Cortinarius sect. Riederi: taxonomy and phylogeny of the new section with European and North American distribution

Article *in* Mycological Progress · November 2018

DOI: 10.1007/s11557-018-1443-0

15 authors, including:

Geert Schmidt-Stohn

35 PUBLICATIONS **322** CITATIONS

SEE PROFILE

Tuula Niskanen

Finnish Museum of Natural History

106 PUBLICATIONS **13,311** CITATIONS

SEE PROFILE

Kare Liimatainen

Royal Botanic Gardens, Kew

100 PUBLICATIONS **11,484** CITATIONS

SEE PROFILE

Tobias Guldberg Frøslev

University of Copenhagen

147 PUBLICATIONS **4,499** CITATIONS

SEE PROFILE

Mycological Progress
https://doi.org/10.1007/s11557-018-1443-0

ORIGINAL ARTICLE

Cortinarius sect. *Riederi*: taxonomy and phylogeny of the new section with European and North American distribution

Tor Erik Brandrud[1] · Geert Schmidt-Stohn[2] · Kare Liimatainen[3] · Tuula Niskanen[3] · Tobias Guldberg Frøslev[4] · Karl Soop[5] · Dimitar Bojantchev[6] · Ilkka Kytövuori[7] · Thomas Stjernegaard Jeppesen[8] · Francesco Bellù[9] · Günter Saar[10] · Bernhard Oertel[11] · Tahir Ali[12,13] · Marco Thines[12,13] · Bálint Dima[14,15]

Received: 29 May 2018 / Revised: 19 September 2018 / Accepted: 25 September 2018

Abstract

Cortinarius is one of the most species-rich genera of mushroom-forming fungi. Based on phylogenetic and morphological evidence, *Cortinarius*, sect. *Riederi*, is introduced at sectional level (= subsect. *Riederi* sensu Brandrud & Melot). The taxonomy, phylogeny, ecology and distribution of not only mainly European but also including some North American taxa of this section are treated, which includes nine species and two varieties. Of these, three taxa are described as new (*C. burlinghamiae*, *C. pallidoriederi* and *C. argenteolilacinus* var. *dovrensis*). The sect. *Riederi* species possess morphological features similar to *Phlegmacium* group(s) and forms a phylogenetically isolated lineage, with no supported affinity to other phlegmacioid groups. Three taxa are known from both Europe and North America, two species are known only from North America and five only from Europe. Altogether, eight of the ten taxa are associated with conifers or northern (boreal-subalpine) deciduous trees (*Betula* spp.). Only two species occur in more temperate forests (*Fagus* forests), and no species have so far been found in thermophilous *Quercus* forests

Keywords Agaricales · Basidiomycota · Ecology · Morphology · nrDNA ITS · Phlegmacioid

Introduction

Cortinarius is by far the largest genus of macromycetes in the Northern Hemisphere. Many groups are still poorly known, and deeper taxonomic studies (including integrative approaches combining morpho-anatomical studies and molecular phylogeny) may lead to a two to three times increase in the number of species (see, e.g. Niskanen et al. 2013 on sect.

Section Editor: Zhu-Liang Yang

✉ Bálint Dima
cortinarius1@gmail.com

[1] Norwegian Institute for Nature Research (NINA), Gaustadalléen 21, 0349 Oslo, Norway

[2] Bienenbüttel, Germany

[3] Jodrell Laboratory, Royal Botanic Gardens, Kew, Surrey TW9 3AB, UK

[4] Natural History Museum of Denmark, University of Copenhagen, Øster Voldgade 5-7, 1350 Copenhagen, Denmark

[5] Department of Botany, Swedish Museum of Natural History, Box 50007, SE-104 05 Stockholm, Sweden

[6] MushroomHobby.com, 345 Shipwatch Lane, Hercules, CA 94547, USA

[7] Finnish Museum of Natural History, University of Helsinki, P.O. Box 7, FI-00014 Helsinki, Finland

[8] Natural History Museum of Denmark, Collections, University of Copenhagen, Universitetsparken 15, 2100 Copenhagen Ø, Denmark

[9] Bolzano, Italy

[10] Lahr-Sulz, Germany

[11] Alfter, Germany

[12] Senckenberg Biodiversität und Klima Forschungszentrum, Senckenberganlage 25, 60325 Frankfurt am Main, Germany

[13] Fachbereich Biowissenschaften, Institut für Ökologie, Evolution und Diversität, Goethe Universität, Max-von-Laue-Str. 13, 60438 Frankfurt am Main, Germany

[14] Department of Plant Anatomy, Institute of Biology, Eötvös Loránd University, Pázmány Péter sétány 1/c, Budapest 1117, Hungary

[15] Department of Biosciences (Plant Biology), Viikki Plant Science Centre, University of Helsinki, P.O. Box 65, FI-00014 Helsinki, Finland

Bovini; Brandrud et al. 2014 on sect. *Multiformes*). According to Garnica et al. (2016), more than 800 species are verified by distinct nrDNA ITS sequences. Niskanen et al. (2012a) estimated the number of species in the Nordic countries of Europe to be approximately 900. A conservative estimate for the amount of species in the Northern Hemisphere is 2000–2500 species. Already, more than 5000 names have been published in *Cortinarius*, worldwide (see Garnica et al. 2016; Index Fungorum). However, this number does not reflect the real diversity in the genus, since studies of type specimens have shown that many names are synonymous (see, e.g. Liimatainen et al. 2014).

Morphologically, *Cortinarius* has traditionally been subdivided into five to eight subgenera (Moser 1967; Brandrud et al. 1989–2012; Knudsen and Vesterholt 2012), of which *Phlegmacium*, *Telamonia* and *Dermocybe* are the largest and most well known. The subdivisions are also supported by phylogenetic data to some degree, with the placement of most phlegmacioid taxa into three major clades (Phlegmacium I and II and Calochroi; in the following referred collectively to as 'phlegmacioid species'), and most *Dermocybe*- + *Telamonia*-like species forming a 'superclade' (Stensrud et al. 2014; Garnica et al. 2016).

Since the monograph of Moser (1961) on *Cortinarius* subgenus *Phlegmacium* in Europe, a number of phlegmacioid groups/sections have been given an extensive taxonomic treatment: sect. *Phlegmacium* (Brandrud 1996a, b), sect. *Phlegmacioides* (Brandrud 1998), sect. *Calochroi* (Frøslev et al. 2006, 2007), (sub)sect. *Elegantiores* (Garnica et al. 2006), sect. *Claricolores* (Brandrud et al. 2013), sect. *Multiformes* (Brandrud et al. 2014) and sect. *Purpurascentes* (Saar et al. 2014). Furthermore, a cautiously updated taxonomy, which includes most North and Central European species is provided in the descriptive key in the Funga Nordica (Jeppesen et al. 2012). But comprehensive, taxonomic studies are still lacking for many groups in Europe. Recent molecular studies of *Phlegmacium* (e.g. Garnica et al. 2003, 2005, 2009, 2016; Peintner et al. 2004; Frøslev et al. 2006, 2007; Liimatainen et al. 2014) identify a number of small well-supported clades of phlegmacioid species with no phylogenetic affinity to the three major *Phlegmacium* clades.

According to phylogenetic studies (Garnica et al. 2016), *Riederi* is such a clade, which is also morphologically well delimited. *Riederi* species were formerly treated either as part of the large sect. *Glaucopodes* (Brandrud et al. 1989–2012; Brandrud and Melot 1990) or included in sections *Glaucopodes* and *Variecolores* (Moser 1961) or *Phlegmacium* (Bidaud et al. 1999; Consiglio et al. 2006).

The aim of this study is to present a detailed species-level study of clade Riederi based on molecular and morphological data, including studies of type specimens. An identification key to all known European species is also provided.

Materials and methods

Molecular data

A total of 112 specimens of clade Riederi from Europe and North America were sequenced (see Collections examined under each species description), including the type specimens of *C. anomaloochrascens* Chevassut & Rob. Henry, *C. argenteolilacinus* M.M. Moser, *C. fallaceicolor* Rob. Henry (incl. 'f. meridionale'), *C. fulvoochrascens* Rob. Henry, *C. fulvoochrascens* var. *cyanophyllus* Rob. Henry, *Cortinarius fulvoochrascens* var. *subcaninicolor* Rob. Henry, *C. glaucocyanopus* Rob. Henry, *C. imbricatoides* Rob. Henry, *C. malachioides* P.D. Orton, *C. marginatoochrascens* Rob. Henry, *C. notabilis* Rob. Henry, *C. parksianus* A.H. Smith, *C. pseudoarquatus* A.H. Smith, *C. riederi* (Weinm.) Fr., *C. stilazureus* Rob. Henry, *Phlegmacium fuscomaculatum* var. *smolandicum* M.M. Moser and *P. fuscomaculatum* var. *umbrinum* M.M. Moser. For the majority of the specimens, the total DNA was extracted from dried material with the NucleoSpin Plant II kit (Macherey-Nagel, Düren, Germany). Primers ITS1F and ITS4 (White et al. 1990; Gardes and Bruns 1993) were used to amplify the internal transcribed spacer region (ITS) of the ribosomal genes. The protocols of the polymerase chain reaction (PCR) followed Niskanen et al. (2009). Some of the specimens were amplified with the Phire® Plant Direct PCR Kit (Thermo Scientific, USA) using the primers ITS1F and ITS4B (Gardes and Bruns 1993) and following the method described in Papp and Dima (2017). Direct sequencing of the amplicons was performed at the University of Helsinki, LGC Genomics (Berlin, Germany), and at the laboratory centre of the Senckenberg Biodiversity and Climate Research Centre (Frankfurt am Main, Germany) with the same primers as those applied in PCR. Chromatograms were assembled and edited with Sequencher 4.1 (Gene Codes, Ann Arbor, MI, USA) and CodonCodeAligner 4.1. (CodonCode Corporation, Centerville, MA, USA). BLAST queries of the public databases (GenBank: http://www.ncbi.nlm.nih.gov/ and UNITE: http://unite.ut.ee/) were used to check for identical or similar sequences.

In order to evaluate the monophyly and phylogenetic placement of clade Riederi, 108 ITS sequences of *Cortinarius* were sampled across the main lineages of the genus known from the Northern Hemisphere. One sequence of each species from clade Riederi was chosen for the analysis, while the other *Cortinarius* lineages were represented by two to four sequences per clade. *Hebeloma* was chosen as an outgroup (Table 1). Sequences were aligned with MAFFT (online version 7) using the E-INS-i strategy with default settings (Katoh and Toh 2008). The alignment was imported to SeaView (Gouy et al. 2010) for visual inspection. Indels were coded as presence/absence characters with FastGap 1.2 (Borchsenius 2009) following the simple indel coding algorithm (Simmons et al. 2001). Adding indel characters to the nucleotide

Table 1 *Cortinarius* sequences used in the dataset 1 that the phylogenetic analysis shown in Fig. 1 is based on

Species	Voucher	Sequence accession No.	Reference
C. acutus	IB19980137	AF325578	Peintner et al. (2001)
C. alboamarescens	H6029887	KR011137	Ariyawansa et al. (2015)
C. alboviolaceus	IB19950329	AF325597	Peintner et al. (2001)
C. anomaloochrascens	O-F-75650	MH923046	This study
C. anomalovelatus	JFA13109[a]	FJ717605	Harrower et al. (2011)
C. anthracinus	TUB 01190	AY669670	Garnica et al. (2005)
C. aprinus	TF-01-034	AJ889942	GenBank
C. argenteolilacinus	MD18/2013	MH923064	This study
C. argenteolil. var. *dovrensis*	TEB312-09	MH923073	This study
C. armeniacus	CFP809	DQ117925	Kytövuori et al. (2005)
C. armillatus	CFP584	DQ114744	Kytövuori et al. (2005)
C. atrovirens	CFP1022	DQ663225	Frøslev et al. (2007)
C. aurantiobasis	F17122	GQ159865	Harrower et al. (2011)
C. badiovinaceus	IB19500061[a]	HQ845169	Niskanen et al. (2011)
C. balaustinus	AT2004219	UDB002172	UNITE
C. balteatoalbus	CFP1083	KF732613	Liimatainen et al. (2014)
C. balteatus	F44758	KF732262	Liimatainen et al. (2014)
C. bivelus	F44841	KP866159	Niskanen et al. (2015)
C. borgsjoeensis	O-F-65492	AY669567	Garnica et al. (2005)
C. bovarius	TN11-188[a]	KC905156	Liimatainen and Niskanen (2013)
C. bovinus	IK04-038[a]	JX407276	Niskanen et al. (2013)
C. brunneus	TN04-932	EU266638	Niskanen et al. (2009)
C. burlinghamiae	IB19970218	AF389139	Peintner et al. (2004)
C. caerulescens	F44815	KF732271	Liimatainen et al. (2014)
C. caesiocortinatus	TSJ2002-028	DQ083774	Frøslev et al. (2005)
C. calochrous	TSJ2000-068	DQ323960	Frøslev et al. (2006)
C. chalybaeus	PDD73146[a]	JQ287671	GenBank
C. cinnabarinus	F248436	JX114944	Ammirati et al. (2013)
C. colymbadinus	CFP1130	JX127302	Ammirati et al. (2013)
C. corrosus	TSJ2000-020	DQ323964	Frøslev et al. (2006)
C. croceus	TN06-295[a]	KP087990	Niskanen (2015)
C. decipiens	IB19740451	AY083180	Peintner et al. (2003)
C. delibutus	OS574	KC842441	Stensrud et al. (2014)
C. dionysae	TUB019718	KJ421178	Garnica et al. (2016)
C. disjungendus	TN03-1701	JX407329	Niskanen et al. (2013)
C. duracinus	TUB011517	AY669674	Garnica et al. (2005)
C. evernius	TUB 011901	AY669686	Garnica et al. (2005)
C. flexipes	AT2005167	UDB002249	UNITE
C. floccopus	GK432472[a]	JQ746616	Niskanen et al. (2012b)
C. fulvoochrascens	O-F-75726	MH923028	this study
C. fuscoperonatus	CFP1470	JX407330	Niskanen et al. (2013)
C. glaucocyanopus	GK5034[a]	MH846274	this study
C. glaucopus	F44760	KF732315	Liimatainen et al. (2014)
C. hedyaromaticus	NAMA 2010-080	KR090562	Cripps et al. (2015)
C. helvelloides	IB19930140	AY083182	Peintner et al. (2003)
C. hemitrichus	TUB 011509	AY669680	Garnica et al. (2005)
C. herpeticus	F44759[a]	KF732321	Liimatainen et al. (2014)
C. hinnuleoarmillatus	GK16160	DQ499464	Niskanen et al. (2006)
C. hinnuleus	TUB011512	AY669665	Garnica et al. (2005)

Table 1 (continued)

Species	Voucher	Sequence accession No.	Reference
C. humicola	F44876	KP866157	Niskanen et al. (2015)
C. illuminus	F16382	FJ039603	Harrower et al. (2011)
C. infractiflavus	OSC 1064084	EU525961	Smith et al. (2002)
C. infractus	F41138[a]	KF732325	Liimatainen et al. (2014)
C. laetus	IB19990518	AF389170	Peintner et al. (2004)
C. laniger	IB19740251	AF325591	Peintner et al. (2001)
C. malachioides	TEB245-13	MH923032	this study
C. malachius	IK98-1298	JX407332	Niskanen et al. (2013)
C. microglobisporus	IB20130101	KF961227	Peintner et al. (2014)
C. montanus	MICH10377[a]	KF732349	Liimatainen et al. (2014)
C. mucosus	IA12	UDB001566	UNITE
C. multiformis	F44806[a]	KF732350	Liimatainen et al. (2014)
C. neosanguineus	TN09-130	JX045678	Niskanen et al. (2012c)
C. neotropicus	NY34729[a]	KJ920032	Harrower et al. (2015)
C. norrlandicus	CFP526	DQ117928	Kytövuori et al. (2005)
C. obtusus	AT2005087	UDB002204	UNITE
C. olidus	KS-CO1159	KJ421068	Garnica et al. (2016)
C. pallidoriederi	Bellu30-09-2011[a]	MH923049	this study
C. paracephalixus	BP50169	KR080708	Cripps et al. (2015)
C. paragaudis	CFP564[a]	HQ845146	Niskanen et al. (2011)
C. parksianus	MICH10393[a]	MH846283	this study
C. percomis	CFP1104	KF732520	Liimatainen et al. (2014)
C. pholideus	TUB011520	AY669694	Garnica et al. (2005)
C. phrygianus	KS-CO584	KJ421031	Garnica et al. (2016)
C. pini	F47382[a]	KF732384	Liimatainen et al. (2014)
C. praestans	CFP482	KF732267	Liimatainen et al. (2014)
C. prasinocyaneus	TSJ2003-033	DQ083806	Frøslev et al. (2005)
C. privignoides	MCVE9443	JF907956	Osmundson et al. (2013)
C. pseudofallax	TEB738-13	KT591593	Brandrud et al. (2015)
C. purpurascens	IK98-2121[a]	KF732406	Liimatainen et al. (2014)
C. raphanoides	IK00-003	JX407333	Niskanen et al. (2013)
C. riederi	TEB407-13/DB5109	MH923051	this study
C. rubrovioleipes	IK04-031	DQ497191	Kytövuori et al. (2005)
C. russus	F44757	KF732416	Liimatainen et al. (2014)
C. saginus	T30	KC842448	Stensrud et al. (2014)
C. salor	MCVE11005	JF907884	Osmundson et al. (2013)
C. sanguineus	SL22091940	JN114099	Niskanen et al. (2012c)
C. saniosus	AT2004044	UDB000947	UNITE
C. saturninus	TAAM128654	UDB016058	UNITE
C. sodagnitus	CFP905	DQ663422	Frøslev et al. (2007)
C. sp. (as uncul. fungus)	3241J9	KF617829	Taylor et al. (2014)
C. splendens	TUB012741	EU057012	Garnica et al. (2009)
C. subbalaustinus	TN02-834	JX407335	Niskanen et al. (2013)
C. subserratissimus	IK11-017[a]	KP165552	Niskanen (2014)
C. subsulfurinus	TN11-093[a]	KT351642	Dima (2015)
C. tabularis	614-HRL	KJ705108	GenBank
C. talus	F44793[a]	KF732457	Liimatainen et al. (2014)
C. torvus	IK98-1973	JX407337	Niskanen et al. (2013)
C. trivialis	TUB011839	AY669593	Garnica et al. (2005)

Table 1 (continued)

Species	Voucher	Sequence accession No.	Reference
C. uraceus	TN04-872[a]	KJ206522	Dima et al. (2014)
C. urbcius	F44893	KP866158	Niskanen et al. (2015)
C. variecolor	F44809[a]	NR 130279	Liimatainen et al. (2014)
C. varius	TUB019761	KJ421000	Garnica et al. (2016)
C. venetus	IB19970371	AF389167	Peintner et al. (2004)
C. vibratilis	M4	KC842440	Stensrud et al. (2014)
C. violaceomaculatus	CFP1449	KF732473	Liimatainen et al. (2014)
C. violaceus	MM1974/0208[a]	KM253741	GenBank
C. viridicoeruleus	TUB023092	KJ421077	Garnica et al. (2016)
C. vulpinus	TUB019728	KJ421189	Garnica et al. (2016)
Hebeloma mesophaeum	KRAM-F47211	KT071031	Eberhardt et al. (2015)
Hebeloma sinapizans	HJB10628	JQ751191	Eberhardt et al. (2013)
Hebeloma velutipes	KRAM-F57419	KT071058	Eberhardt et al. (2015)

[a] Sequence from type material

alignment of ITS sequences increases the robustness of the phylogenetic analyses (Nagy et al. 2012; Brandrud et al. 2015; Seress et al. 2016).

