margin. Also see comments under the non-fibrillose scaly form (described below). The pileus epicutis hyphae of *C. clandestinus* exsiccatae in KOH are typically black to gray unlike the mainly olivaceous to yellow olivaceous epicutis hyphae of *C. atro-*

*squamosus*, another common western species. *Cortinarius fuscotomentosus* is morphologically similar to *C. clandestinus* but it has smaller, more subglobose basidiospores and occurs in broadleaf and mixed broadleaf-conifer forests. All of the collections from eastern North America have a  $\pm$  fibrillose scaly pileus surface and are morphologically similar to western collections of *C. clandestinus*. Intraspecific variation in *C. clandestinus* is around 1 %, with typical *C. clandestinus* and the non-fibrillose scaly form intermixed throughout the clade, and for the most part irrespective of phenology.

***Cortinarius clandestinus* (non-fibrillose scaly form)** — Fig. 3d, 5h

*Pileus* 30–80 mm diam, rounded conic, conic-convex to convex,  $\pm$  umbonate, margin decurved, glabrous to finely fibrillose or finely fibrillose scaly on disc, typically lacking conspicuous, dark fibrillose scales, colour ochraceous, brownish yellow, yellow brown, brown or reddish brown, sometimes mottled olive brown, some young stages more olive coloured, sometimes with more blackish olive to blackish colouration, especially on the disc. *Lamellae* adnexed to slightly subdecurrent, ochraceous to ochraceous brown becoming orange, deep orange to golden orange with reddish spots, edges concolourous. *Stipe* 40–70 mm long, 8–20 mm thick,  $\pm$  equal or gradually thicker towards base, pale yellow, pale olive yellow, yellow ochre to brownish orange; *veil* lemon yellow, yellow or pale yellow, sheathing or forming bands below annular zone, sometimes also with brown fibrils below. *Context* yellow ochre to buff, yellow or watery orange yellow becoming watery brown or discoloured reddish, stem hollow in age. *Odour* and *taste* of flesh  $\pm$  raphanoid. *Exsiccatae*. Pileus light medium brown to grayish, lamellae rusty brown, flesh light dull creamy to brownish, stipe pale yellowish white, cream colour or brownish, basal mycelium whitish to dull cream colour. *UV*. Fresh basidiomata  $\pm$  bright yellow; exsiccatae lamellae pale to light yellow, otherwise  $\pm$  negative reaction overall or sometimes  $\pm$  yellow on stipe and context.

*Basidiospores* 6.3–8.1  $\times$  5.2–5.9  $\mu\text{m}$ ,  $L \times W_m$  7.3  $\times$  5.6  $\mu\text{m}$ ,  $Q$  1.2–1.45,  $Q_m$  1.3, subglobose to broadly ellipsoid, moderately to coarsely verrucose, slightly to moderately dextrinoid. *Basidia* 4-spored, 26–31  $\times$  6.5–9  $\mu\text{m}$ , clavate, colourless, some with refractive granules or yellowish pigment. *Pileipellis*: epicutis  $\pm$  well developed, hyphae interwoven to entangled, 4.5–12.5 (–16)  $\mu\text{m}$ ,  $\pm$  cylindrical, some grayish to pale blackish otherwise colourless to yellowish or containing orange to yellow pigment, walls smooth or encrusted, refractive,  $\pm$  thickened; hypocutis poorly developed, hyphae interwoven, radially arranged, 5–26  $\mu\text{m}$  wide, cylindrical to broadly cylindrical to enlarged, colourless or yellowish to orange yellow, wall refractive, smooth.

**Habitat & Distribution** — Montane, subalpine and boreal conifer forests of *Abies*, *Pinus*, *Picea*, *Pseudotsuga* and/or *Tsuga*, and mixed conifer boreal forests with *Alnus*, *Betula* and *Populus*. It reproduces only in the spring and early summer, from California into the Pacific Northwest and Rocky Mountains as well as eastern North America.

**Specimens examined.** USA, California, El Dorado County, Crystal Basin Wilderness, mixed conifers, 22 May 2009, coll. *D. Bojantchev*, DBB15293, GenBank MT853248, DBB15563 (WTU, Pers. Herb.), GenBank MT853249; Sierra County, McNair Meadow, mixed conifers, 13 June 1984, coll. *H.D. Thiers*, JFA8916, JFA8917 (WTU); Colorado, Jackson County, Cameron Pass, subalpine, mixed conifers, *Picea*, 4 Aug. 1984, coll. *A. Methven*, JFA9011 (WTU), GenBank MW009212; Idaho, Adams County, Lower Brundage Mountain, mixed conifers, 10 June 1966, coll. *O.K. Miller*, OKM3923 (NYBG); Valley County, Upper Payette Lake, *Picea*, *Pinus*, *Abies*, 13 June 1986, coll. *J. Ammirati*, JFA9286 (WTU), GenBank MW009213; Minnesota, Lake County, Knife River, Westover Road, below Steelhead Sanctuary, *Abies*, *Alnus*, 28 May 2005, coll. *B. Dentinger*, BD325 (MIN), GenBank MW009208; Montana, Gallatin County, *Picea*, *Pinus*, *Abies*, 3 July 2006, coll. *C.L. Cripps*, CLC2335E (2339) (MONT); Fridley, *Picea*, *Pinus*, *Abies*, 9 June 2006, coll.