The second dataset to study the species limits within the clade Riederi was assembled using 99 sequences of the target clade of which 87 were generated for this study and 12 were downloaded from public repositories (Table 2). Multiple sequence alignment was done with PRANK (Löytynoja and Goldman 2005, 2008) as implemented in its graphical interface (PRANKSTER) under default settings. The resulting alignment contained 574 positions. Indels were coded with the same indel coding algorithm as described above. The final matrix was composed of 609 positions (nucleotides + binary data). New sequences were submitted to GenBank, and the accession numbers are available in Tables 1 and 2. The alignment was deposited at TreeBase (TB2:S22806).

Phylogenetic analyses

Maximum Likelihood (ML) analysis was carried out for both datasets using RAxML (Stamatakis 2014) as implemented in raxmlGUI (Silvestro and Michalak 2012). For testing the support of the branches, rapid bootstrap analysis with 1000 replicates and ML search were chosen. For the partitioned dataset, the GTRGAMMA substitution model for the DNA and the default set for binary (indel) characters were applied. The resulting ML phylogenetic tree (Fig. 1) was edited with MEGA6 (Tamura et al. 2013).

For the dataset 2, Bayesian inference (BI) analysis was performed with MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003). The alignment was partitioned and the GTR + G model of evolution was applied for the ITS and the two-state Markov model for the indel characters. Four Markov chains and two independent runs were performed for 10,000,000 generations, sampling every 1000 steps, resulting in overall sampling of 10,001 trees. The first 4000 of the sampled trees (40%) was excluded before constructing the 50% majority rule consensus tree and calculating the posterior probabilities (PP). The Markov Chain Monte Carlo (MCMC) convergence was checked with AWTY online (Nylander et al. 2007).

Tree topologies of both BI and ML analyses were checked visually, and no incongruence was observed, only the ML tree is shown in Fig. 2. Branches were considered strongly supported when BI posterior probability values (PP) exceeding at least 0.90 and ML bootstrap values (BS) at least 70%. Phylogenetic trees were visualised and edited in MEGA6 (Tamura et al. 2013) (Figs 1 and 2).

Morphological studies

Fresh material was examined mainly from N, C, W and S Europe and some from N America. More collections than those used for DNA sequencing were studied morphologically, but the character variation described in the 'Taxonomy' section is based on the sequenced material alone, as no obvious discrepancies were observed. Collections sequenced and examined morphologically are listed under each species description (and in Table 2). Most specimens (except some types) were examined both macro- and micromorphologically. The morphological descriptions are only based on specimens studied by the authors. The measurements of macromorphological characters were based on expanded, but never old (and then often aberrant) basidiocarps. The terminology of characters follows Brandrud et al. (1990) and Brandrud (1996a).

Microscopical structures were observed either from fresh material mounted in H_2O, often with a drop of 40% KOH added subsequently or from dried material mounted in H_2O

Table 2 *Cortinarius* sequences used in the dataset 2 that the phylogenetic analysis shown in Fig. 2 is based on

Taxon name	Voucher	Geographic origin	ITS acct. No.
C. anomaloochrascens (as *C. riederi*)	MCVE16165	Italy	JF907910 (Osmundson et al. 2013)
C. anomaloochrascens (as *C.* sp.)	TUB019758	Germany	KJ420997 (Garnica et al. 2016)
C. anomaloochrascens (as *C. riederi*)	TUB019769	Germany	KJ421008 (Garnica et al. 2016)
C. anomaloochrascens (as *C. riederi*)	TUB019770	Germany	KJ421012 (Garnica et al. 2016)
C. anomaloochrascens	PRM924382	Czech Republic	MH923043
C. anomaloochrascens	IK92-2028	Finland	MH846273
C. anomaloochrascens	Henry 2807 (isotype)	France	MH846270
C. anomaloochrascens	Henry 2805 (holotype)	France	MH846269
C. anomaloochrascens	TSJ2006-095	France	MH923036
C. anomaloochrascens (*C. imbricatoides*)	Henry 395 (holotype)	France	MH846271
C. anomaloochrascens (*C. stilazureus*)	Henry 85.13 (holotype)	France	MH846272
C. anomaloochrascens	TEB762-12/DB4814	Germany	MH923048
C. anomaloochrascens	MD28/2013	Germany	MH923042
C. anomaloochrascens	Bellu 13-08-2012	Italy	MH923037
C. anomaloochrascens	Rossi 07-09-2017	Italy	MH923040
C. anomaloochrascens	Bellu 30-07-2012	Italy	MH923045
C. anomaloochrascens	TEB175-07	Norway	MH923041
C. anomaloochrascens	TEB252-07	Norway	MH923039
C. anomaloochrascens	TEB316-10	Norway	MH923038
C. anomaloochrascens	O-F-75650	Norway	MH923046
C. anomaloochrascens	EB-TEB6-05	Norway	MH923044
C. anomaloochrascens	CFP1539	Sweden	MH923047
C. argenteolilacinus	MM 48/752 (holotype)	Austria	MH846277
C. argenteolilacinus	TSJ2010-004	Denmark	MH923066
C. argenteolilacinus	TSJ2011-025	Denmark	MH923062
C. argenteolilacinus	DB3312	France	MH846278
C. argenteolilacinus	MD18/2013	Germany	MH923064
C. argenteolilacinus	NL-5262	Hungary	MH923063
C. argenteolilacinus	TEB052-01	Norway	MH923061
C. argenteolilacinus	ILF2013-98	Norway	MH923067
C. argenteolilacinus	TEB281-17/DB6361	Norway	MH923065
C. argenteolilacinus	IK98-2617	Sweden	MH846279
C. argenteolilacinus	CFP1608	Sweden	MH923068
C. argenteolilacinus var. *dovrensis* (as *C. elotus*)	MCVE6043	Italy	JF907933 (Osmundson et al. 2013)
C. argenteolilacinus var. *dovrensis* (as *C. argenteolilacinus*)	KS-CO770	Sweden	KJ421064 (Garnica et al. 2016)
C. argenteolilacinus var. *dovrensis*	TN11-319	Canada, AB	MH923078
C. argenteolilacinus var. *dovrensis*	TEB312-09	Norway	MH923073
C. argenteolilacinus var. *dovrensis*	KB-EB-TEB79-10	Norway	MH923077
C. argenteolilacinus var. *dovrensis*	TEB112-80 (holotype)	Norway	MH923071
C. argenteolilacinus var. *dovrensis*	TEB217-08	Norway	MH923069
C. argenteolilacinus var. *dovrensis*	KB-EB-TEB78-10	Norway	MH923072
C. argenteolilacinus var. *dovrensis*	KS-CO1821	Sweden	MH923075
C. argenteolilacinus var. *dovrensis*	KS-CO1703	Sweden	MH923074
C. argenteolilacinus var. *dovrensis*	KS-CO2130	Sweden	MH923076
C. argenteolilacinus var. *dovrensis*	TSJ2006-010	Sweden	MH923070
C. burlinghamiae (as *C. fulvoochrascens*)	IB19970218	USA, WY	AF389139 (Peintner et al. 2004)
C. burlinghamiae	DBB37303 (holotype)	USA, MO	KX768115
C. burlinghamiae	DBB57001	USA, CA	KX768116
C. fulvoochrascens (as *C. riederi*)	TUB019735	Germany	KJ420976 (Garnica et al. 2016)
C. fulvoochrascens (as *C. riederi*)	TUB020433	Germany	KJ421204 (Garnica et al. 2016)
C. fulvoochrascens (*Phl. fuscomaculatum* var. *umbrinum*)	MM 49/137 (holotype)	Austria	MH923027
C. fulvoochrascens	Henry 314 (holotype)	France	MH846266
C. fulvoochrascens	Henry 71.732 (‘heterotype’)	France	MH846267
C. fulvoochrascens (*C. fulvoochrascens* var. *cyanophyllus*)	Henry 3258-a-29 (‘heterotype’)	France	MH923021
C. fulvoochrascens (*C. fulvoochrascens* var. *subcaninicolor*)	Henry 82/77 (holotype)	France	MH923017
C. fulvoochrascens (*C. marginatoochrascens*)	Henry 643 (holotype)	France	MH923018
C. fulvoochrascens (*C. notabilis*)	Henry 3258-a-16 (holotype)	France	MH846268
C. fulvoochrascens	TEB437-10	Germany	MH923022
C. fulvoochrascens	Rossi 31	Italy	MH923030
C. fulvoochrascens	TEB725-17/DB6542	Norway	MH923016
C. fulvoochrascens	TEB667-80	Norway	MH923025
C. fulvoochrascens	TEB172-04	Norway	MH923020
C. fulvoochrascens	O-F-75726	Norway	MH923028
C. fulvoochrascens	TEB530-13/DB5210	Norway	MH923023
C. fulvoochrascens	TEB292-13	Norway	MH923026

Table 2 (continued)

Taxon name	Voucher	Geographic origin	ITS acct. No.
C. fulvoochrascens	DB4408	Romania	MH923029
C. fulvoochrascens	JB-6858-09	Spain	MH923019
C. fulvoochrascens	TSJ2004-052	Sweden	MH923024
C. glaucocyanopus	GK5034 (holotype)	France	MH846274
C. glaucocyanopus	AL99/51	Hungary	MH846275
C. glaucocyanopus	DB2072	Hungary	MH846276
C. malachioides (as *C.* sp.)	KS-CO1708	Sweden	KJ421177 (Garnica et al. 2016)
C. malachioides	TN07-313	Canada, NL	MH846281
C. malachioides (*C. fallaceicolor* '*f. meridionale*')	Henry 80.811 (holotype)	France	MH846282
C. malachioides	TEB245-13	Norway	MH923032
C. malachioides	TEB562-08	Norway	MH923034
C. malachioides	TEB176-07	Norway	MH923035
C. malachioides	CFP980	Sweden	MH923031
C. malachioides	TEB340-16/DB6138b	Sweden	MH923033
C. malachioides	K(M)94426 (holotype)	UK	MH846280
C. pallidoriederi	Bellu 30-09-2011 (holotype)	Italy	MH923049
C. pallidoriederi	Bellu 30-09-2011b (isotype)	Italy	MH923050
C. parksianus	MICH10393 (holotype)	USA, CA	MH846283
C. riederi	IK98-1171	Finland	MH846263
C. riederi	IK93-664	Finland	MH846264
C. riederi	TG25-08-2013	Italy	MH923053
C. riederi	Bellu 12-08-2012	Italy	MH923057
C. riederi	Rossi 19-08-2005	Italy	MH923052
C. riederi	KB-EB-TEB2-10	Norway	MH923055
C. riederi	TEB258-17	Norway	MH923058
C. riederi	TEB407-13/DB5109	Norway	MH923051
C. riederi	TSJ2001-004	Norway	MH923059
C. riederi	TEB141-10/SSt10-066	Sweden	MH923056
C. riederi (*Phl. fuscomaculatum* var. *smolandicum*)	MM 57/60 (holotype)	Sweden	MH923054
C. riederi	GK13347 (neotype)	Switzerland	MH923060
C. riederi (*C. pseudoarquatus*)	MICH10397 (holotype)	USA, WA	MH846265
C. sp. (*Picea* sp. EcM)	183E	Canada, BC	UDB031686 (UNITE)
C. sp. (as uncultured fungus)	clone 3241J9	USA, AL	KF617829 (Taylor et al. 2014)
C. sp.	TN11-362	Canada, AB	MH846284

and then in KOH. Basidiospore measurements were made at × 1000 magnification with a calibrated optical micrometer or on a flat screen with the program ProgRes® CapturePro from Jenoptik. The measurements are based on at least 20 spores from each specimen/basidiocarp; numbers in square brackets refer (in this order) to the number of collections they originate from, the number of basidiocarps (sometimes more than one basidiocarp has been measured per collection) and the number of spores measured, respectively. Spore measurements are given as follows: length range × width range followed by the mean values in brackets then the variation of the MVs. Q values were calculated as follows: Q = length divided by width. Mean values of the Q is also presented. To exclude aberrant spores, the given values are based only on spores within the 95% confidence interval. For comparative spore measurements, see also Table 3.

The photo micrographs of the spores (Fig. 3) are created using z-stacking (Schmidt-Stohn 2011). For this, about ten pictures taken with a Jenoptik ProgRes® C10 plus digital camera, at different focus heights, were combined into the final picture with the Helicon Focus 6.5 program. For the correction and the final arrangement of the spores on the plates Adobe Photoshop CS5 was used. The column graph of mean values of spore lenghts (Fig. 4), the scatter diagram of spore mean values (Fig. 5) and the 95% confidence ellipses of spore variations (Figs. 6 and 7) were calculated with a special Microsoft Excel file (Documenta Geigy, pers. com. of H. Clémençon). For generating figures, the graphics were copied from Excel and edited with Adobe Photoshop CS5.

Results and discussion

Molecular phylogeny

The ML analysis (Fig. 1) of the dataset 1 confirmed that the clade Riederi is a well-supported monophyletic group within genus *Cortinarius*, in line with the results of Garnica et al. (2016). According to multigene phylogenetic analysis using the ITS, LSU and *rpb1* gene regions performed by Garnica et al. (2016), the clade Riederi nested basally in a large well-supported group called 'Phlegmacioid clade II', together with, e.g. sect. *Multiformes*, sect. *Scauri* and the *C. lustratus* and *C. pinophilus* groups. ITS sequences of clade

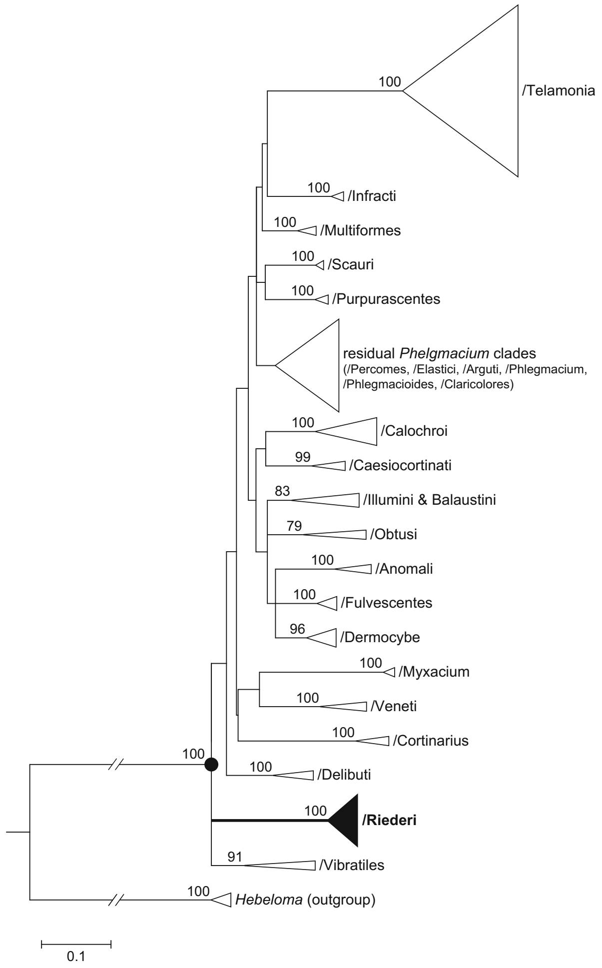


Fig. 1 Compressed phylogenetic tree based on RAxML analysis of the ITS region showing the main infrageneric clades within *Cortinarius* in Europe. The clade Riederi is highlighted in black. The genus *Hebeloma* was chosen as outgroup. Bootstrap supports values (> 70%) are shown at the branches. The bar indicates 0.1 expected change per site per branch

Riederi species were relatively dissimilar to other *Cortinarius* taxa when evaluating BLAST hits, with only 88% similarity to the best match in GenBank (e.g. *C. borgsjoeensis*). Molecularly, the Riederi species also differ from typical phlegmacioid species in other lineages (e.g. Calochroi, Infracti, Phlegmacioides) in the length of the ITS region, which in clade Riederi is more similar to that of species in the Telamonia lineage (= *Telamonia* s. str.). Both our analyses and those of Garnica et al. (2016) clearly indicate that clade Riederi is an isolated lineage within *Cortinarius*, and this is also supported by morphological data (see below). Therefore, we here present this well-circumscribed group and combine it formally to section level (see 'Taxonomy' section). For a more precise infrageneric placement of this clade, multigene phylogenetic analyses combined with deeper taxon sampling will need to be done in the future.

The analysis of the second dataset revealed 11 OTUs within the clade Riederi (Fig. 2). Nine of these have a distinct 'barcoding gap', each OTU being separated by at least 1.2% (seven substitutions and indel positions) from sister species and with little internal variation (0–0.7%, 0–4 changes). Eight of these OTUs can also be morphologically distinguished and are here treated as species (see Taxonomic part). Two OTUs in the *C. argenteolilacinus* complex showed only a small barcoding gap of 0.5% (three substitutions and indel positions). This percentage is smaller than normally used 1% as a minimum cut-off value for recognising species of *Cortinarius* based on ITS sequences (see, e.g. Frøslev et al. 2007; Liimatainen et al. 2014; Garnica et al. 2016). Therefore, we have decided to treat these clades as varieties although they also have morphological and ecogeographical differences (see Taxonomic part). The one additional unsupported OTU (probably a complex of several species) from N America assigned here as *Cortinarius* sp. is not further studied due to lack of data.

Morphological and ecological characters used to circumscribe the species in sect. *Riederi*

Stipe shape Already, Fries (1836) and then later Moser (1961) made a major distinction between phlegmacia with a marginate bulb and those with a cylindric-clavate stipe. This is still largely a good diagnostic character to distinguish major phylogenetic lineages such as sect. *Phlegmacioides* (cylindric stipe) and sect. *Calochroi* (flattened, marginate bulb) (see Garnica et al. 2006; Frøslev et al. 2007). In sect. *Riederi*, however, this feature is less relevant as a diagnostic character, since the species have a rather irregular stipe shape, some with a mainly clavate-bulbous stipe and some with a more marginate bulb, but usually with a fairly large infraspecific variation.

Lamellae colour A bright, deep violaceous colour is present in young lamellae and stipe of most *Riederi* species (paler bluish in *C. malachioides*). However, this pigment vanishes with age and exposure, resembling the situation with bright bluish coloured species in sect. *Glaucopodes*.

Pileus colour and structure In contrast with the above-mentioned features, pileus colour is an important diagnostic character on the species level in sect. *Riederi*; ranging from vivid redbrown-ochre colours in *C. fulvoochrascens* and *C. riederi* to pale (bluish-)grey in *C. argenteolilacinus*. The *Riederi* species normally possess a finely innately fibrillose structure of the pileus cuticle. This is due to darker pigmented, innate filaments that form a braided-veined structure towards the margin, and a denser, almost marbled pattern towards the centre. The structure is especially distinct in specimens of *C. riederi* with a strong ochraceous-redbrown colouration but can be seen in all taxa (see also under Micromorphology). Although seen in some other species, such as *C. dionysae*,

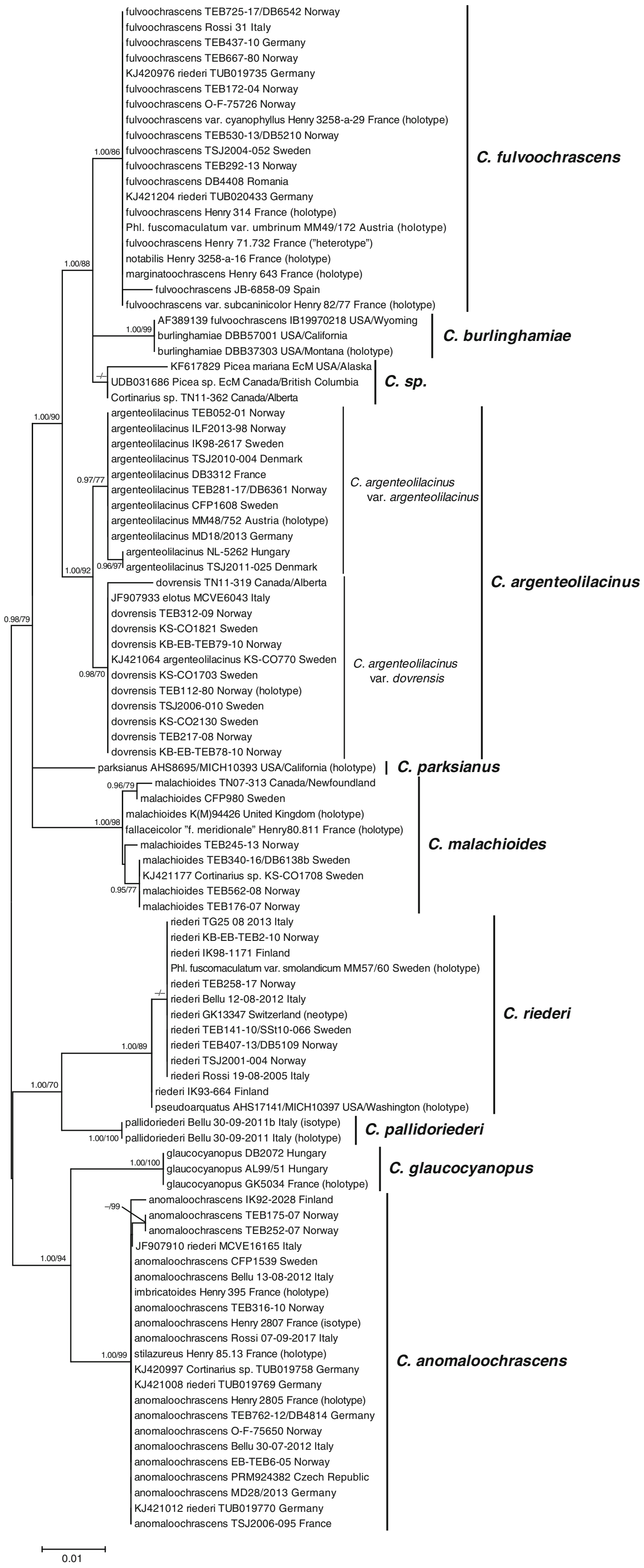


Fig. 2 Mid-point-rooted phylogenetic tree of sect. *Riederi* inferred from ITS dataset and RAxML analysis. Bayesian posterior probabilities (> 0.90) and RAxML bootstrap supports values (> 70%) are indicated on the branches at nodes (PP/ML). The bar indicates 0.01 expected change per site per branch

Table 3 Spore characteristics of the species of sect. *Riederi*

Taxon	*n* coll.	*n* frb.	*n* spores	Length (*L*) × width (*W*) 95% variation (µm)	Length (*L*) × width (*W*) total (µm)	Variation in MVs (µm)	*Q L*/*W* 95% variation	*Q L*/*W* total
C. anomaloochrascens	7	11	168	10.2–***11.5***–12.8 × 6.3–***7.2***–8.1	9.8–***11.5***–13.3 × 6.0–***7.2***–8.5	***10.9–11.9*** × ***6.9–7.6***	1.43–***1.60***–1.78	1.39–***1.61***–1.86
C. argenteolilacinus var. *argent.*	8	16	319	10.7–***12.2***–13.7 × 6.7–***7.5***–8.3	10.7–***12.2***–14.2 × 6.5–***7.5***–8.5	***11.6–12.9*** × ***7.1–7.9***	1.42–***1.63***–1.84	1.40–***1.63***–1.91
C. argenteolilacinus var. *dovren.*	9	16	264	11.2–***12.5***–13.8 × 6.8–***7.7***–8.6	11.0–***12.5***–14.0 × 6.7–***7.7***–8.9	***11.8–13.5*** × ***7.3–8.2***	1.45–***1.62***–1.79	1.43–***1.62***–1.86
C. malachioides	9	15	276	9.6–***10.7***–11.8 × 5.9–***6.7***–7.4	9.3–***10.7***–12.0 × 5.8–***6.7***–7.5	***10.1–11.3*** × ***6.3–7.1***	1.42–***1.61***–1.79	1.33–***1.61***–1.93
C. fulvoochrascens	7	11	206	11.1–***12.5***–13.8 × 7.2–***7.9***–8.6	10.7–***12.5***–14.5 × 6.8–***7.9***–9.0	***12.1–12.7*** × ***7.6–8.2***	1.43–***1.59***–1.75	1.40–***1.59***–1.81
C. riederi	10	15	249	11.6–***12.9***–14.2 × 7.3–***8.2***–9.0	10.9–***12.9***–15.0 × 7.1–***8.2***–9.1	***12.3–13.6*** × ***7.9–8.7***	1.44–***1.58***–1.72	1.39–***1.58***–1.86
C. glaucocyanopus	2	2	68	10.3–***11.7***–13.1 × 6.6–***7.2***–7.8	9.7–***11.7***–13.7 × 6.5–***7.2***–7.9	***11.2–12.0*** × ***7.2–7.3***	1.41–***1.63***–1.85	1.37–***1.63***–1.86
C. pallidoriederi	1	4	65	11.1–***12.4***–13.8 × 6.3–***7.4***–8.5	10.9–***12.4***–14.0 × 6.1–***7.4***–8.5	***12.1–12.7*** × ***6.9–7.7***	1.45–***1.69***–1.92	1.44–***1.69***–1.95
C. burlinghamiae	1	1	21	11.2–***12.2***–13.2 × 6.9–***7.5***–8.2	11.0–***12.2***–13.2 × 6.9–***7.5***–8.3	***12.2*** × ***7.5***	1.51–***1.63***–1.75	1.51–***1.63***–1.78
C. parksianus	1	1	50	9.8–***10.7***–11.6 × 6.3–***6.7***–7.1	9.4–***10.7***–11.6 × 6.0–***6.7***–7.2	***10.7*** × ***6.7***	1.45–***1.61***–1.77	1.43–***1.61***–1.79

C. napus and *C. aureopulverulentus*, such regular, densely braided pattern of innate fibrils is rarely encountered in other phlegmacioid taxa.

Universal veil Unlike most related groups, the universal veil in most taxa of sect. *Riederi* is sparse, leaving almost no visible traces on the pileus or the stipe surface. Only in *C. fulvoochrascens* and sometimes in *C. argenteolilacinus* can distinct veil remnants be seen, near the bulb and pileus margin.

KOH reactions Macrochemical reactions with KOH are always negative (slightly grey brownish discolouring) and are not further mentioned in the Taxonomic part.

Basidiospores The spore shape and ornamentation is fairly uniform in sect. *Riederi*. The entire group is characterised by rather ellipsoid-shaped spores with a more or less rounded apex, never with a sharply pointed-elongated apex as seen in the spores of many other phlegmacioid species (Fig. 3). Such ellipsoid-subamygdaloid spores occur also in *C. glaucopus* agg. and in *C. eucaeruleus*-*C. coerulescentium* complex. The ornamentation also resembles that of the spores of the latter mentioned taxa with a pattern of rather dense, discrete warts without interconnected ridges and crusts as seen in sect. *Calochroi*. A characteristic feature of the spores of the species of sect. *Riederi* is the apex, where the ornamentation often is more or less confluent, forming an apical 'lense', sometimes also with some prominent, subapical 'teeth'. This feature is especially pronounced in *C. argenteolilacinus*. The *Q* value (spore length/width ratio) is very similar in all species, with average values ranging from 1.59 to 1.69 (Table 3).

The spore size is the most important diagnostic character at the species level (Figs. 4, 5, 6 and 7). When spores are measured from the stipe/cortina (excluding aberrant, unripe ones), and mean values (MVs) from each measurement series are compared, many species show considerable differences. For instance, among the coniferous forest species, the comparatively small-spored *C. anomaloochrascens* (spore MVs 10.9–11.9 × 6.9–7.6 µm) can be distinguished from the sometimes co-occurring, large-spored *Cortinarius riederi* (spore MVs 12.3–13.6 × 7.9–8.7 µm) and *C. fulvoochrascens* (spore MVs 12.1–12.7 × 7.6–8.2 µm) (Figs. 4 and 6), and the small-spored, *Betula*-associated *C. malachioides* (spore MV 10.1–11.3 × 6.3–7.1 µm) from the co-occurring, large-spored *C. argenteolilacinus* var. *dovrensis* (spore MV 11.8–13.5 × 7.3–8.2 µm) (Figs. 4 and 7).

Pileus cuticle A major subdivision of *Phlegmacium* can be performed based on the structure of pileipellis (Brandrud et al. 1990). Sect. *Riederi* shares with sections such as

Cortinarius anomaloochrascens (coll. Bellù 30.07.2012)

Cortinarius fulvoochrascens (coll. TEB748-11)

Cortinarius riederi (coll. TEB141-10)

Cortinarius pallidoriederi (coll. Bellù 30.09.2011b)

Cortinarius burlinghamiae (coll. DBB37303)

Cortinarius argenteolilacinus var. argenteolilacinus (coll. I-LF2013-98)

Cortinarius argenteolilacinus var. dovrensis (coll. KS-CO1821)

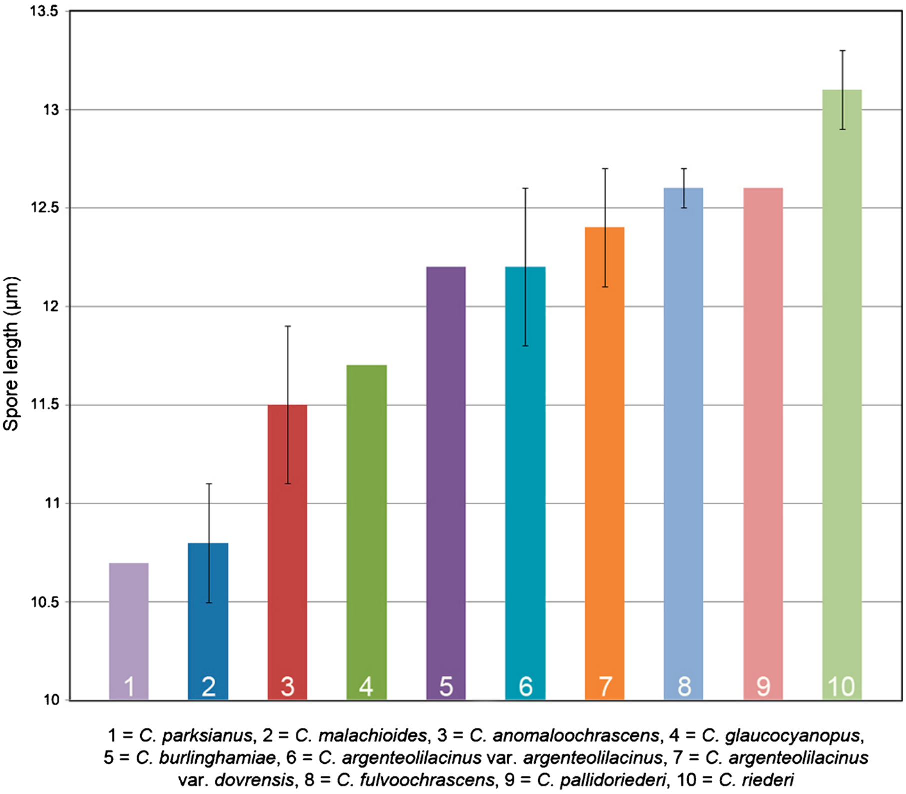
Cortinarius malachioides (coll. I-LF2013-98)

Cortinarius glaucocyanopus (coll. DB2072)

Cortinarius parksianus (coll. 10393)

Fig. 3 Spore photos of selected specimens of each species in sect. *Riederi*

Fig. 4 Mean values of spore lengths of species in sect. *Riederi*. Bars indicate 95% confidence interval. The missing bars are due to the limited number of available collections of those species



Glaucopodes and *Scauri* a duplex structure of pileipellis with a thin epicutis of narrow hyphae and a subcutis/hypodermium consisting of broader, shorter, tightly cemented, 'subcellular' elements. Some sections such as *Calochroi*, *Cliduchi* and *Phlegmacioides*, on the other hand, are characterised by a simplex pileipellis consisting of a thick, more or less homogeneous layer of thin, long, usually loosely entangled hyphae. In sect. *Riederi* species, the transition layer between the epicutis and the hypodermium consists of irregularly interconnected bundles of rather narrow, long hyphae with more or less encrusted pigment, giving rise to the innately fibrillose structure described under macrocharacters. The degree of encrustations of these long, transition hyphae is an important diagnostic character of some species. The major part of the hypodermium consists in sect. *Riederi* species of moderately inflated, 15–20-µm-wide elements. In *C. argenteolilacinus*, the hypodermium is weakly developed, and elements are only little inflated.