*C.L. Cripps*, CLC2233 (MONT), GenBank MW009211; Hyalite Canyon, *Pinus contorta*, 31 May 2017, coll. *C.L. Cripps*, CLC3340 (MONT); Madison County, Gravelly Mountain, *Pinus*, *Picea*, 6 July 2005, coll. *C. Cripps*, CLC2112 (MONT); Missoula County, Missoula area, mixed conifers, May 1984, coll. *S. Rehner*, JFA8909 (WTU); Washington, Pend Oreille County, Powerline Corridor & Hanks Butte Road South of Lone, *Pinus contorta*, *Abies grandis*, 15 May 2009, coll. *A.D. Parker*, ADP090515-1 (WTU), GenBank MW009214; Wyoming, Albany County, Medicine Bow Mts, Snowy Range, subalpine, mixed conifers, 27 July 1983, coll. *M. Moser*, IBF19830140 (IBF); Teton County, Shoshone National Forest, *Picea engelmannii*, *Pinus albacaulis*, 28 July 1997, coll. *M. Moser*, IBF19970069 (IBF), GenBank MW009215.

**Notes** — Some collections lack dark fibrillose scales (CLC2233), while other collections have some fibrillose scales on the disc (CLC2112) and even onto margin (JFA8917). The stature is variable, from slender basidiomata to larger ones with a thick stipe and pileus context. Collected only in the spring and early summer months. See comments under *C. clandestinus*.

***Cortinarius flavifolius* Peck, Rep. (Annual) Trustees State Mus. Nat. Hist., New York 41: 72. 1888 — IF 221292; Fig. 2c, 3g**

*Holotype*. USA, New York, Catskill Mountains, woods, Sept. 1887, coll. *C.H. Peck*, NYSf1209, (NYS)

*Epitype*. USA, Tennessee, Robertson County, Greenbrier, *Quercus*, 30 Aug. 2013, coll. *E. Harrower*, EH 230 (TENN 068695, *epitypus hic designatus*); ITS barcode GenBank MW009217. MycoBank MBT 393868.

= *Cortinarius rubroclavus* L. Krieg., Mycologia 19: 309. 1927. IF 161713.

Forming a monotypic well-supported lineage with more than twenty-two differences in ITS from other *Leprocyebe* species, a similarity of 96.4 %.

*Pileus* 33–75 mm diam, rounded umbonate to convex or nearly plane, fibrillose to squamulose, sometimes longitudinally rimose, not truly hygrophanous, varying in colour from pale yellow to creamy yellow or sordid buff to tawny yellow, sometimes reddish tinged. *Lamellae* subdistant, adnexed, at first a rich sulfur yellow to mustard yellow then yellowish cinnamon, edges eroded. *Stipe* 48–100 mm long, 10–18 mm thick, slightly tapering upward, bulbous (up to 35 mm thick), whitish to white or pale yellowish, sometimes changing to a deep saffron red (from handling), basal mycelium pale yellow, peronate and slightly annulate from a copious, silky white to whitish veil. *Context* solid, creamy white to whitish or pale yellow, staining reddish saffron. *Odour* of context raw potato, pungent or not distinctive; *taste* mild, slightly bitter or fungoid. *Exsiccatae*. Pileus surface light medium brown, with reddish tints on disc, lamellae rich medium rust brown, pileus and stipe flesh pale with brownish and grayish discolourations, stipe pale with brownish tones on lower stipe, base with some whitish mycelium. *UV*. Pileus surface brown with some light yellowish areas, context of stipe and pileus pale yellow, the lamellae and stipe light to bright yellow; exsiccatae pileus brown, context, lamellae and stipe bright yellow.

*Basidiospores* (6.7–)7.0–8.1 (–8.9)  $\times$  (4.8–)5.6–5.9  $\mu\text{m}$ ,  $L \times W_m$  7.6  $\times$  5.6  $\mu\text{m}$ ,  $Q$  1.25–1.51,  $Q_m$  1.36, broadly ellipsoid to subglobose, very coarsely verrucose, slightly to moderately or more strongly dextrinoid. *Basidia* 4-spored, 26–35  $\times$  7.5–9.0  $\mu\text{m}$ , clavate, colourless, often with refractive granules or yellow contents. *Pileipellis*: epicutis thin to more developed, hyphae interwoven and radially arranged, with some clusters of entangled hyphae, cylindrical to broadly cylindrical, 4–17  $\mu\text{m}$  wide, colourless, to yellowish or with yellow contents, walls  $\pm$  thickened, refractive, colourless to yellowish, smooth or some slightly encrusted; hypocutis poorly developed, hyphae radially oriented, interwoven, cylindrical to broadly cylindrical or  $\pm$  enlarged, 4.5–19.0  $\mu\text{m}$  wide, colourless to yellowish or with yellow contents, walls refractive, colourless to yellowish.

**Habitat & Distribution** — Broadleaf and mixed broadleaf-conifer forests, *Pinus*, *Tsuga*, *Quercus*, *Betula*, *Fagus*, *Acer*, and/or *Fraxinus*, eastern North America.