Fig. 5 Scatter diagram of mean values of spores of each measured collection in sect. *Riederi*

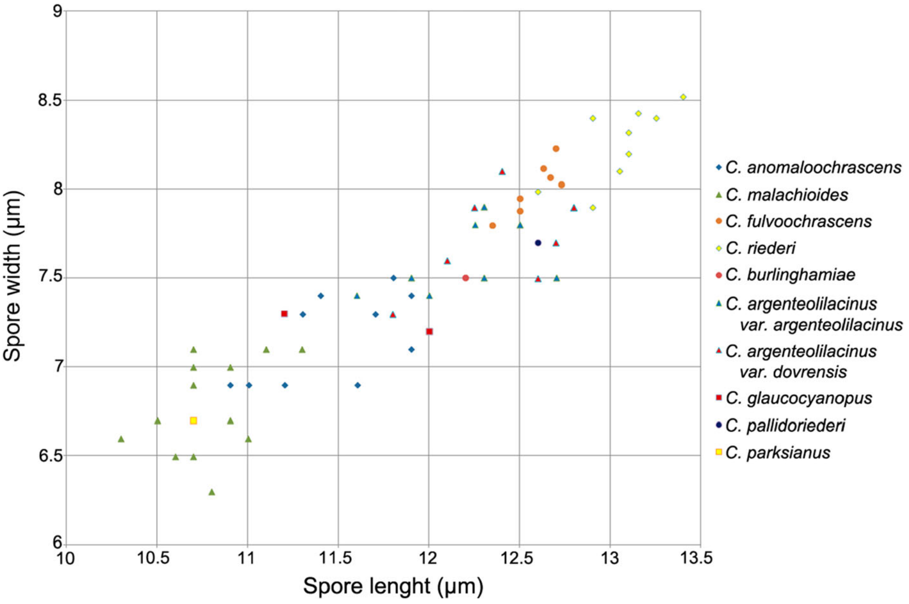
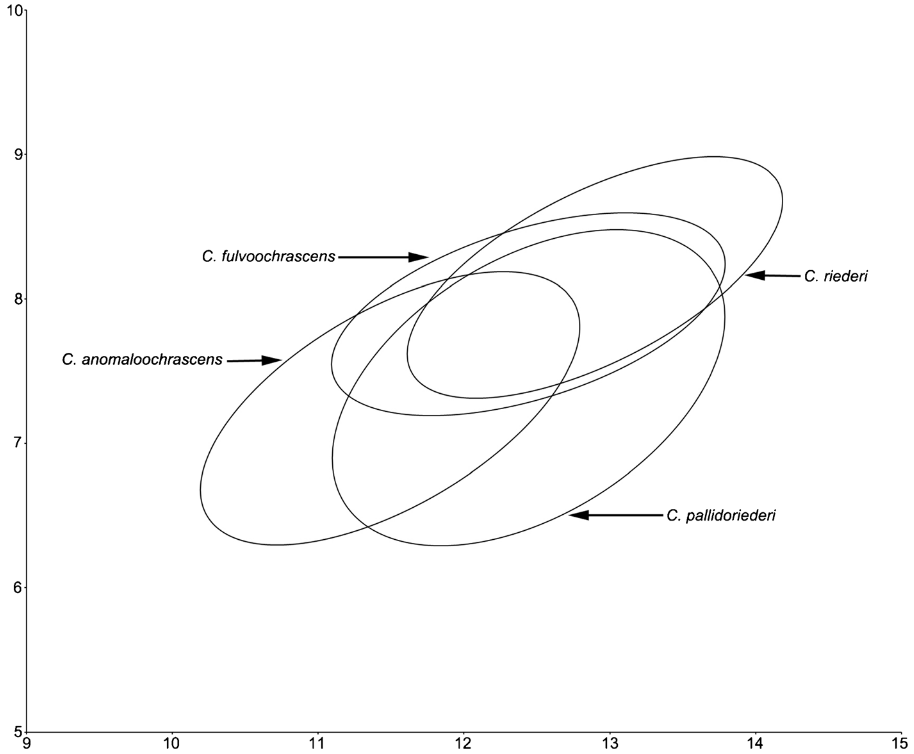
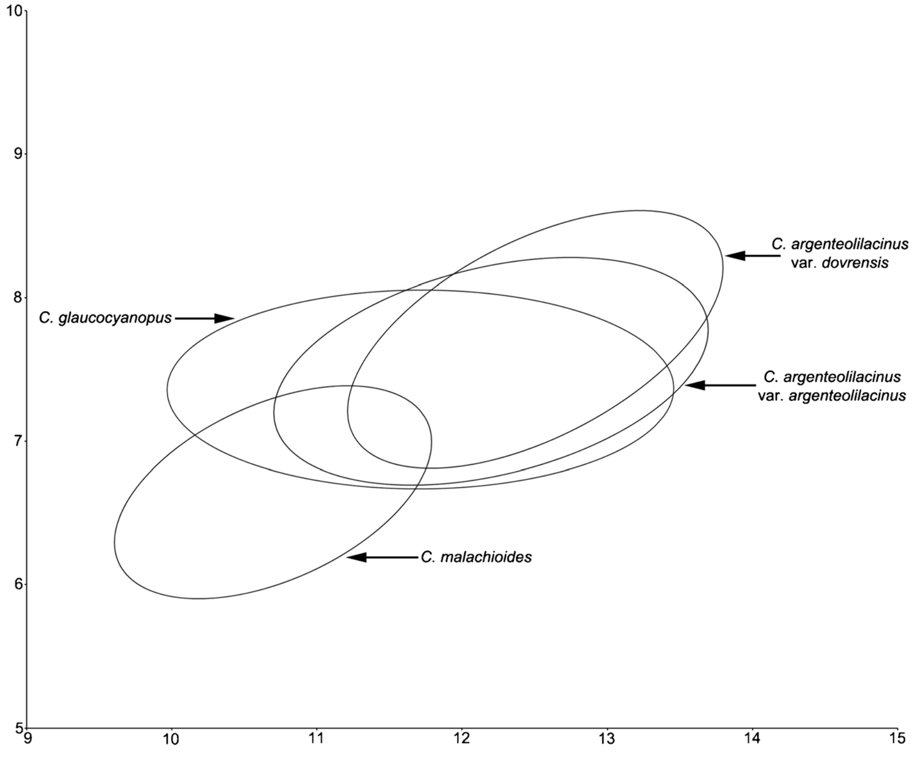


Fig. 6 95% confidence ellipses of spore variations of the conifer-associated species in sect. *Riederi*



Distinguishing features towards similar sections/clades Morphologically, the species of sect. *Riederi* resemble those of the *C. glaucopus* group (deep violet lamellae/stipe), the *C. talus*-*C. multiformis* group (ochre yellow pileus with a similar surface structure) as well as the *C. largus* complex (bluish-greyish pileus). The most important character for distinguishing the *Riederi* species from these are the large spores > (10.5) 11 μm long. Furthermore, the innately fibrillose surface of the pileus and the lack of a distinctly marginate bulb also clearly differ from other taxa. Section *Riederi* is further characterised by the lack of distinct smells.

Fig. 7 95% confidence ellipses of spore variations of the species associated with deciduous trees in sect. *Riederi*



Habitat and distribution Half of the eight European taxa are associated with coniferous trees, the other half with deciduous ones. The widespread *C. riederi*, *C. anomaloochrascens* and *C. fulvoochrascens* are mainly associated with *Picea abies*. *Cortinarius argenteolilacinus* var. *argenteolilacinus* is found under *Fagus sylvatica* in nemoral/temperate regions of C Europe and S Scandinavia, and under *Tilia* and *Corylus* in S Sweden and S Norway. *Cortinarius argenteolilacinus* var. *dovrensis* and *C. malachioides* are recorded mainly under *Betula pubescens subsp. tortuosa* in Scandinavian mountains.

For most species, a preference for boreal-montane regions can be assumed. At least five of the eight European taxa are associated with boreal-montane coniferous trees or with boreal deciduous trees. Only *C. argenteolilacinus* var. *argenteolilacinus* and *C. glaucocyanopus* seem to have a preference for more temperate (mixed) *Fagus* forests. Most species show an overlapping distribution in the boreonemoral region of S Scandinavia, which can be regarded as a region of high diversity for sect. *Riederi* in Europe. In contrast, none of the species occurs in thermophilous (sub)mediterranean *Quercus* forests. The taxa of sect. *Riederi* are also characterised by less calciphilous requirements than most other phlegmacioid species. *Cortinarius riederi* prefers oligotrophic sites, and also the other taxa rarely grow on calcareous ground, and rarely occur in typical *Phlegmacium* hotspots (the exception being *C. fulvoochrascens*).

Comparatively little is known about the distribution of the species of sect. *Riederi* outside Europe. The two preferentially boreal(-subalpine) taxa *C. riederi* and *C. argenteolilacinus* var. *dovrensis* are also found in N America and probably have a circumpolar distribution. Two western N American (non-European) species are included in sect. *Riederi* (*C. parksianus* and *C. burlinghamiae*), as well as one unknown species complex from Canada and Alaska (Fig. 2), but generally, the *Riederi* group seems to be understudied in N America, and more taxa are probably to be discovered.

Taxonomy

Cortinarius sect. ***Riederi*** (Brandrud & Melot) Brandrud, Dima, Niskanen & Liimat., stat. nov.

MycoBank: MB 827874

Basionym: *Cortinarius* subsect. *Riederi* Brandrud & Melot in Nord. J. Bot. 10: 538 (1990). MycoBank: MB 828282

Basidiocarps fleshy and phlegmacioid. Pileus glabrous and viscid-glutinous, more or less innately fibrillose, vividly yellow brown to redbrown, pale greybrown to almost whitish. Lamellae usually deep violaceous blue when young, soon fading to greyish brown. Stipe with a clavate-bulbous base (rarely slightly marginate-bulbous), glossy, initially usually deep (greyish) violet in upper part, soon fading to greyish white, often developing glossy brass brown patches. Universal veil very sparse and hardly visible on most species. Context fugacious violet.

Basidiospores large (10–14(15) × 6–9 μm), ellipsoid to subamygdaloid, densely verrucose (with discrete warts), sometimes with an apical 'lense' of confluent warts. Lamellar edge more or less fertile. Pileipellis duplex, composed of thin, gelatinised epicutis and subcellular subcutis/hypodermium with brown parietal-encrusting pigment, in transition to epicutis many species with bundles of zebra-striped-crustulose encrusted hyphae.

Type species: *Cortinarius riederi* (Weinm.) Fr.

Cortinarius riederi (Weinm.) Fr., Epicr. Syst. mycol.: 259 (1838).

MycoBank: MB 155615, Fig. 8a, b

Basionym: *Agaricus riederi* Weinm., Hymenom. Gasterom. Imp. Ross.: 161 (1836). MycoBank: MB 244037. Type: Switzerland, Graubünden, Engadin, J. Favre, 26 Aug 1944 (sub nom. *C. lilacinopes*), GK13347 (G), neotype designated in Melot (1986). GenBank: MH923060.

Synonyms: *Cortinarius pseudoarquatus* A.H. Smith, Lloydia 7(3): 181 (1944). MycoBank: MB 285764. Holotype: USA, Washington, Olympic National park, near Olympic Hot Springs, 22 Sept 1941, A.H. Smith, AHS17141 (MICH10397).

Phlegmacium fuscomaculatum var. *smolandicum* M.M. Moser, Die Gatt. Phlegm.: 355 (1961). MycoBank: MB 349991. Holotype: Sweden, Småland, Femsjö, 9 Sept 1957, M. Moser, MM 57/60 (M).—*Cortinarius fulvoochrascens* var. *smolandicus* (M.M. Moser) Rob. Henry, Bull. trimest. Soc. mycol. Fr. 105(4): 331 (1989). MycoBank: MB 126140.—*Cortinarius fuscomaculatus* f. *smolandicus* (M.M. Moser) Nespiak, Flora Polska, Grzyby (Mycota), 7, Basidiomycetes, Agaricales, Cortinariaceae, Cortinarius 1 (Warszawa-Krakow): 147 (1975). MycoBank: MB 347980.

Selected icones: Moser (1961), Die Gatt. Phlegm.: Pl. XVII, 95 (as *C. lilacinopes*—neotype for *C. riederi*), Pl. XXII, 127 (as *P. fuscomaculatum* var. *smolandicum*); Soop 2017, Pl. 5:17 as *C. pseudoarquatus.*

Pileus 5–10(12) cm, (hemi-)spherical(-campanulate), then plano-convex (to broadly umbonate), viscid-glutinous and glossy when dry, towards margin distinctly to strongly innately fibrillose-rivulose, centre with a fine-marbled structure from darker, innate fibres, sometimes with darker hygrophanous spots or veins towards margin, a few also with a narrow hygrophanous ring near margin; ochraceous brown-fulvous to somewhat more orange-red brown tinged at the centre, the involute margin whitish brown. Universal veil remnants very sparse, hardly visible.

Fig. 8 Basidiocarps of *Cortinarius* species in sect. *Riederi* associated with coniferous trees: **a**, **b** *C. riederi* (**a** TEB258-17 Norway, **b** SSt10-066 Sweden); **c**, **d** *C. fulvoochrascens* (**c** TEB530-13 Norway, **d** TEB-292-13 Norway); **e**–**g** *C. anomaloochrascens* (**e** TEB762-12/DB4814 Germany, **f** SSt17-202 Germany, **g** PRM924382 Czech Republic); **h** *C. pallidoriederi* (FB30-09-2011 Italy). Photos: **a**, **c**, **e** B. Dima; **b**, **f** G. Schmidt-Stohn; **d** T.E. Brandrud; **g** J. Borovička; **h** E. Castellini

Lamellae crowded ($L = 80–110$), 0.5–1-cm broad, initially deep violet to greyish violet, but soon fading to paler bluish grey and then greyish brown; edge even to crenulate.

Stipe 6–12 × 1–2(2.5) cm, with a clavate-bulbous base (up to 4.5 cm), bulb rarely slightly (irregularly) marginate, glossy, initially deep (greyish) violet in upper part and with a pale bluish tinge downwards, soon fading to greyish white-pale ochraceous brown, often developing glossy brass brown patches (like *C. glaucopus*, *C. multiformis*), often with distinct patches of watery bluish white tomentum towards base (sometimes developing strongly with age). Universal veil very sparse and hardly visible.

Context initially deep violet to greyish violet in (upper part) of stipe, bluish white in pileus and bulb, violet colour soon fading, becoming whitish with brass brown spots where damaged.

Macrochemical reactions: negative, KOH somewhat brownish in context.

Smell faint, sometimes yeast-like with age.

Exsiccata pale brownish with vivid brown-redbrown pileus.

Basidiospores [10, 15, 249], 11.6–14.2 × 7.3–9 μm (MV = 12.9 × 8.2 μm); variation of MVs, 12.3–13.6 × 7.9–8.7 μm; $Q = 1.44–1.72$ (MV = 1.58), ellipsoid-subamygdaloid, medium to strongly and densely verrucose, sometimes with an apical 'lense' of confluent warts; suprahilar plague hardly visible.

Lamellar edge more or less fertile, sterile cells small, clavate or cylindrical.

Pileipellis duplex. Epicutis thin. At surface 2–5 μm wide, loosely erect-entangled, gelatinous hyphae, hyaline, or with pale, refractive pigment when collapsed. Subcutis/hypodermium hyphae 5–20 μm wide, tightly cemented, with brown parietal-encrusting pigment, forming an amber-like embedment; in transition to epicutis with subparallel, interconnected bundles of 3–6(10)-long and rather narrow 5–7(10)-μm-wide hyphae, with distinct to strong, brown, zebra-striped-crustulose encrusted pigment. These bundles are normally easy visible when the thin pellicle is peeled off.

Veil at pileus surface: absent or very thin, of narrow, hyaline hyphae.

Habitat: Associated with *Picea abies*, probably also *Pinus sylvestris* (cf. Favre 1960, Moser 1961 as *C. lilacinopes*). In oligotrophic *Vaccinium myrtillus* type of forests, sometimes also in richer/mesotrophic low-herb spruce forests, sometimes in bog rims. Frequently in young, mossy *Picea* plantations.