**Additional specimens examined.** CANADA, Quebec, Boucherville, *Quercus rubra*, 19 July 1998, coll. Y. Lamoureux, CMMF003226, GenBank MW009220; Notre-Dame-du-Mont-Carmel, *Fagus*, *Tsuga*, 28 Aug. 2016, coll. R. Lebeuf, A. Paul, HRL2287 (Pers. Herb.); Pointe-au-Chêne, *Fagus*, 23 Sept. 2011, coll. R. Lebeuf, A. Paul, HRL0942 (Pers. Herb.); Sainte-Anne-de-Bellevue, Morgane Arboretum, *Quercus rubra*, 21 Sept. 2011, coll. R. Lebeuf, A. Paul, HRL0925 (Pers. Herb.). — USA, Florida, Alachua County, High Springs, O'Leno State Park, xeric oak-pine hammock, 13 Jan. 2015, coll. K. Liimatainen, T. Niskanen, 14-227 (H), GenBank MW009218; Iowa, Webster County, Diggings Preserve, Fort Dodge, mixed woods, 7 Sept. 2006, coll. R. Healy, RH72 (ISC), GenBank MW009219; Maryland, Anne Arundel County, near the Severn River, 3 Oct. 1919, coll. H.A. Kelly, No. 256 (holotype, *C. rubroclavus*) (MICH), GenBank MW009238; Michigan, Mackinac County, Mackinac City, broadleaf forest, 18 Aug. 1949, coll. A.H. Smith, 33105, IBF19490344 (IBF); New York, Catskill Mountains, woods, Sept. 1887, coll. C.H. Peck, NYSf1209, (holotype, *C. flavifolius*) (NYS); Tennessee, Robertson County, Greenbrier, *Quercus*, 30 Aug. 2013, coll. E. Harrower, EH 230, TENN 068695, epitype, GenBank MW009217; Union County, Ghost Loop Trail, Big Ridge State Park, *Pinus*, *Fagus*, *Quercus*, *Carya*, 11 Sept. 2017, coll. A.M. Overholt, AMO4, TENN 071880, GenBank MG663246; Vermont, Chittenden County, Indian Brook Conservation Area, Essex, mixed woods, 31 July 2000, M. Seidl, MTS4789 (WTU), GenBank AF389166.

**Notes** — Based on the original descriptions of *C. flavifolius* and *C. rubroclavus*, their microscopic features, and the UV + yellow fluorescence of the exsiccatae, these are the same species. The application of the name *C. flavifolius* matches the current interpretation of *C. rubroclavus*. The exsiccatae of *C. flavifolius* indicate a medium to larger *Leproclybe* with an enlarged stipe base (clavate-bulbous) which is not indicated in the original description by Peck but has been recorded for other collections. The basidiospores, basidia and lamellae are very similar in the two type collections. Somehow L.C.C. Krieger focused on the red discolouration of his specimens, which also was noted in the collection from Vermont (MTS4789) and Florida (TN14-227). This is a rather frequent and widespread species that has long gone under the name *C. flavifolius*. We could not get a sequence of the ITS from the holotype of *C. flavifolius*; however, we were able to sequence the holotype of *C. rubroclavus*. The sequence of the latter matches with several other collections of this species, therefore, we have selected an epitype (EH 230, TENN 068695) for *C. flavifolius* to stabilize the long standing and accurate use of the name.

***Cortinarius olivaceosquamosus*** Niskanen, A. Paul, Lebeuf, Y. Lamoureux, J. Landry, Matheny & Liimat., *sp. nov.* — MycoBank MB 837399; Fig. 2d, 3h

**Etymology.** For olivaceous colour of squamulose pileus surface.

**Typus.** CANADA, Newfoundland, West coast, Gros Morne National Park, W side of Lomond River, trail to Stuckless Pond, mesic to damp coniferous forest (*Abies balsamea*, *Picea*) with some *Betula*, on calcareous ground, 19 Sept. 2010, coll. K. Liimatainen, T. Niskanen (holotype H 7068353), (isotype K); ITS barcode GenBank MW009231.

**Diagnosis** — Alaska and eastern North America: mixed conifer-broadleaf forest; basidiomata medium sized; pileus olive to olive yellow with small, dark blackish fibrillose scales; stipe clavate; veil forming a sock-like covering on the lower stipe; basidiospores small ( $L \times W_m$ ,  $6.6 \times 5.5 \mu\text{m}$ ). Forming a strongly supported monotypic lineage with more than twenty-one differences in ITS from other *Leproclybe* species, a similarity of 96.5 %.

**Pileus** 35–60 mm diam, at first hemispherical, later low convex to plane, somewhat hygrophanous, olive yellow in the center, yellow towards the edge, with small, dark, brownish black to blackish fibrillose scales. **Lamellae** adnexed, somewhat crowded, yellow to olive yellow. **Stipe** 50–80 mm long, 6–10 mm thick above, base 9–15 mm, clavate, at first covered with white fibrils, later becoming very pale brownish yellow; **veil** yellow, thin, forming a

sock-like sheet on the lower part of the stipe. **Context** yellow in stipe, somewhat paler in the pileus, brownish yellow at the very bottom of the stipe. **Odour** of lamellae strongly raphanoid. **Taste** not recorded. **Exsiccatae.** Pileus surface light brown to darker brown, disc blackish brown in places, lamellae medium brown to rusty medium brown, stipe light gray brown to olive brown, base light brown, flesh light gray brown to light olive brown. **UV.** Exsiccatae stipe bright yellow including cortex, lamellae light yellow, pileus surface and flesh negative.

**Basidiospores** (6–)6.3–7.0(–7.6)  $\times$  (5.2–)5.4–5.6(–6.3)  $\mu\text{m}$ ,  $L \times W_m$  6.6  $\times$  5.5  $\mu\text{m}$ ,  $Q$  1.1–1.3,  $Q_m$  1.2, subglobose to broadly ellipsoid, moderately to  $\pm$  coarsely verrucose,  $\pm$  moderately dextrinoid. **Basidia** 4-spored, clavate, 24–36  $\times$  7.4–8.1  $\mu\text{m}$ , colourless, grayish or with yellow pigment, some with granules, some with darkened walls. **Pileipellis:** epicutis well developed, hyphae on disc entangled to interwoven, forming mounds and ascending clusters, on margin interwoven,  $\pm$  radially arranged, forming some mounds, 4–15  $\mu\text{m}$  wide, cylindrical to broadly cylindrical or enlarged, grayish to blackish, with yellow to brownish pigment or colourless, walls refractive,  $\pm$  thickened, colourless or darkened, smooth or encrusted; hypocutis poorly developed,  $\pm$  radially arranged and interwoven on margin, on disc more strongly interwoven, hyphae 4–17  $\mu\text{m}$  wide, cylindrical to broadly cylindrical or more enlarged, colourless, walls refractive, colourless or slightly darkened, smooth or slightly encrusted.

**Habitat & Distribution** — In mesic to damp mixed forests, calcareous soil, *Abies*, *Picea*, *Pinus*, *Alnus* and *Populus*. Known from Alaska, Quebec, Newfoundland and Tennessee.

**Additional specimens examined.** CANADA, Newfoundland, West coast, Gros Morne National Park, W side of Lomond River, hiking trail to Stuckless Pond, mesic to damp coniferous forest, *Abies balsamea*, *Picea*, some *Betula*, 19 Sept. 2010, coll. K. Liimatainen, T. Niskanen, TN10-105 (holotype H), GenBank MW009231; Quebec, Hébertville, Lac-Saint-Jean, Road 169, 3 km south entrance Laurentides Wildlife Reserve, 31 Aug. 2014, coll. H. Aubin, A. Paul, R. Lebeuf, HRL1790 (pers. herb., TENN 071110), GenBank KX897409; Rawdon, near Lake Brennan, *Abies balsamea*, *Picea glauca*, *P. mariana*, *Betula* and *Populus*, 26 Sept. 2000, coll. Y. Lamoureux, CMMF003539, GenBank MW009233. — USA, Alaska, Fairbanks NW, George Park Hwy, by the Gold Hill Rd, *Picea*, *Betula*, *Populus*, 17 Aug. 2011, K. Liimatainen, T. Niskanen, TN11-118 (H), GenBank MW009232; Tennessee, Knox County, Obed, Boulder Fields, mixed conifer-broadleaf forest, 14 Oct. 2015, coll. E. Harrower, EH304B (TENN).

**Notes** — The olive yellow to brownish yellow colouration and the blackish brown to blackish scales on the pileus surface together with smaller basidiospores make *C. olivaceosquamosus* a rather distinctive species.

***Cortinarius parkeri*** Ammirati, M.T. Seidl & O. Ceska, *Botany* 90 (4): 329. 2012 — IF 518768; Fig. 2e, 3i

Forming a strongly supported monotypic lineage, sister to *C. atrotomentosus*.

**Pileus** 20–70 mm diam, convex, plane or uplifted, shallowly depressed, margin decurved, moist to dry, somewhat hygrophanous, fibrillose streaked, slightly olive yellow to dull yellow from veil at first, basic colour yellow brown, brown, orange brown, in age with reddish tones. **Lamellae** adnexed to sinuate, close to crowded, light yellow olive to brownish yellow buff becoming orange brown then rusty brown. **Stipe** 33–49 mm long, 7–13 mm thick above, base 9–20 mm thick, rounded to bulbous, surface shiny, whitish to pallid, yellowish or slightly yellowish with light watery brown streaks, rusty orange in age; **veil** sheathing to volva-like, membranous, yellow to brownish yellow. **Context** in pileus pale yellowish brown or pale brownish, fading to pallid watery brown with reddish tones in place, in stipe stuffed to hollow, pale yellowish brown, whitish or watery brown with reddish or orange brown discolourations. **Odour** of context typically

strongly raphanoid or rarely garlic-like. Taste of context mildly raphanoid. *Exsiccatae*. Pileus light brown with slight reddish tones, lamellae rich rust brown from spores, flesh creamy white with some brownish areas, stipe creamy white to slightly brownish, base pale yellowish white to creamy, membranous veil creamy white or rusty from spores. UV. Fresh basidiomata bright yellow stipe, lamellae and context; surface of pileus and veil slightly yellow to negative; *exsiccatae* pileus brown, flesh pale to light yellow, lamellae rusty brown with spores, stipe pale yellow with some brownish areas below.