Distribution: Mainly recorded from Fennoscandia where the species is widespread and rather frequent in boreal regions (Moser 1961 as *Phlegmacium fuscomaculatum* var. *smolandicum*; Soop 2011 as *C. fulvoochrascens* p.p.; Jeppesen et al. 2012). Rarely occurring also in subalpine *Picea-Pinus* forests in the Alp-Prealp regions, so far recorded from S Tyrol, Italy and Swiss national park, Engadin (neotype; see Moser 1961 as *C. lilacinopes*), probably also in French Jura and French Alps (Bidaud et al. 1999 as *C. fulvoochrascens* var. *umbrinus* and *C. lilacinopes*, material not sequenced). Recorded up to 2150 m asl. in the Swiss Alps (Favre 1960, as *C. lilacinopes*). Probably wider distributed in C Europe but little known due to confusion with the more frequent *C. fulvoochrascens* and *C. anomaloochrascens*. Recorded also in western North America (Smith 1944, as *C. pseudoarquatus*; type conspecific with *C. riederi*).

Comments: *Cortinarius riederi* is characterised by its (i) distinctly innately fibrillose and vividly ochre brown-redbrown pileus, (ii) deeply, but fugacious violet lamellae and stipe, (iii) irregularly bulbous stipe, and (iv) (very) large spores. The stipe is furthermore glossy-shiny often with watery blue tomentum in lower part and it soon becomes brass-brown spotted. The watery blue felt is often a very characteristic feature, but is not constant, and seems often to develop with age. The species has a mainly northern distribution in Europe, preferring oligotrophic-acidophilous spruce forest types. It sometimes occurs in large groups in young, mossy *Picea* plantations. In montane-subalpine sites in C Europe, acidophilous habitats such as margins of bogs might be characterising. *Cortinarius riederi* (= *C. fulvoochrascens* s. auct.) has by most authors been treated collectively, including taxa with innately fibrillose and vividly fulvous, umber to ochre brown pileus, initially deeply violet lamellae and stipe and large, ellipsoid-subamygdaloid spores. However, according to molecular studies, the *C. riederi* complex in its widest sense can be separated into a number of well-supported taxa. On closer examination, these are also distinguishable morphologically and partly ecogeographically; for instance, the large-spored *C. riederi* s. str., *C. fulvoochrascens* and *C. pallidoriederi* as well as *C. anomaloochrascens* with somewhat smaller spores. In Fennoscandia, more than half of the *C. riederi* s. lato collections belong to the present species, the remaining mainly to *C. anomaloochrascens*. In C Europe, about 50–50 of the collections belong to *C. fulvoochrascens* versus *C. anomaloochrascens*, whereas *C. riederi* s. str. apparently is rare and restricted to (montane-)subalpine *Picea-Pinus* forests.

Cortinarius riederi s. str. is often confused with the large-spored *C. fulvoochrascens*, and there is no consistent name-use for these in the literature. *Cortinarius fulvoochrascens* can be distinguished by the distinct veil remnants on stipe when very young, and it has furthermore (i) a more uniform ochre-fulvous-umber brown, less glabrous, less innately fibrillose pileus, (ii) usually a more clavate-bulbous stipe, (iii) lack of watery bluish mycelia tomentum on the bulb, and (iv) on average slightly smaller and more strongly verrucose spores. According to the spore-measurement series performed of sequenced collections (12 specimens from 10 collections), the mean values of spore length of *C. riederi* in half of the measurement-series exceed 13.0 μm, whereas MVs > 13.0 μm are not observed from *C. fulvoochrascens* so far (11 specimens from 7 collections; see Table 3). *Cortinarius fulvoochrascens* also apparently has its main distribution in montane C Europe (where *C. riederi* s. str. Can hardly be found). In N European regions where both species might co-occur, *C. fulvoochrascens* occurs in richer, often calcareous forest types, whereas *C. riederi* is confined to more oligotrophic/acid sites. *Cortinarius fulvoochrascens* reported in Moser et al. (1995) from N America might belong to *C. riederi*, based on the spore measurements given (see discussion under *C. fulvoochrascens*).

According to molecular data, *C. riederi* is more closely related to *C. anomaloochrascens* than to *C. fulvoochrascens*. *Cortinarius anomaloochrascens* sometimes occurs in the same, acidophilous habitats as *C. riederi*, but is well distinguished by smaller and often more amygdaloid spores. Furthermore, *C. riederi* normally has somewhat more vivid/warmer and darker pileus colours, larger basidiocarps with a more clavate stipe and stronger, encrusting pigment of pileipellis.

According to the protologue of Weinmann (1836), *C. riederi* might be a collective species, including at least *C. riederi* in our sense and *C. anomaloochrascens* which is widely distributed in boreal areas resembling the St Petersburg region where Weinmann collected. *Cortinarius fulvoochrascens* is less likely to be included in the protologue, since calcareous coniferous forests seem to be lacking or rare in the St Petersburg region. A neotype of *C. riederi* was selected by Melot (1986), representing a collection of *C. lilacinopes* as described and depicted by Favre in Favre (1960) and in Moser (1961). With the wide concept in the protologue, *C. riederi* s. str. might well be included here, so the selection of neotype can hardly be regarded as in serious contradiction with the protologue and should be accepted. The type has been studied microscopically, and corresponds well with the present species, but could also cover *C. fulvoochrascens*. However, the mean value 13.0 × 8.2 μm of spores (from stipe surface) is larger than that of all measured collections of *C. fulvoochrascens* and fits well with our species. The collection of Favre is from a subalpine coniferous forest of the Engadin valley in the Alps, and this high-altitude site on siliceous soils corresponds well with the present species. Furthermore, after several sequencing attempts, the type yielded an ITS1 sequence corresponding to the present taxon (Fig. 2).

Collections examined: **Finland**. Savonia Borealis, Vehmersalmi, Pitkälahti, J. Vauras, JV 1475F (herb. TUR). Uusimaa, Luukki, I. Kytövuori, IK93-664 (H). Kittilän Lappi, Kolari, I. Kytövuori, IK98-1171 (H). **Italy**. S Tyrol, Anterselva, 19 Aug 2005, *C. Rossi*, Rossi 19-08-2005 (herb. Rossi); S Tyrol, 25 Aug 2013, G. Turrini, TG25-08-2013 (herb. Turrini); 12 Aug 2012, F. Bellù, Bellu 12-08-2012 (herb. BOZ), 14 Aug 2012, *C. Rossi* (herb. Rossi). **Norway**. Oppland, Søndre Land, Hov NW, T.E. Brandrud, B. Dima, TEB407-13/DB5109 (O); Vestre Slidre, Einang Bridge S, T.E. Brandrud, TEB443-11 (O). Etnedal, Solbjør N, T.E. Brandrud & B. Dima, TEB258-17 (O). Sør-Trøndelag, Trondheim, Ranheimsskogen, T.S. Jeppesen TSJ2001-004 (C), Nord-Trøndelag, Lierne, K. & E. Bendiksen, TE. Brandrud; KB-EB-TEB 2-10 (O). **Sweden**. Jämtland, Bräcke, Ammersön, T.E. Brandrud, TEB141-10/SSt10-066 (O). Småland, Femsjö, M. Moser, MM 57/60 (M, holotype of *Phlegmacium fuscomaculatum* var. *smolandicum*). **Switzerland**. Graubünden, Engadin, J. Favre, 26 Aug 1944, GK13347 (G, neotype). **U.S.A.** Washington, Olympic National Park, Olympic Hot Springs, A.H. Smith, AHS17141 (MICH10397, holotype of *C. pseudoarquatus*).

Cortinarius pallidoriederi Brandrud, Dima & Bellù, sp. nov. MycoBank: MB 827875, Fig. 8h

Etymology: the epithet refers to the paler colour of the pileus than that of *C. riederi.*

Holotype: Italy, S Tyrol, Val d'Ega (Eggental), Novale (Rauth), Wald Lagarn, between Underkor and Oberkor, E. Castellini, F. Bellù, 30 Sept 2011, Bellu 30-09-2011 (BOZ). GenBank: MH923049.

Pileus: 4–8 cm, (hemi-)spherical, then plano-convex, viscid-glutinous, finely innately fibrillose-rivulose from darker, innate fibres; uniform pale ochraceous yellow to ochraceous brown, with an olivaceous ochre tinge. Universal veil remnants sparse, rendering surface shiny-micaceous-marbled when young.

Lamellae: crowded ($L = 80–90$), 0.4–0.8 cm broad, initially deep violet to greyish violet, but soon gradually fading to greyish brown; edge even to slightly sinuate.

Stipe: 5–8 × 1.2–2 cm, with a slightly marginate bulb (up to 3 cm), glossy, longitudinally striate, initially deep, metallic (greyish) violet in upper part and with a pale bluish tinge downwards, soon fading to greyish white-pale ochraceous brown, often developing glossy brass brown-golden brown patches, especially when bruised. Universal veil very sparse and hardly visible.

Context: initially violet to greyish violet in upper part of stipe, mainly in cortex, otherwise whitish, violet colour soon fading, some yellow brown spots where damaged.

Smell: faint, indistinct.

Exsiccata: pale brownish with almost whitish pileus.

Basidiospores: [1, 4, 65], 11.1–13.8 × 6.3–8.5 μm (MV = 12.4 × 7.4 μm); variation of MVs: 12.1–12.7 × 6.9–7.7 μm; $Q = 1.45–1.92$ (MV = 1.69), subamygdaloid-ellipsoid, strongly and densely verrucose, sometimes with an apical 'lense' of confluent warts; suprahilar plague hardly visible.

Pileipellis: duplex. Epicutis thin. At surface 3–4 μm wide, loosely erect-entangled, gelatinous hyphae, hyaline or with pale, refractive pigment when collapsed, some terminal hyphae clavate (up to 6 μm wide). Subcutis/hypodermium distinct, hyphae 5–20 μm wide, tightly cemented, with pale yellow brown parietal-encrusting pigment, forming an amber-like embedment, some dark brown oleifers intermixed; in transition to epicutis with subparallel, interconnected bundles of two to four hyphae, rather narrow (5–8 µm wide), pale, hyaline, or a few pale zebra-striped encrusted pigment.

Veil at pileus surface: thin, of narrow, hyaline hyphae or collapsed with some golden yellow necropigment.

Habitat: Montane forest with *Fagus sylvatica* and some *Picea abies* (ca. 1300 m asl.).

Distribution: Known only from the type locality in Val d'Ega, S Tyrol, N Italy.

Comments: *Cortinarius pallidoriederi* is characterised by the rather pale ochraceous yellow pileus with an olivaceous green tinge, marbled-micaceous, and innately fibrillose surface, deeply violaceous colours of lamellae and stipe (apex), glossy stipe with slightly marginate bulb, large spores and with only few, pale encrusted hyphae in pileipellis. Phylogenetically, it is close to *C. riederi* s. str. (distinguished by 3% dissimilarity, i.e. 16 substitutions and indel differences) but differs in its paler olive-tinged pileus with less encrusted hyphae and a slightly marginate bulb. The spores are also slightly smaller and narrower than typical *C. riederi* spores. The species might also be mixed with the pale *C. anomaloochrascens*, but the latter has smaller spores with MVs always < 12.0 µm. With its pale, somewhat micaceous, olive ochre pileus, the species may look also like *C. herpeticus* (but this is never deep violet and has much smaller spores).

The species is known only from the type locality, but yet its specific rank seems well-documented, since it is (i) quite dissimilar from closest relatives phylogenetically (two specimens of the type collection were sequenced in the ITS region, both were identical and differing in 16 changes from *C. riederi*), and in addition, (ii) possesses differential macroscopical characters (pale olivaceous ochre pileus) and microscopically (little encrusted pileipellis hyphae). Thus, it is described here as a new species. *Cortinarius pallidoriederi* was found in a mixed *Fagus-Picea* forest, apparently in a forest opening or rim with some grass-herb vegetation (not in deep *Fagus* litter). It remains an open question if this is a *Fagus* or *Picea* associate (or with both), but according to habitat preferences of the related species *C. riederi* and *C. anomaloochrascens*, it seems probable that also this could be a major *Picea* associate.

Collections examined: **Italy**. S Tyrol, Val d'Ega (Eggental), Novale (Rauth), Wald Lagarn, between Underkor and Oberkor, leg. E. Castellini, F. Bellù, 30 Sept 2011, Bellu 30-09-2011 (BOZ, holotype; O, isotype).

Cortinarius fulvoochrascens Rob. Henry, Bull. trimest. Soc. myc. Fr. 59: 55 (1943).

MycoBank: MB 539413, Fig. 8c, d

Holotype: France, Doubs, R. Henry 314 (PC). GenBank: MH846266.

Synonyms: *Cortinarius notabilis* Rob. Henry, Bull. trimest. Soc. mycol. Fr. 73(1): 53 (1957). MycoBank: MB 295899. Holotype: France, Doubs, R. Henry 3258-a-16 (PC).

Cortinarius marginatoochrascens Rob. Henry, Doc. Mycol. 19(73): 67 (1988). MycoBank: MB 134954. Holotype: France, Doubs, R. Henry 643 (PC0085905).

Cortinarius fallaceicolor Rob. Henry, Doc. Mycol. MycoBank: MB 111326. Holotype: France, Doubs, under *Picea abies*, R. Henry 80.800 (PC).

Cortinarius fulvoochrascens var. *cyanophyllus* Rob. Henry, Doc. Mycol. 19(73): 67 (1988). MycoBank: MB 134961. Type: France, Doubs, R. Henry 3258-a-29 (PC, as héterotype).

Cortinarius fulvoochrascens var. *subcaninicolor* Rob. Henry, Bull. trimest. Soc. mycol. Fr. 105(2): 115 (1989). MycoBank: MB 581142. Holotype: France, Doubs, under *Picea abies*, R. Henry 82.77 (PC).

?Cortinarius fuscomaculatus Jul. Schäff., Ber. Bayer. Bot. Ges. 27: 211 (1947). MycoBank: MB 329045.

Phlegmacium fuscomaculatum var. *umbrinum* M.M. Moser, Die Gatt. Phlegm.: 355 (1961). MycoBank: MB 353720. Holotype: Austria, Tyrol, Gschnitztal, under *Picea abies*, *Larix decidua*, M. Moser, MM 49/137 (M).—*Cortinarius fulvoochrascens* var. *umbrinus* (M.M. Moser) Quadr., Doc. Mycol. 14(56): 29 (1984). MycoBank: MB 116631.—*Cortinarius fuscomaculatus* f. *umbrinus* Nespiak, Flora Polska, Grzyby (Mycota), 7, Basidiomycetes, Agaricales, Cortinariaceae, Cortinarius 1: 147 (1975). MycoBank: MB 352736.

Pileus: 5–10(12) cm, (hemi-)spherical, then plano-convex, viscid-glutinous, towards margin more or less distinctly innately fibrillose-rivulose, somewhat micaceous, but not glossy, often slightly fibrillose and towards centre faintly tomentose due to diffuse veil remnants, when young in dry weather sometimes distinctly fibrillose-tomentose(-squamulose) like a *C. balteatus*; usually rather homogeneous ochraceous brown, fulvous brown to more umber brown, when very young sometimes with a faint greenish ochre brown tinge towards margin; young margin often white fibrillose due to abundant veil remnants, sometimes also whitish from veil remnants at centre.

Lamellae: crowded ($L = 80–110$), 0.5–1 cm broad, initially deep violet to greyish violet, but soon fading to paler bluish grey and then greyish brown; edge even to crenulate.

Stipe: 5–10 × 1–2.5 cm, with a more or less distinct marginate bulbous base (up to 5 cm), sometimes very robust and *Boletus* like; initially deep (greyish) violet in upper part and with a pale bluish tinge downwards, soon fading to greyish white-pale ochraceous brown, often turning somewhat brass brown, sometimes with diffuse patches of watery bluish white tomentum towards base. Universal veil near the bulb margin when young distinct, often forming a slight bluish white, then ochraceous yellow, partly gelatinous girdle.

Context initially deep violet to greyish violet in (upper part) of stipe, bluish white in pileus and bulb, violet colour soon fading, becoming whitish with brass brown spots where damaged.

Macrochemical reactions: negative.

Smell: faint, indistinct.

Exsiccata: pale brownish with vivid brown-redbrown pileus.

Basidiospores: [7, 11, 206], 11.1–13.8 × 7.2–8.6 μm (MV = 12.5 × 7.9 μm); variation of MVs: 12.1–12.7 × 7.6–8.2 μm; Q = 1.43–1.75 (MV = 1.59), ellipsoid-amygdaloid, rather strongly and densely verrucose, suprahilar plague hardly visible. *Lamella edge* more or less fertile, sterile cells small, clavate or cylindrical.

Pileipellis: duplex. Epicutis thin. At surface 3–5 μm wide, loosely erect-entangled, gelatinous hyphae, hyaline or with pale, refractive pigment when collapsed, terminal hyphae sometimes clavate. Subcutis/hypodermium, hyphae 5–20 μm wide, tightly cemented, with brown parietal-encrusting pigment, often forming an amber-like embedment; in transition to epicutis with narrow (5–8 μm wide), long hyphae with strong, brown, parietal to zebra-striped encrusted pigment, tightly cemented to and sometimes intermixed in hypodermium, or forming more loose, subparallel, interconnected bundles.

Veil at pileus surface: on young specimen often prominent, at least two to three layers, hyphae rather thick (4–8(12) μm wide), some interconnected (H-shaped connections), some terminal elements slightly inflated; many with yellow parietal pigment, some with zebra-striped encrustrations, some filled with brown, oleiferous necropigment.