*Basidiospores* (6.5–)7.0–9.0(–9.5) × 5.0–6.0(–6.5) μm, L × W<sub>m</sub> 7.4 × 5.6 μm, Q 1.2–1.5, Q<sub>m</sub> 1.3, broadly ellipsoid to subglobose, moderately to very coarsely verrucose, non-dextrinoid to slightly dextrinoid. *Basidia* 4-spored, 26–30 × 7–9 μm, clavate, colourless, grayish or with dull yellowish to brownish yellow pigment, some with darkened walls. *Pileipellis*: epicutis well developed, hyphae ± radially arranged, interwoven, 3.5–9.5 μm wide, cylindrical, colourless, pale yellowish, pale orange yellow, some containing dull yellow orange to reddish orange pigment, walls refractive, smooth or slightly encrusted; hypocutis poorly developed, hyphae cylindrical to broadly cylindrical, 4–12 μm wide, colourless to yellowish or containing yellowish pigment, walls refractive, smooth.

**Habitat & Distribution** — Occurring from March to early July, conifer forests, including combinations of *Abies*, *Larix*, *Pinus*, *Picea*, *Pseudotsuga*, *Thuja* and *Tsuga*, or mixed forest of conifers with *Arbutus*, *Vaccinium*, *Corylus*, *Lonicera*, *Populus*, *Acer* and/or *Quercus*. British Columbia, Washington, Oregon, Idaho.

**Specimens examined.** CANADA, British Columbia, Vancouver Island, Saanich, Observatory Hill, 11 Mar. 2007, coll. O. Ceska, A. Ceska, OC 181 (UBC, F17253). — USA, Idaho, Boise County, Anderson Creek Road, 14 June 1986, coll. C.J. Byrne, JFA9290 (WTU); Oregon, Hood River County, Surveyor's Ridge Trail #688, 19 May 1999, coll. J. Lindgren, JEL9914 (WTU); Jefferson County, Suttle Lake, 14 May 2010, coll. M. Beug, 02MWB051410 (WTU); Linn County, Mt Jefferson Lake trailhead, 15 June 1984, coll. S. Miller, SM737 (WTU); Wasco County, Southeast of Mt Hood, 18 May 1986, coll. D. Sieger, JFA9262 (WTU); Washington, Chelan County, Lake Wenatchee, 1 mi from mouth of White River, 8 May 1982, coll. J. Sherman, JFA8584 (WTU); Kittitas County, Lake Kachess Campground, 25 May 2001, coll. J. Ammirati, JFA12885 (WTU); Klickitat County, Trout Lake area, 4 May 2007, coll. D.B. Bishop, PNWKC07-124-04 (WTU); Pend Oreille County, Crawford State Park, near Gardener Cave parking lot, 2 May 2000, coll. A.D. Parker, ADP000502-1 (holotype WTU); FS road 190, about 9 mi N. of Metaline Falls, *Abies grandis*, 11 May 2009, coll. A. Parker, ADP090511-2 (WTU); Skamania County, Steamboat Research Natural Area, 11 July 1999, coll. J. Lindgren, JEL9961 (WTU); Whatcom County, Canyon Creek, Mt Baker, 8 June 2010, coll. B. McAdoo, JFA13399 (WTU).

**Notes** — *Cortinarius parkeri* is a small to medium sized, somewhat compact, yellow to yellow brown species that is distinctive by the presence of a volvate to sheathing veil on the lower stipe. The spores are often more broad, short ellipsoid than subglobose. Found in spring to early summer in conifer forests of the Pacific Northwest.

## KEY TO SPECIES OF *C.* SUBGENUS *LEPROCYBE* FROM NORTH AMERICA

### Cautions

- 1 compare specimens with photos whenever possible;
  - 2 be certain the specimens (fresh or *exsiccatae*) are strongly UV + bright yellow in some part, since there are some species such as *C. tofaceus* that look like *Leprocycbe* but they are not;
  - 3 if collection is from a mixed conifer broadleaf forest, try both key leads; and
  - 4 species distributions may be poorly known, particularly where there is limited sampling.
1. Found in association with broadleaves (*Quercus*, *Notholithocarpus*, *Ostrya*, *Carya*, *Fagus*), sometimes conifers present (*Pinus*, *Pseudotsuga*, *Tsuga*) . . . . . 2