Veil at stipe surface: (ochre parts) with many pale golden yellow, refractive, collapsed, gelatinous hyphae (a few dark brown oleifers), wider hyphae (5–7(10) μm) faintly zebra-striped-verrucose encrusted.

Habitat: Associated mainly with *Picea abies*, but probably also with *Pinus sylvestris*. In rich low-herb spruce-pine forests, according to Moser (1961) also on rather acid ground. In S Scandinavia, mainly in calcareous spruce forests.

Distribution: Mainly distributed in C Europe, especially in the Alp/Prealp region. Rare in Fennoscandia, but exact distribution unknown due to confusion with the similar *C. riederi*. Just a few collections known so far from SE and C Norway and S/C Sweden. Widespread, but apparently rare in montane-subalpine districts of C (-S) Europe. Reported from subalpine sites in Tyrol, Austria (Moser 1961 as *Phlegmacium fuscomaculatum* incl. var. *umbrinum*), and from montane areas of the Jura region of France (Henry 1943, 1966, 1988; Bidaud et al. 1999), various parts of Germany (Schäffer 1947; Moser 1961; Krieglsteiner 1991) and from Spain (Ballarà 1999). The species is also collected in N Italy and Romania (Transylvania) (see collection list). So far not confirmed from N America.

Comments: *Cortinarius fulvoochrascens* is characterised by uniformly fulvous(-umber) brown, somewhat fibrillose pileus when young, more or less marginate bulbous stipe with initially distinct veil remnants and large, ellipsoid-subamygdaloid spores. The often-robust stature with veil remnants at bulb and pileus margin is well illustrated by Bidaud et al. (1999, Pl. 217 as *C. fulvoochrascens* var. *marginato-ochrascens*). This has frequently been treated as part of the collective species *C. riederi* s. lato (see comments under *C. riederi*). However, this is well separated phylogenetically from *C. riederi* s. str., and on closer examination, these are normally also well-distinguished morphologically. *Cortinarius riederi* differs by its smooth, glossy pileus, with more vividly yellow-orange tinges, almost lack of veil remnants, watery bluish mycelial felt and a hardly marginated stipe bulb. On average, the spores are slightly smaller and more strongly verrucose on *C. fulvoochrascens*, but the overlap in spore features is considerable (see comment on *C. riederi*).

Ecologically, *C. fulvoochrascens* is characterised by occurrence mainly in C European, richer to calcareous spruce-pine forests, whereas *C. riederi* s. str. is mainly N European, in C Europe more subalpine, and it mainly occurs in oligotrophic/acid spruce forests. *Cortinarius fulvoochrascens* also resembles *C. anomaloochrascens*. The former is, however, normally distinguished by its darker, more fibrillose pileus colours, and larger, more robust basidiocarps with pronounced veil remnants, distinctly larger spores, and stronger encrusting pigment of pileipellis. The species is further distinguished from *C. argenteolilacinus* and *C. malachioides* by darker coloured pileus, more distinct veil remnants as well as habitat in coniferous forests. *Cortinarius fuscomaculatus* (Schäffer 1947) is very likely synonymous with our species, but no original material of Schäffer exists. However, the type of *Phlegmacium fuscomaculatum* var. *umbrinum* described by Moser (1961) was sequenced and turned out to be conspecific with *C. fulvoochrascens*. The species is treated under six different names by R. Henry (see synonymy list), according to our sequence study of R. Henry types. Among the Henryian names cited as synonyms is *C. fulvoochrascens* var. *cyanophyllus*, which has not infrequently been regarded as a variety or a species in literature (see, e.g. Ballarà 1999). Moser et al. (1995) reported *C. fulvoochrascens* from W North America based on many collections, but the spore sizes indicated, fits better to *C. riederi* than to *C. fulvoochrascens*. Future sequencing of these collections might give more information on their identity. However, only one N American collection of *C. fulvoochrascens* identified by M. Moser was sequenced (GenBank: AF389139), but it belongs to *C. burlinghamiae*.

Collections examined: **Austria**. Tyrol, Gschnitztal, MM 49/172 (M, holotype of *Phlegmacium fuscomaculatum* var. *umbrinum*). **France**. Doubs, R. Henry 314 (PC, holotype); R. Henry 71.732 (PC, hétérotype of *C. fulvoochrascens*); R. Henry 3258-a-16 (PC, holotype of *C. notabilis*); R. Henry 643 (PC, holotype of *C. marginatoochrascens*); R. Henry 80.800

(PC, holotype of *C. fallaceicolor*); R. Henry 3258-a-29 (PC, héterotype of *C. fulvoochrascens* var. *cyanophyllus*); R. Henry 82/77 (PC, holotype of *C. fulvoochrascens* var. *subcaninicolor*). **Germany**. Baden-Württemberg, Schwaben, Ehingen a.d. Donau, T.E. Brandrud, TEB437-10 (O). **Italy**. Trentino-Alto-Adige, Alto-Badia, La Valle Badia, 7 Sept 2008, *C. Rossi*, Rossi 31 (herb. Rossi); Naz-Sciaves, Springa, 14 Oct 2000, G. Turrini, TG2000-198 (herb. Turrini). **Norway**. Oppland, Jevnaker, Rustad, T.E. Brandrud, TEB667-80 (O); Lunner, S. Oppdalen, T.E. Brandrud, TEB172-04 (O); Gran, Lygna N, 11 Sept 2013, T.E. Brandrud & B. Dima, TEB530-13/DB5210 (O/BP); Vestre Toten, Eriksrudtjern, T.E. Brandrud & B. Dima, TEB725-17/DB6542 (O). Buskerud, Hole, Nes, T.E. Brandrud, TEB748-11 (O). Nord-Trøndelag, Levanger, Ytterøya, TEB292-13 (O). Oslo, Oslo, Østmarksetra, 13 Sept 2014, T. Berg-Hansen, F-75726 (O). **Romania**. Partium, Bihar, Pádis, 10 Oct 2010, Z. Erdei, DB4408 (BP). **Spain**. Catalunya, J. Ballarà, JB 6858-09. **Sweden**. Västergötland, Kinnekulle, Hällekis, Gössäter, T.S. Jeppesen, TSJ2004-052 (C).

Additional ITS sequence data from the public sequence repositories: **Germany**. KJ421204/TUB020433 (as *C. riederi*), KJ420976/TUB019735 (as *C. riederi*).

Cortinarius anomaloochrascens Chevassut & Rob. Henry, Doc. Mycol. 16(63–64): 84 (1986).

MycoBank: MB 129655, Fig. 8e–g

Holotype: France, Doubs, R. Henry 2805 (PC). GenBank: MH846269.

Synonyms: *Cortinarius imbricatoides* Rob. Henry, Bull. trimest. Soc. mycol. Fr. 105(1): 92 (1989). MycoBank: MB 136657. Holotype: France, Doubs, R. Henry 395 (PC).

Cortinarius stilazureus Rob. Henry, Bull. trimest. Soc. mycol. Fr. 105(2): 125 (1989). MycoBank: MB 136688. Holotype: France, Doubs, Frasne, R. Henry 85.13 (PC).

Selected icones: Soop (2017, Pl. 5: 19).

Pileus: 4–8 cm, (hemi-)spherical(-campanulate), then plano-convex (to broadly umbonate), viscid-glutinous and glossy when dry, towards margin distinctly innately fibrillose-rivulose, centre with a marbled structure from darker, innate fibres, sometimes with hygrophaneous veins or spots towards margin; pale ochraceous brown to greybrown, sometimes with an olivaceous tinge when young, the involute margin whitish. Universal veil remnants very sparse, hardly visible.

Lamellae: crowded (L = 70–100), 0.4–0.8 cm broad, initially deep violet to greyish violet, but soon fading to paler bluish grey and then greyish brown; edge even to crenulate.

Stipe: 5–10 × 0.8–1.5 cm, with a clavate-bulbous to slightly marginate bulbous base (up to 3.5 cm), glossy, initially deep (greyish) violet in upper part and with a pale bluish tinge downwards, soon fading to greyish white-pale ochraceous brown, often developing glossy brass brown patches, sometimes with patches with watery bluish white tomentum towards base. Universal veil near the bulb margin very sparse.

Context: initially deep violet to greyish violet in (upper part) of stipe, bluish white in pileus and bulb, violet colour soon fading, becoming whitish with brass brown spots where damaged.

Macrochemical reactions: negative, KOH somewhat brownish in context.

Smell: none or faint, sometimes yeast-like with age.

Exsiccata: pale brownish.

Basidiospores: [7, 11, 168], 10.2–12.8 × 6.3–8.1 μm (MV = 11.5 × 7.2 μm); variation of MVs: 10.9–11.9 × 6.9–7.6 μm; *Q* = 1.43–1.78 (MV = 1.60), ellipsoid to subamygdaloid, distinctly and densely verrucose, suprahilar plague hardly visible.

Pileipellis: duplex. Epicutis thin. At surface of 3–5 μm wide, loosely erect-entangled, gelatinous hyphae, hyaline, or with pale pigment, some pale verrucose to zebra-striped. Subcutis/hypodermium hyphae 5–20 μm wide, tightly cemented, with brown parietal-encrusting pigment, often forming an amber-like embedment; in transition to epicutis with subparallel, interconnected bundles, with some, encrusted pigment.

Habitat: Associated with *Picea abies*, also in *Picea* plantations outside the natural distribution of Norway spruce; in a few cases also seen in pure *Pinus sylvestris* forests in W Norway, possibly also associated with *Abies alba* in mixed stands. Preferentially in oligotrophic-mesotrophic spruce forests, rarely on calcareous ground (Krieglsteiner and Gminder 2010; Jeppesen et al. 2012).

Distribution: Widely distributed in boreal-montane districts in Europe, but apparently everywhere rather rare. Reported from C and S Fennoscandia (Soop 2011 as *C. fulvoochrascens* p.p.; Jeppesen et al. 2012), from The Black Forest region of Germany (Krieglsteiner and Gminder 2010) and from the Jura region of France (Henry 1989a, b; Bidaud et al. 1999). In The Black Forest, the species occurs in the montane zone (450)600–1000 m asl., and in the lower montane mixed *Picea*-*Abies* forests, it seems to be more frequent than *C. riederi* (Krieglsteiner and Gminder 2010, pers. obs.). The species is further collected by us in N Italy and the Czech Republic (see list of collections examined). Moser (1961) may have included *C. anomaloochrascens* in his wide concept of *Phlegmacium fuscomaculatum* which is reported not to be rare in the Alp-Prealp region.

Comments: *Cortinarius anomaloochrascens*, although widespread, is very little known and described, apparently mainly included in a broad concept of *C. riederi*. The species seems well illustrated in Bidaud et al. (1999; Pl. 213) and Soop (2017), although these specimens are not verified by sequencing. *Cortinarius anomaloochrascens* is characterised by its rather small and slender basidiocarps, pale ochraceous greybrown pileus, and smaller spores compared with *C. riederi* and *C. fulvoochrascens*. The spores are usually also somewhat more amygdaloid than those of *C. riederi* and *C. fulvoochrascens*. The contrast between the initially bright violaceous stipe and the pale greyish ochre pileus margin is often striking. The stipe furthermore normally has a more marginate bulb than that of *C. riederi*. Misidentifications under the name *C. riederi* or *C. fulvoochrascens* can easily be sorted out by the smaller spores of *C. anomaloochrascens*, which show no overlap with the spores of *C. riederi*/*C. fulvoochrascens*, when mean values for measurement series are compared (spore MVs for *C. anomaloochrascens* always < 12 μm long). *Cortinarius glaucocyanopus* and *C. malachioides* also have comparatively small spores, but these are associated with deciduous trees, mainly *Fagus* and *Betula*, respectively. These also have a paler coloured pileus, and *C. malachioides* usually lacks deep violet tinges on young lamellae and stipe.

Collections examined: **Czech Republic**. C Bohemia, Prague region, Borovsko, Hadce u Želivky Nature Reserve, mixed forest with *Picea*, *Pinus*, *Betula* on serpentinite soil, J. Borovicka 140519-29 (PRM 924382). **Denmark**. Northern Jutland, Faurholt hede, A. Eriksen, AE2009-65377 (C77672). **Finland**. Kainuu, Paltamo, I. Kytövuori, IK92-2028 (H). **France**. Doubs, R. Henry 2805 (PC, holotype), R. Henry 2807 (PC, isotype); R. Henry 395 (PC, holotype for *C. imbricatoides*); R. Henry 85.13 (PC, holotype for *C. stilazureus*). Doubs, Levier, T.G. Frøslev, T.S. Jeppesen, TSJ2006-095 (C). Auvergne-Rhone-Alpes, Oyonnax, I. Kytövuori, IK94-1743 (H). **Germany**. Baden-Württemberg, Rottweil, Dunninger Wald, T.E. Brandrud, B. Dima, G. Saar, TEB762-12/DB4814 (O). Bayern, Sachsenkamm, Kirchsee Nord, 7 Oct 2013, M. Dondl, MD28/2013; Bayern, Mittenwald, Kranzbergregion, 21 Sept 2013, M. Dondl, MD 27/2013. **Italy**. Trentino-Alto-Adige, St. Valentin Atzwang, 30 July 2012, F. Bellù, Cester, Bellu 30-07-2012 (BOZ); Riscone, 14 Aug 2012, *C. Rossi*, Rossi 14-08-2012 (herb. Rossi); Redensberg, Nähe Olang, 13 Aug 2012, F. Bellù & Fuman, Bellu 13-08-2012 (BOZ). S Tyrol, Jenesien, Remphof, 4 Sept 2017, T. Errico, Bellu 04-09-2017 (O); Bolzano, Villnösstal, Malga Zannes, Val di Funes, *C. Rossi*, Rossi 31-08-2017 (O); Mölten, Kirchebene, pr. Mettina, *C. Rossi*, Rossi 07-09-2017 (O). **Norway**. Oppland, Lunner, S. Oppdalen, E. Bendiksen, TEB316-10 (O). Østfold, Halden, Idd, T.E. Brandrud, TEB252-07 (O). Hordaland, Ulvik, Åsen peninsula, T.E. Brandrud, TEB175-07 (O). Nord-Trøndelag, Nærøy, Saglivatn, E. Bendiksen & T.E. Brandrud, EB-TEB 6-05 (O). Oslo, Oslo, Enebakkveien 866, 12 Sept 2014, T. Blakar, F-75650 (O). **Sweden**. Ångermanland, Säbrå, H. Marklund, CFP 1539 (S).

Additional ITS sequence data from the public sequence repositories: **Germany**. KJ420997/TUB019758 (as *C. riederi*); KJ421008/TUB019769 (as *C. riederi*); KJ421012/TUB019770 (as *C. riederi*). **Italy**. JF907910/MCVE16165 (as *C. riederi*).

Cortinarius glaucocyanopus Rob. Henry, in Bidaud et al., Atlas des Cortinaires IX: 371 (1999).

MycoBank: MB 461065, Fig. 9h, i

Holotype: France, Ardennes, Bois de Toges, 6 Oct 1995, P. Reumaux, GK5034 (G). GenBank: MH846274.

Synonym: *Cortinarius glaucocyanopus* Rob. Henry, Bull. trimest. Soc. myc. Fr: 73: 32 (1957), nom. inval.

Pileus: 2.5–7 cm, (hemi-)spherical, then plano-convex, viscid-glutinous, innately fibrillose-rivulose; pale ochraceous (grey)brown to cream yellow, with an olivaceous tinge (resembling the colour of *C. anserinus*), sometimes with lilac tinged spots; the involute margin whitish. Universal veil remnants very sparse, hardly visible.

Lamellae: crowded, initially deep violet to pale greyish violet or bluish lilac, soon fading to greyish brown; edge even.

Stipe: 5–8 × 0.7–1.5 cm, with a slightly marginate bulbous base (up to 3 cm), glossy, initially pale (greyish) violet-bluish lilac, developing brass brown patches. Universal veil near the bulb margin very sparse.

Context: initially pale bluish violet in (upper part) of stipe, white in bulb, bluish white in pileus, violet colour soon fading, becoming whitish with brass brown spots where damaged. *Macrochemical reactions*: negative.

Smell: indistinct.

Exsiccata: pale brownish.

Basidiospores: [2, 2, 68], 10.3–13.1 × 6.6–7.8 μm (MV = 11.7 × 7.2 μm), variation of MVs: 11.2–12.0 × 7.2–7.3 μm; *Q* = 1.41–1.85 (MV = 1.63), ellipsoid to subamygdaloid, distinctly and densely verrucose, suprahilar plague hardly visible.

Pileipellis: duplex. Epicutis thin. At surface of 3–5 μm wide, loosely erect-entangled gelatinous hyphae, hyaline or with pale pigment. Subcutis/hypodermium hyphae 5–20 μm wide, tightly cemented, with brown parietal-encrusting pigment, often forming an amber-like embedment; in transition to epicutis with subparallel, interconnected bundles, some hyphae with weakly encrusted pigment.

Habitat: Apparently associated with *Fagus*, possibly also other deciduous trees; collected in *Fagus* dominated forest with small *Picea* trees and *Betula* in Hungary and reported from *Fagus* forests in the Ardennes and French Jura (Bidaud et al. 1999).