1. Found in association with conifers (*Abies*, *Picea*, *Pinus*, *Pseudotsuga*, *Tsuga*), broadleaves sometimes present (*Betula*, *Alnus*, *Populus*, *Quercus*, *Notholithocarpus*) . . . . . 10
2. Species primarily found in western North America . . . . . 3
2. Species primarily found in mid-western and eastern North America . . . . . 7
3. Pileus surface typically lacking distinct fibrillose scales, somewhat hygrophanous, pale brownish yellow; lamellae yellowish brown; stipe 8–11 mm thick, cylindrical to clavate; veil pale yellow, forming a sock-like sheet on lower stipe; basidiospores L × W<sub>m</sub> 7.2 × 5.6 μm, subglobose to broadly ellipsoid; associated with live oaks (*Quercus*) . *C. subleproleptopus*
3. Pileus surface distinctly fibrillose tomentose to fibrillose scaly . . . . . 4
4. Basidiospores subglobose, L × W<sub>m</sub> ≤ 7 × 5.5 μm . . . . . 5
4. Basidiospores subglobose to broadly ellipsoid, L × W<sub>m</sub> ≥ 7.5 × 5.5 μm . . . . . 6
5. Pileus ± finely fibrillose scaly, disc and inner margin rich brown to blackish brown, outer margin lighter brown to tan; lamellae yellow to yellow brown; stipe 8–19 mm thick, cylindrical to subclavate; veil white, leaving a slight creamy zone above; odour fragrant; basidiospores L × W<sub>m</sub> 6.5 × 5.3 μm . . . . . *C. loringii*
5. Pileus ± fibrillose tomentose to ± fibrillose scaly overall, brown to black centrally, margin olive, olive gray or olive brown; lamellae pale yellow to pale olive; stipe 20–35 mm thick, cylindrical to subclavate; veil olive to olive brown, partially covering lower stipe, occasionally forming a distinct zone; associated with tan oak (*Notholithocarpus*); odour raphanoid; basidiospores L × W<sub>m</sub> 6.7 × 5.3 μm . . . . . *C. fuscotomentosus*
6. Pileus ± fibrillose, fibrillose-tomentose and fibrillose scaly, olive brown to blackish brown, typically discolouring reddish brown; lamellae yellowish to brownish yellow; stipe 15–18 (–28) mm thick, typically tapered to base; veil yellowish, thinly coating stipe; odour of marjoram or raphanoid; basidiospores L × W<sub>m</sub> 8 × 6.4 μm . . . . . *C. brunneofibrillosus*
6. Pileus appressed fibrillose, ± tomentose to finely fibrillose scaly, pale chamois buff to dark brown or olive brown to medium brown; lamellae dull yellow brown; stipe 20–35, cylindrical to subclavate; veil brownish olive, forming patches and zones on stipe; odour raphanoid; basidiospores L × W<sub>m</sub> 8.6 × 7.4 μm, subglobose to broadly ellipsoid . . . . . *C. aff. cotoneus*
7. Pileus surface with olive brown to yellow olive colours; veil yellow olive to brownish olive . . . . . 8
7. Pileus surface yellowish to brownish yellow; veil white to slightly yellow . . . . . 9
8. Pileus ± tomentose, appressed fibrillose to finely fibrillose scaly, pale chamois buff, grayish yellow, olive brown or brown; lamellae dull yellow brown; stipe 7–17 mm thick, clavate; veil forming brownish to brownish olive zones on stipe; odour raphanoid to mild; basidiospores L × W<sub>m</sub> 8.2 × 6.2 μm, subglobose . . . . . *C. hughesiae*
8. Pileus dark brown olive to yellow olive, tomentose, fibrillose and appressed squamulose; lamellae yellow olive; stipe 10–25 mm thick, clavate; veil yellow olive; odour strongly fruity herbaceous; basidiospores L × W<sub>m</sub> 7.6 × 6 μm, ± subglobose . . . . . *C. apius*
9. Pileus pale yellow to tawny yellow, slightly fibrillose scaly, sometimes dull reddish; lamellae pale yellow; stipe 10–35 mm thick, bulbous to clavate bulbous; veil white, peronate; odour pungent, raw potatoes or mild; basidiospores L × W<sub>m</sub> 7.6 × 5.6 μm, broadly ellipsoid to subglobose . . . . . *C. flavifolius*

9. Pileus yellow to brownish yellow, very finely brown fibrillose to fibrillose scaly; lamellae yellow to brownish yellow; stipe up to 20 mm thick, clavate; veil thin, whitish with some yellowish tints, annulate; odour raphanoid; basidiospores  $L \times W_m$   $7.3 \times 5.6 \mu\text{m}$ ,  $\pm$  subglobose . . . . . *C. atkinsiae*
10. Found in western North America, Rocky Mountains to the Pacific Coast and Alaska . . . . . 11
10. Found in mid-western to eastern North America . . . . . 19
11. Species producing basidiomata in primarily spring or early summer, coastal to subalpine forests . . . . . 12
11. Species producing basidiomata later in the season, summer well into fall, but typically not occurring early in the season, coastal to subalpine forests . . . . . 14
12. Pileus distinctly fibrillose scaly overall, dark olive brown, blackish olive or black; lamellae brownish chamois to yellow brown; stipe 5–18 mm thick, equal, clavate or somewhat bulbous; veil yellow, light greenish yellow, pale olivaceous or dark olivaceous, annulate; basidiospores  $L \times W_m$   $7.5 \times 5.8 \mu\text{m}$ , subglobose to broadly ellipsoid . . . . . *C. clandestinus*
12. Pileus surface fibrillose to fibrillose streaked, sometimes finely fibrillose scaly on the disc, but not distinctly fibrillose scaly . . . . . 13
13. Pileus fibrillose streaked, yellow brown, brown, orange brown; lamellae light yellow olive to brownish yellow buff; stipe 7–20 mm thick, base rounded to bulbous; veil sheathing, forming membranous volva at base, yellow to brownish yellow; basidiospores  $L \times W_m$   $7.4 \times 5.6 \mu\text{m}$ , broadly ellipsoid to subglobose; reproducing in the spring and early summer . . . . . *C. parkeri*
13. Pileus ochraceous, yellow brown, olive brown, brown or reddish brown, typically lacking dark fibrillose scales; lamellae ochraceous to ochraceous brown; stipe 8–10 mm thick, equal or slightly enlarged toward base; veil yellow, annulate; basidiospores  $L \times W_m$   $7.3 \times 5.6 \mu\text{m}$ , subglobose to broadly ellipsoid; spring and summer, mostly subalpine . . . . . *C. clandestinus* (non-fibrillose scaly form)
14. Pileus velvety to tomentose scaly to  $\pm$  fibrillose scaly, black, blackish brown, dark brown or olivaceous brown; lamellae olive yellow to olive brown; stipe 4–12 mm thick, cylindrical to narrowly clavate; veil thin, whitish with yellow to brown tints; basidiospores  $L \times W_m$   $7.2 \times 5.4 \mu\text{m}$ , shape variable, subglobose to broadly ellipsoid and ellipsoid (sometimes common); conifer and mixed forests . . . . . *C. atrosquamosus*
14. Not with the above combination of characteristic . . . . . 15
15. Basidiospores  $\pm$  subglobose to broadly ellipsoid,  $L_m \leq 7 \mu\text{m}$  . . . . . 16
15. Basidiospores subglobose to broadly ellipsoid or ellipsoid,  $L_m > 7 \mu\text{m}$  . . . . . 18
16. Pileus olive yellow in center, yellow towards margin, with small, brownish black to blackish fibrillose scales; lamellae yellow to olive yellow; stipe 6–15 mm thick, clavate; veil yellow, thin, forming a sock-like sheath on the lower stipe; basidiospores  $L \times W_m$   $6.6 \times 5.5 \mu\text{m}$ , subglobose to broadly ellipsoid; boreal forests . . . . . *C. olivaceosquamosus*
16. Not with the above combination of characteristics . . . . . 17
17. Pileus surface yellow to olive-yellow, with blackish brown fibrillose scales, especially on disc; lamellae yellowish brown, edges yellow; stipe 6–10 mm thick, cylindrical to somewhat clavate; veil yellow, forming zones and incomplete girdles on the stipe; basidiospores  $L \times W_m$   $6.9 \times 5.7 \mu\text{m}$ ,  $\pm$  subglobose; boreal forests . . . . . *C. squamivenetoideus*
17. Pileus densely fibrillose scaly, especially on disc, dull olive yellow to blackish brown; lamellae dark brown to rich brown, edges yellowish buff; stipe 5–13 mm thick, clavate tapered; veil light yellow, leaving small patches and slight strands; basidiospores  $L \times W_m$   $6.7 \times 5.4 \mu\text{m}$ ,  $\pm$  subglobose to broadly ellipsoid; conifer forests . . . . . *C. fuscoflavidus*
18. Pileus distinctly fibrillose scaly overall, dark olive brown, blackish olive or black; lamellae brownish chamois to yellow brown stipe 5–18 mm thick, equal, clavate or bulbous; veil yellow, light greenish yellow, pale olivaceous or dark olivaceous; basidiospores  $L \times W_m$   $7.5 \times 5.8 \mu\text{m}$ , subglobose to broadly ellipsoid; coastal to subalpine and boreal forests . . . . . *C. clandestinus*
18. Pileus tomentose to minutely fibrillose scaly, dark yellowish brown, pale olive brown to olive yellow; lamellae olive yellow to yellowish brown; stipe 6–13 mm thick, cylindrical to clavate; veil pale greenish yellow to pale yellow; basidiospores  $L \times W_m$   $c. 7.5 \times 6 \mu\text{m}$ , subglobose to broadly ellipsoid . . . . . *C. veneto-occidentalis* (see text to compare *C. aff. veneto-occidentalis*)
19. Producing basidiomata in the spring and early summer . . . . . 20
19. Producing basidiomata in the summer and well into fall . . . . . 21
20. Pileus mustard yellow to golden yellow with conspicuous olive brown to dark yellow brown fibrillose scales; lamellae light yellow; stipe to 12 mm thick, equal or slightly enlarged above, base slightly bulbous; veil yellow; basidiospores  $L \times W_m$   $7.5 \times 5.8 \mu\text{m}$ ,  $\pm$  subglobose to broadly ellipsoid . . . . . *C. clandestinus*
20. Pileus ochraceous, yellow brown, olive brown, brown or reddish brown, typically lacking dark fibrillose scales; lamellae ochraceous to ochraceous brown; stipe 8–10 mm thick, equal or slightly enlarged toward base; veil yellow, annulate; basidiospores  $L \times W_m$   $7.3 \times 5.6 \mu\text{m}$ , subglobose to broadly ellipsoid . . . . . *C. clandestinus* (non-fibrillose scaly form)
21. Stipe distinctly clavate, habit rather stout (up to 15 mm thick) . . . . . 22
21. Stipe cylindrical to somewhat clavate, habit more slender (up to 10 mm thick) . . . . . 23
22. Pileus olive yellow in center, yellow towards margin, with small, brownish black to blackish fibrillose scales; lamellae yellow to olive yellow; stipe 6–15 mm thick, clavate; veil yellow, thin, forming a sock-like sheath on the lower stipe; basidiospores  $L \times W_m$   $6.6 \times 5.5 \mu\text{m}$ , subglobose to broadly ellipsoid; boreal forests . . . . . *C. olivaceosquamosus*
22. Pileus coarsely fibrillose to scaly, dark olivaceous gray to olivaceous yellow or reddish yellow to reddish brown with blackish brown scales; lamellae pale ochraceous to olivaceous; stipe 5–12 mm thick, clavate; veil blackish brown to olivaceous gray forming distinct girdles and scales on the stipe; basidiospores  $L \times W_m$   $6.2 \times 4.7 \mu\text{m}$ , broadly ellipsoid to subglobose; mixed woods with *Pinus* . . . . . *C. phrygianus*
23. Pileus innately fibrillose to finely scaly, yellowish to greenish yellow with brown to blackish brown colours centrally; lamellae yellow; stipe 4–8 mm thick, equal to narrowly clavate; veil dingy yellow, subannulate; basidiospores  $L \times W_m$   $7.2 \times 5.7 \mu\text{m}$ , subglobose to broadly ellipsoid; boreal to northern, conifer or mixed woods . . . . . *C. lutescens*
23. Pileus somewhat hygrophanous, yellow to olive-yellow with dark scales, center almost blackish brown; lamellae yellowish brown, edges yellow; stipe 6–10 mm thick cylindrical to somewhat clavate; veil yellow, forming zones and incomplete girdles on the stipe; basidiospores  $L \times W_m$   $6.9 \times 5.7 \mu\text{m}$ ,  $\pm$  subglobose; boreal forests . . . . . *C. squamivenetus* (morphologically similar to *C. squamivenetoideus*)