Distribution: So far, known only from temperate/nemoral regions of French Ardennes-Jura and western Hungary. Apparently a very rare species.

Comments: The description of macromorphology is based on the protologue and on own materials from Hungary. *Cortinarius glaucocyanopus* is a very rare species, so far known only from one site (two collections) in western Hungary, and from the type

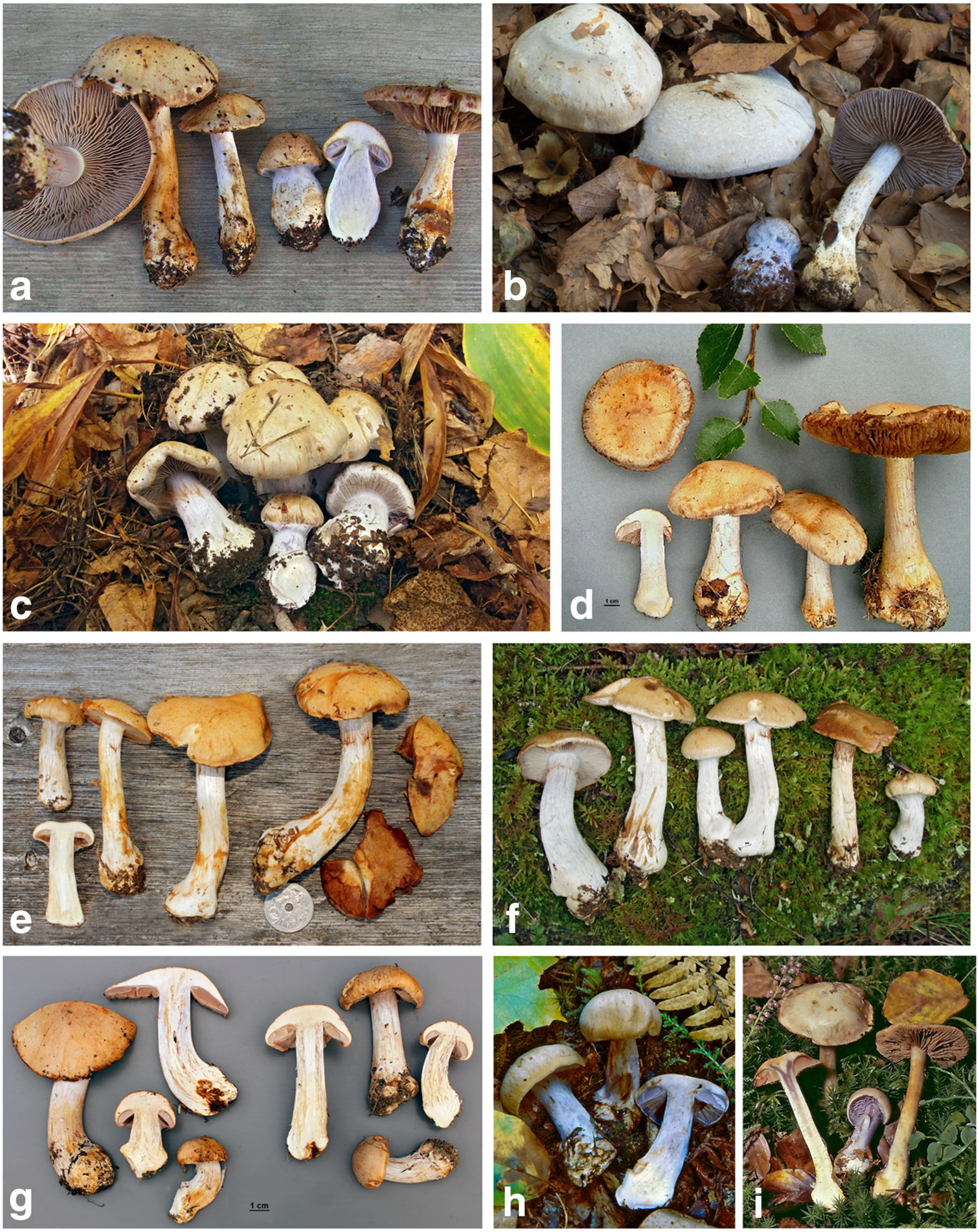


Fig. 9 Basidiocarps of species in sect. *Riederi* associated with deciduous trees: **a**–**c** *C. argenteolilacinus* var. *argenteolilacinus* (**a** ILF2013-98 Norway, **b** TSJ2011-025 Sweden, **c** TEB281-17 Norway); **d** *C. argenteolilacinus* var. *dovrensis* (KS-CO1703 Sweden); **e**–**g** *C. malachioides* (**e**–**f** TEB245-13 Norway, **g** TEB340-16/DB6138 Sweden); **h**–**i** *C. glaucocyanopus* (**h** DB2072 Hungary, **i** AL99/51 Hungary). Photos: **a** I.-L. Fonneland; **b** T.S. Jeppesen; **c**, **e**, **f** T.E. Brandrud; **d** K. Soop; **g**, **h** B. Dima, **i** L. Albert

collection from the French Ardennes, possibly also from one (not sequenced) collection from French Jura (see Bidaud et al. 1999).

The species is genetically well-distinguished, separated from its sister species *C. anomaloochrascens* by 10 substitution and indel positions in the ITS regions. They also have different habitats; *C. glaucocyanopus* growing in *Fagus* forests, *C. anomaloochrascens* in *Picea* forests. Morphologically, the former seems to differ by a paler, more olive-ochre pileus, according to the protologue resembling the colour of *C. anserinus* (=*C. amoenolens*) (Henry in Bidaud et al. 1999). However, more material is needed to confirm the morphological-ecological characteristics of this species. *Cortinarius glaucocyanopus* was introduced by Henry (1957), but this description is invalid since lacking a Latin diagnosis. Moreover, the short description seems to cover one of the large-spored *Riederi* taxa rather than the relatively small-spored *C. anomaloochrascens*/*C. glaucocyanopus* ('spores … de 15/8.8 μ.'). In fact, the scetched specimen and the description of the pileus ('ochracée … mate, devenant café au lait avec des plages d'un glauque bleuâtre sur le disque plus ou moins pseudo-squamuleuse à la fin'.) seems to cover *C. argenteolilacinus* better than our species. However, the species was validated and re-described by Henry in Bidaud et al. (1999). The description is based on two collections; the type from the Ardennes, and another collection from the Jura (Brandrud 1998). The type has been sequenced, and the type and our Hungarian collections have identical sequences. The description (protologue) and depicted specimens in Bidaud et al. (1999) correspond rather well with our find from Hungary, but again the spores are given (very) large; (11)12–15(17) × 7.5–8.5(9) μm, of the same size as those of *C. fulvoochrascens*, and considerably larger than our measurements.

Collections examined: **France**. Ardennes, Bois de Toges, 06 Oct 1995, P. Reumaux, GK5034 (G, holotype). **Hungary**. Vas, Farkasfa (lake Fekete-tó), 3 Oct 1999, L. Albert, AL 99/51 (BP), 1 Oct 2005, B. Dima, DB2072 (BP, O).

Cortinarius argenteolilacinus* var. *argenteolilacinus M.M. Moser, Sydowia 6(1–4): 151 (1952).

MycoBank: MB 295797, Fig. 9a–c

Holotype: Austria, Holltal, 16 Oct 1948, M. Moser, MM 48/752 (M). GenBank: MH846277.

Synonym: *Phlegmacium argenteolilacinum* (M.M. Moser) M.M. Moser, Die Gatt. Phlegm. 241 (1961). MycoBank: MB 302878.

Selected icones: Moser (1961, Pl. XVII 96), Læssøe (2011), Svampe 64: 57, Soop (2011, Pl. 11, Fig. 43).

Pileus: 4–10 cm, (hemi-)spherical, then plano-convex (to broadly umbonate), viscid-glutinous, towards margin weakly, often finely (sometimes distinctly) innately fibrillose-rivulose, somewhat silvery-micaceous, but hardly glossy-polished (like *C. riederi*), often faintly fibrillose-tomentose; pale grey, greyish ochre to greyish white, often slightly more ochraceous brown at centre, initially often with a bluish tinge towards margin, the involute margin (bluish) whitish. Universal veil remnants sparse, sometimes with whitish veil fibres towards margin when young.

Lamellae: crowded ($L = 80–110$), 0.5–1 cm broad, initially deep violet to greyish violet, but (very) soon fading to paler bluish grey and then greyish brown, edge often paler crenulate-serrulate.

Stipe: 6–10(11) × 1–2.5 cm, often robust, with a bulbous to often slightly marginate-bulbous base (up to 4.5 cm), glossy to slightly fibrillose, initially greyish violet to deep violet in upper part, (bluish) white downwards (sometimes distinctly violet down to bulb), bluish tinges fades soon, but more slowly than that of the lamellae, and in some stages violet blue stipe apex contrasts the already greyish brown lamellae; sometimes turning (spot wise) brass-brown with age. Universal veil sparse to rather abundant, and then forming a girdle at or just above the bulb margin; white to sometimes bluish when very young.

Context initially deep violet to greyish violet in upper part of stipe (especially towards cortex), bluish white in pileus and bulb, violet colour soon fading, becoming whitish with brass brown spots where damaged.

Macrochemical reactions: negative, sometimes yellow-brownish with KOH in bulb context.

Smell: faint, indistinct.

Exsiccata: brownish to almost whitish.

Basidiospores: [8, 16, 319], 10.7–13.7 × 6.7–8.3 μm (MV = 12.2 × 7.5 μm), variation of MVs: 11.6–12.9 × 7.1–7.9 μm; $Q = 1.42–1.84$ (MV = 1.63), ellipsoid to subamygdaloid, rather strongly to very strongly and rather densely verrucose, perisporium sometimes visible, ornaments often lense-like coalescent at apex, sometimes prominent, giving the spore a slightly citriform outline, often also with prominent, tooth-like warts subapically; suprahilar plague rarely visible.

Lamellar edge: more or less fertile, sterile cells small, clavate or cylindrical.

Pileipellis: duplex. Epicutis thin. At surface 3–5 μm wide, loosely erect-entangled, gelatinous hyphae, hyaline or with pale, refractive pigment (especially when collapsed). Subcutis/hypodermium weakly developed, hyphae 5–15 μm wide, tightly cemented, with pale yellow brown parietal-encrusting pigment, often forming an amber-like embedment; in transition to epicutis with subparallel, interconnected bundles of long and rather narrow hyphae (5–10 μm wide), with distinct to strong zebra-striped/crustulose brown encrusting pigment, encrustration especially prominent on some slightly wider hyphae (8–10 μm wide). *Veil hyphae at pileus surface*: scattered, mainly narrow (3–6 μm), hyaline; some hyphae interconnected.

Habitat: Associated mainly with *Fagus sylvatica*, in boreonemoral region also sometimes found under *Tilia cordata* and *Corylus avellana*, in richer to somewhat calcareous forests.

Distribution: Distributed mainly in nemoral-(sub)montane areas of C Europe and S Scandinavia, more rare in boreonemoral areas of S Scandinavia. Apparently rare everywhere, very rare in S Europe. Little known, recorded only from SE Norway, S Sweden and Denmark (cf. Læssøe 2011, pers. obs.), Tyrol, Austria (Moser 1961), Germany (Krieglsteiner 1991, pers. obs.) and the French Jura (see collections examined). According to Mahiques (1999), it is found also in NE Spain (Catalonia).

Comments: *Cortinarius argenteolilacinus* s. lato is characterised by its pale greyish, almost fibrillose pileus with bluish tinges when (very) young, and the initially deep violet lamellae and stipe. The basidiocarps are often robust. The spores often possess an apical, irregular, lense-like structure due to coalescent warts. *Cortinarius argenteolilacinus* var. *argenteolilacinus* and var. *dovrensis* deviate genetically by only two to three nucleotide and indel differences in the ITS region.

Cortinarius argenteolilacinus var. *dovrensis* is a N European subalpine *Betula* forest taxon, whereas var. *argenteolilacinus* is a C European–S Scandinavian (boreo-)nemoral *Fagus-Tilia-Corylus* forest species. *Cortinarius argenteolilacinus* var. *argenteolilacinus* has so far never been found in subalpine birch forests, and the distribution of the two varieties shows almost no overlap in Scandinavia. The latter differs morphologically by the more strongly ornamented spores, and the strongly zebra-striped encrusted 8–10-μm-wide subsurface pileipellis hyphae. With this combination of (i) a small, constant genetic differentiation, (ii) a considerable ecogeographical differentiation and (iii) a subtle micromorphological differentiation, we have decided to treat these as two infraspecific taxa (varieties). Due to geographical differences, these taxa might also be treated as subspecies, but we think it is wise to stick to only one infraspecific rank (subspecies is nowadays very little applied in agaric taxonomy).

Cortinarius argenteolilacinus var. *argenteolilacinus* also resembles *C. malachioides* but is distinguished by the larger spores and more zebra-striped encrusted pileipellis subsurface hyphae. It usually also has a larger, more fibrillose and more (bluish) grey pileus, and initially deeper violet colours of lamellae and stipe. It is further distinguished from *C. riederi* and *C. anomaloochrascens* by the less smooth, less innately fibrillose and a paler (and bluish tinged) pileus. The present species has traditionally been classified with the *C. variecolor*-*C. largus* group, and not with *C. riederi*, but the micromorphology as well as genetic data show a close relationship to the latter. *Cortinarius argenteolilacinus* might look like a *C. caesiocanescens*, *C. coerulescentium* or a *C. largus,* but has larger, more ellipsoid spores. Furthermore, the bulb is more marginated on *C. caesiocanescens* and *C. coerulescentium*, and the former has more abundant (volva-like) veil remnants, and the latter has a more distinctly bluish, strongly innately fibrillose pileus when young. *Cortinarius largus* is distinguished by the yellow KOH reaction (context), and never marginate bulbous stipe. *Cortinarius argenteolilacinus* var. *argenteolilacinus* is so far known from a few nemoral lowland (S Sweden, Denmark), submontane (French Jura, S Germany) to upper montane (Austria and NE Hungary) *Fagus* sites. Furthermore, it is found in a few boreonemoral *Tilia*(-*Quercus*) forests in SE Norway, and under *Corylus* at Öland, SE Sweden. The taxon is probably distributed further East in Europe (e.g. in the Carpathians).

Collections examined: **Austria**. Holltal, M. Moser, MM 48/752 (M, holotype). **Denmark**. Sjælland, Vejlø skov, T.S. Jeppesen, TSJ2010-004 (C), TSJ2012-044 (C). **France**. Jura, Prénovel, 10 Oct 2008, B. Dima, DB3312 (BP). **Germany**. Baden-Württemberg, Schwaben, Ehingen a.d. Donau, T.E. Brandrud, G. Schmidt-Stohn et al., TEB 418-10/SSt10-174 (O). Bayern, Tegernsee, Riederstein, M. Dondl, MD18/2013. **Hungary**. Heves, Mátra Mts, L. Nagy, NL-5262 (herb. L. Nagy). **Norway**. Telemark, Drangedal, Sannes-Langen, T.E. Brandrud, TEB52-01 (O). Aust-Agder, Risør, Dalsvann SW, Grønnfjell, I.L. Fonneland, ILF2013-98 (O); Vestfold, Larvik, Kjose, T.E. Brandrud, TEB370-08 (O); T.E. Brandrud, TEB381-08 (O). Buskerud, Hole, Bråtåfjellet SV, T.E. Brandrud & B. Dima, TEB281-17/DB6361 (O). **Sweden**. Bohuslän, Tanum, T.E. Brandrud et al., CFP1608 (S). Öland, Borg, I. Kytövuori, IK98-2617 (H). Skåne, Ivön, C. Ingvert, T.G. Frøslev, T.S. Jeppesen TSJ2011-025 (C).

Cortinarius argenteolilacinus* var. *dovrensis Brandrud, var. nov.

MycoBank MB 827876, Fig. 9d

Etymology: the epithet refers to the Dovre Mountains of S Norway, from where the type was collected.

Holotype: Norway, Sør-Trøndelag, Oppdal, Kongsvoll, Dovre Mountains, 10 Aug 1980, T.E. Brandrud, TEB112-80 (O). GenBank: MH923071.

Selected icones: Soop 2017, Pl. 5:20 as *C.* '*dovrensis*'.

Pileus: 4–10 cm, (hemi-)spherical, then plano-convex (to broadly umbonate), viscid-glutinous, towards margin weakly, finely (sometimes distinctly)innately fibrillose-rivulose, somewhat silvery-micaceous, often faintly fibrillose-tomentose; pale grey, greyish ochre to greyish white, often slightly more ochraceous brown at centre, sometimes almost whitish, initially often with a bluish tinge towards margin, the involute margin (bluish) whitish. Universal veil remnants very sparse, sometimes with whitish veil fibres towards margin when young.

Lamellae: crowded ($L = 80$–110), 0.5–1 cm broad, initially deep violet to greyish violet, but (very) soon fading to paler bluish grey and then greyish brown; edge even to crenulate.