## DISCUSSION

In this study a total of 18 species are recognized from North America, and the diversity of the species is remarkably higher than previously thought. Revision of all North American names is provided here and old European names have been typified. Releasing 27 new ITS sequences from type specimens, in addition to the previously released four type sequences, will highly improve the barcode database of subg. *Leprocybe* in public sequence repositories.

The phylogenetic analysis of North American species of subg. *Leprocybe* shows a very high diversity of species with a number of strongly supported lineages. Some of these lineages form well-supported sections composed of two or more species. These include sections *Leprocybe*, *Fuscotomentosi*, *Melanoti*, *Squamiveneti* and *Veneti*. In addition, there are a number of well supported monotypic lineages which are given the status of *incertae sedis* until further study. These include *Cortinarius atrosquamosus*, *C. brunneofibrillosus*, *C. clandestinus*, *C. flavifolius*, *C. olivaceofuscus* and *C. parkeri*. Interestingly, to date no species from sect. *Melanoti* have been reported from North America while species of the sections *Leprocybe*, *Fuscotomentosi*, *Squamiveneti* and *Veneti* are found on both continents. Central American *C. aureopigmentatus* was currently placed in *incertae sedis* due to the large genetic difference to the sister clade, sect. *Leprocybe*, as well as morphological differences although both groups have large basidiospores.

The species of *Cortinarius* in subg. *Leprocybe* present considerable variation in morphology and ecology. Using molecular data it was possible to recognize the diversity in the subgenus, evaluate convergence in morphological and microscopical characteristics, and look more carefully at ecological and distributional data.

The main morphological characteristics useful in section level classification and species identification are, the nature of the pileus surface (appressed fibrillose to densely fibrillose scaly), overall size, shape and colouration of the basidiomata, and basidiospore size and degree of ornamentation. The pigmentation of the epicutis hyphae observed from exsiccatae mounted in KOH is a helpful secondary characteristic but difficult to use for identification unless correlated with morphology and basidiospores characteristics. Ecological features such as tree host, general habitat and soil (calcareous or acidic soils) are also helpful in defining taxa.

The distribution of many *Leprocybe* species in North America is incompletely known due to inadequate sampling, however, some trends can be seen. There is a large number of species only known from western North America, *C. atrosquamosus*, *C. brunneofibrillosus*, *C. fuscoflavidus*, *C. fuscotomentosus*, *C. loringii*, *C. parkeri*, *C. squamivenetoideus*, *C. subleproleptopus* and *C. veneto-occidentalis*. Exceptions to this pattern are *C. clandestinus*, known from western North America, the Great Lakes region and eastern Canada, and *C. olivaceosquamosus* which occurs in Alaska and eastern North America. *Cortinarius flavifolius* is widespread, occurring from eastern to mid-western North America. The distributions of other species, *C. apius*, *C. atkinsiae*, *C. hughesiae* and *C. lutescens*, are poorly known, but so far only included eastern North America. Only two species are shared with Europe, *C. phrygianus* and *C. squamivenetus*, both occur in boreal forests.

*Cortinarius atrosquamosus*, *C. clandestinus*, *C. fuscoflavidus*, *C. lutescens*, *C. olivaceosquamosus*, *C. parkeri*, *C. phrygianus*, *C. squamivenetoideus*, *C. squamivenetus* and *C. veneto-occidentalis* are associated with conifer forests or in mixed forests where conifers are the dominant ectomycorrhizal host. *Cortinarius loringii* is from a mixed broadleaf conifer habitat, the ectomycorrhizal host is uncertain but likely *Quercus*. Species asso-

ciated with broadleaves, mainly the *Fagaceae*, include *C. apius*, *C. atkinsiae*, *C. brunneofibrillosus*, *C. flavifolius*, *C. fuscotomentosus*, *C. hughesiae* and *C. subleproleptopus*.

**Acknowledgements** Support from the D.E. Stuntz Memorial Foundation. A number of individuals have made significant contributions to this paper, including S. Adams, M. Beug, A. Bidaud, O. Ceska, M. Gordon, Y. Lamoureux, J. Landry, R. Lebeuf, J. Melot, A. Paul and N. Siegel. Collections managers have been very helpful in providing type collection and other materials, O. Lee (UBC), L. Leonardi (NYS), M. Oliver (TENN), P. Rogers (MICH), K. Hansen (S) and R. Archambault (CMMF).

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