Stipe: 6–10(11) × 1–2.5 cm, often robust, with a bulbous to often faintly marginate-bulbous base (up to 4.5 cm), glossy to slightly fibrillose, initially greyish violet to deep violet in upper part, whitish downwards (sometimes violet down to bulb), bluish tinges soon fading, sometimes turning (spot wise) somewhat brass-brown with age. Universal veil near the bulb sparse and hardly visible; white to sometimes bluish when very young.

Context initially deep violet to greyish violet in upper part of stipe (especially towards cortex), bluish white in pileus and bulb, violet colour soon fading, becoming whitish with brass brown spots where damaged.

Macrochemical reactions: negative, sometimes yellow-brownish with KOH in bulb context.

Smell:faint, indistinct.

Exsiccata: whitish to (pale) brownish.

Basidiospores: [9, 16, 264], 11.2–13.8 × 6.8–8.6 μm (MV = 12.5 × 7.7 μm); variation of MVs: 11.8–13.5 × 7.3–8.2 μm; *Q* = 1.45–1.79 (MV = 1.62), ellipsoid to subamygdaloid, medium to rather strongly and densely verrucose, ornaments often lense-like coalescent at apex, sometimes prominent; suprahilar plague rarely visible.

Lamellar edge: more or less fertile, sterile cells small, clavate or cylindrical.

Pileipellis: duplex. Epicutis thin, at surface of 3–5 μm wide, loosely erect-entangled, gelatinous hyphae, hyaline or with pale, refractive pigment (when collapsed). Subcutis/hypodermium weakly to distinctly developed, hyphae 5–15 μm wide, basally sometimes with inflated elements up to 20 μm wide, tightly cemented, with pale yellow brown parietal-encrusting pigment, often forming an amber-like embedment; in transition to epicutis with subparallel, interconnected bundles of 5–8 μm wide hyphae, sometimes with weak zebra-striped encrusting pigment (never distinct encrustrations like in the main variety).

Veil hyphae at pileus surface: scattered to almost lacking, mainly narrow (3–6 μm) and hyaline.

Habitat: Associated mainly with *Betula pubescens subsp. tortuosa*, also with *Betula pendula* and *Tilia cordata*, more rarely with *Corylus avellana*.

Distribution: So far, mainly known from NW Europe. Most records from subalpine/northern boreal areas of Fennoscandia (known north to Nordland in Norway, Umeå in Sweden, and N Finland (Lapland)) and also found in some boreonemoral fjord districts of W Norway. Apparently, no finds from nemoral-montane regions of C Europe. Once collected in Alberta, Canada, indicating a probably wide, circumpolar distribution.

Comments: *Cortinarius argenteolilacinus* var. *dovrensis* is characterised by its pale greyish-whitish, almost fibrillose pileus with bluish tinges when (very) young, and the initially deep violet lamellae and stipe. The taxon is phylogenetically very closely related to *C. argenteolilacinus* var. *argenteolilacinus* and differs only in two to three substitution and indel positions in the ITS region. With this more or less constant differences the sequences cluster in two rather well-supported clades in our phylogenetic analysis (Fig. 2). Since these genotypes are (i) considerably differentiated ecogeographically (var. *dovrensis* mainly a northern, subalpine *Betula* taxon, var. *argenteolilacinus* a mainly nemoral-montane *Fagus*(-*Tilia*) taxon) and (ii) slightly differentiated also morphologically (*C. argenteolilacinus* var. *dovrensis* with less ornamented spores, less encrusted pileipellis hyphae and on average paler pileus), these are treated as separate varieties (see also comments under *C. argenteolilacinus* var. *argenteolilacinus*).

Most of our collections of *C. argenteolilacinus* var. *dovrensis* were found under *Betula* (mainly subalpine *B. pubescens* subsp. *tortuosa*), whereas three collections were found under *Corylus* (-Betula?)). No collections were from *Fagus* forests, which seems to be the major habitat for *C. argenteolilacinus* var. *argenteolilacinus*. All the 16 DNA-analysed *C. argenteolilacinus* var. *dovrensis* collections have almost identical ITS sequences, but in some cases, we observed single nucleotide polymorphisms in two sites. The specimen found in Canada differs by three indels from the European sequences. More material is needed to see if there is a phylogeographical differentiation within *C. argenteolilacinus* var. *dovrensis*. For the time being, we keep this Canadian collection under var. *dovrensis* based on our phylogenetic analysis (Fig. 2).

Cortinarius argenteolilacinus var. *dovrensis* may sometimes be difficult to separate macromorphologically from the often co-occurring *C. malachioides*. However, the var. *dovrensis* is distinguished by the larger spores. It usually also has a larger and more fibrillose pileus and brighter violet colours on lamellae and stipe.

Collections examined: **Canada**. Alberta, Hinton, 3 Sept 2011, TN11-319 (H). **Finland**. Perä-Pohjanmaa, Yltornio, I. Kytövuori, IK 97-1137 (H). **Norway**. Oppland, Dovre, Kongsvoll, 10 Aug 1980, T.E. Brandrud, TEB112-80 (O, holotype); Lunner, Skøien, T.E. Brandrud, TEB682b-11 (O). Hedmark, Engerdal, Femunden, T.E. Brandrud, TEB217-08 (O). Aust-Agder, Froland, Ytre Lauvrak, T.E. Brandrud, TEB312-09 (O); Dalsvann SW, I.L. Fonneland, 2013-119 (O); Nordland, Hattfjelldal, Storveltlia nature reserve, Ø. Weholt, KB-EB-TEB 78-10 (O), Ø. Weholt, KB-EB-TEB 79-10 (O). Hordaland, Granvin, T.S. Jeppesen, TSJ2005-042 (C). **Sweden**. Härjedalen, Hamrafjället, 13 Aug 2008, K. Soop, KS-CO1703 (S-F251128); 20 Aug. 2008, K. Soop, KS-CO1821 (S). Dalarna, Sollerön, Klikten, 11 Sept 2013, K. Soop, KS-CO2130 (S). Öland, Gråborg, T.G. Frøslev, T.S. Jeppesen TSJ2006-010 (C).

Additional ITS sequence data from the public sequence repositories: **Italy**. JF907933/MCVE6043 (as *C. elotus*). **Sweden**. KJ421064/KS-CO770 (as *C. argenteolilacinus*), Öland, Gråborg, 28 Sept 1996, K. Soop, herb. S-F44342.

Cortinarius malachioides P.D. Orton, Naturalist (Suppl.): 148 (1958)

MycoBank MB 295890, Fig. 9e–g

Holotype: UK, Inverness-shire, Rothiemurchus, Loch-an-Eilean, P.D. Orton 29/9/55 (K(M)94,426). GenBank: MH846280.

Icone: Soop (2011, Pl. 6, Fig. 23, as *C. coniferarum* (M.M.Moser) Moënne-L & Reum); Soop 2017, Pl. 5:18 as *C. jotunae.*

Pileus: 3–7(8) cm, (hemi-)spherical, then plano-convex to broadly umbonate, viscid-glutinous, towards margin finely and rather weakly innately fibrillose-rivulose, with a more net-like pattern at centre, somewhat silvery-micaceous when young, smooth to sometimes faintly fibrillose; initially rather uniformly and pale ochraceous yellow to almost ochraceous white, resembling *C. talus*, sometimes pale grey to greyish ochre, with a faint, fugacious, blush tinge towards margin, with age discolouring patchwise to ochraceous brown (almost redbrown). Universal veil remnants very sparse, hardly visible, sometimes with silky, white remnants at margin.

Lamellae: crowded (*L* = 60–90), 0.4–0.8 cm broad, initially pale greyish blue, especially towards pileus margin, very soon fading to pale greyish brown; edge even to crenulate.

Stipe: 5–10 × (0.8)1–1.5(2) cm, rather slender, with a faintly to rather distinctly marginate-bulbous base (up to 3 cm), glossy to slightly fibrillose, initially pale greybluish white in upper part, but soon almost white, sometimes more distinctly, fugacious violet at apex, turning brass brown spotted with age (especially when bruised). Universal veil at or near the bulb very sparse and hardly visible, whitish. Basal mycelium sparse, white.

Context: initially pale greybluish in upper part of stipe (especially towards cortex), rarely more pronounced violaceous; bluish colours soon fading, otherwise whitish, often with a brownish line under pileipellis and with brass brown spots where damaged.

Macrochemical reactions: negative (NaOH somewhat brownish).

Smell: faint, indistinct to somewhat like bread dough.

Exsiccata: more or less brownish; pileus margin and stipe sometimes remain whitish.

Basidiospores: [9, 15, 276], 9.6–11.8 × 5.9–7.4 μm (MV = 10.7 × 6.7 μm); variation of MVs: 10.1–11.3 × 6.3–7.1 μm; *Q* = 1.42–1.79 (MV = 1.61), ellipsoid to subamygdaloid, rather strongly and densely verrucose, warts diffuse or sometimes lense-like coalescent at apex, suprahilar plague rarely visible.

Lamella edge: more or less fertile, sterile cells small, clavate or cylindrical.

Pileipellis: duplex. Epicutis thin, at surface of 3–5 μm wide, loosely erect-entangled, gelatinous hyphae, hyaline, collapsed hyphae with pale, refractive pigment. Subcutis/hypodermium weakly to distinctly developed, hyphae 5–15 μm wide, basally usually with inflated elements up to 20 μm wide, tightly cemented, with pale yellow brown parietal-encrusting pigment, often forming an amber-like embedment; in transition to epicutis with subparallel, interconnected bundles of 5–8 μm wide hyphae with pale yellow brown parietal pigment, sometimes a few hyphae with weak zebra-striped encrusting pigment.

Veil hyphae at pileus surface: scattered or absent, hyaline and narrow (3–6 μm).

Habitat: Associated mainly with *Betula pubescens subsp. tortuosa* (subalpine), also with other *Betula* taxa (boreal) and probably also *Tilia cordata* and *Corylus avellana* (boreonemoral), possibly also with *Fagus* (subalpine). In somewhat richer low-herb birch forests, also found in more open transition to alpine heaths (with *Betula nana* and *Betula pubescens subsp. tortuosa* thickets), in fjord sides in rich *Tilia-Betula* scree forests, sometimes also in mixed boreal coniferous forests with some *Betula pubescens* (Trøndelag, C Norway). In SW France recorded in a subalpine *Fagus-Picea* forest (Henry 1981 as *C. fallaceicolor* 'forma méridionale'). In N America, recorded with *Betula pumila*.

Distribution: Apparently with a mainly subalpine northern distribution in Europe. So far known only from Norway and Sweden (12 DNA-verified records), one record from Scotland, one from France (Henry 1981 as *C. fallaceicolor* 'forma méridionale'), and one from Canada in Newfoundland. Most finds are from (middle boreal-)subalpine central parts of S Norway and adjacent parts of Sweden but some also from boreonemoral fjord districts of Hardanger-Sogn-Geiranger (three DNA-verified records). The species reaches up to the tree limit of ca. 1000–1100 m asl. in Jotunheimen, S Norway. Rare to very rare.

Comments: *Cortinarius malachioides* is characterised by its pale, uniformly ochraceous yellow to pale ochraceous grey pileus, pale to very pale, fugacious bluish colours, a more or less marginate bulbous stipe base and comparatively small spores. A few specimens with somewhat stronger bluish pigment are seen, but normally bluish tinges on lamellae and stipe are very pale and fugacious. The almost lack of bluish tinges even on very young specimens is a unique feature within the sect. *Riederi*. The discolouring (to brown) of the pileus on mature specimens, may also be a diagnostic character. The species looks much like a *C. talus* but is distinguished from the latter by pale blue-greyish lamellae, the larger spores and lack of a honey smell. The co-occurring *C. argenteolilacinus* var. *dovrensis* is distinguished by the larger spores, less bluish-violet colours and a more fibrillose pileus. On material studied so far, there is hardly any overlap in spore size between these two. When occurring in mixed forests, *C. malachioides* may be mistaken for the coniferous forest species *C. anomaloochrascens*. This species also has rather small spores (slightly larger than *C. malachioides*) but is distinguished by the quite glossy pileus and the initially deep violet lamellae and stipe. Henry (1981) described a 'forme méridionale' of *C. fallaceicolor* Rob. Henry (an otherwise invalid name according to Art. 40.1 of Melbourne Code, see Index Fungorum), which belongs here. This form was collected under *Fagus* and *Picea* on Mont Aigoual (Cévennes, Massif Central, S France), and the referred material (R. Henry 80.811) appears to have an identical ITS sequence to our species. However, the holotype of *C. fallaceicolor*, collected from young *Picea* forest in

French Jura (R. Henry 80.800; Henry 1981) has a different ITS sequence, a sequence which (although only partial) seems to correspond with that of *C. fulvoochrascens*.

According to present data, *C. malachioides* seems to be a mainly northern species in Europe and is one of very few phlegmacia with a major habitat in the subalpine birch forest belt of the Scandinavian mountain chain. Only the here described *C. argenteolilacinus* var. *dovrensis*, as well as *C. blattoi* and *C. durus* share this habitat preference (see Brandrud et al. 2013). Like *C. blattoi* and *C. durus*, *C. malachioides* is likely to occur also in birch forests on Iceland, and probably has a wider, circumpolar distribution, following the subarctic *Betula* forest range. The one Canadian find from Newfoundland of this little known and probably very much overlooked species, indicates such a wide distribution.

The nomenclature of *C. malachioides* is a complex matter. The type of *C. malachioides* undoubtly represents the present taxon. That is clear both from microscope examination (pers. obs.) and from ITS sequencing. However, Orton (1958) in the protologue, treated *C. malachioides* as one of three taxa around *C. malachius*, as a complex belonging to *Telamonia* s. lato (*Sericeocybe* s. Orton), and not to *Phlegmacium*. So, the question remains, could Orton (i) regard this phlegmacioid taxon belonging to sect. *Riederi* as a *Telamonia* species close to *C. malachius* or (ii) did he make a mistake when he chose the type specimen—selecting a collection belonging to another species than his real, telamonioid *C. malachioides*? In other words; to what extent are our species and the type of *C. malachioides* in contradiction with the description in the protologue?

Although not very clear, we think that the first alternative cannot be ruled out; that Orton consciously included our species in his (broader?) concept of *C. malachioides*, and that he believed this to be a *Telamonia/Sericeocybe*. His description seems largely to cover a *C. malachius* s. lato, but our species could also be involved:

1. *The pileus*: Orton (1958) never mentioned a sticky-viscid pileus: 'pileus … overgrown by silky-white fibrils, then, around the margin innate fibrils'. This description does not fit very well with the often glabrous-glossy-sticky pileus of our species. But still, such an appearance could be within the variation spectrum. It is possible to take a *Riederi* species for a *Sericeocybe* (*Telamonia* s. lato) when collected in dry conditions.
1. *The stipe*: Here, the same applies; our species has a glossy, smooth stipe almost without universal veil, whereas Orton (1958) describes the malachioides-stipe as 'veil forming sometimes rather vague ring zone' (which is typical for the *C. malachius* group). However, the 'sometimes ring zone' could possibly refer to elements in the protologue not covering our species.
2. Habitat: Orton (1958) mentions 'under conifers' whereas our species is a *Betula*(-*Tilia*) species. However, *Betula pubescens* is often present at the classical, Scottish localities of Orton, and could well have been overlooked.

As a conclusion, we emend the description in the protologue so that it is in accordance with the type.

Collections examined: **Canada**. Newfoundland, Avalon Peninsula, Cape St. Mary, 28 Sept 2007, Andrus Voitk TN07-313, H7000977 (H). **France**. Languedoc, Gard, Mont Aigoual, M. Chevassut 10 Oct 1980, R. Henry 80.811 (PC, type of *C. fallaceicolor* 'forme méridionale'). **Norway**. Hordaland, Granvin, Åsen, T.E. Brandrud, TEB176-07 (O); Granvin, Håstabbaneset V, T.S. Jeppesen, B. Dima, TSJ2005-043/TEB371-05/DB2002 (C/O/BP); Ulvik, Eddagilet T.E. Brandrud, TEB155-07 (O). Aust-Agder, Froland, Myklandvatna nature reserve, T.E. Brandrud, TEB562-08 (O). Nord-Trøndelag, Høilandet, Folldalen, E. Bendiksen, T.E. Brandrud, EB-TEB 58-05 (O); Levanger, Ytterøya, Sandstadkammen E, TEB245-13 (O). Oppland, Vågå, Jotunheimen, Gjende, TEB469-11 and TEB473-11. **Sweden**. Ångermanland, H. Marklund et al., CFP980 (S). Härjedalen, Tännäs, S Malmagen, S. Jacobsson, SJ 80075 (GB). Medelpad, Dysjöberget, D. Laber, K. Pätzold, TEB340-16/DB6138b (O). **UK**. Inverness-shire, Rothiemurchus, Loch-an-Eilean, P.D. Orton 29/9/55 (holotype, K(M)94,426).

Additional ITS sequence data from the public sequence repositories: **Sweden**. KJ421177/KS-CO1708 (as *Cortinarius* sp.) (Holmvallen, 17 Aug 2006, J. Vesterholt, herb. S, F251129).

Cortinarius parksianus A.H. Smith, Contr. Univ. Mich. Herb. 2: 16 (1939).

MycoBank: MB 253834.

Holotype: U.S.A., California, near Trinidad, 12 Nov 1937, A.H. Smith 8695 (MICH 10393). GenBank: MH846283.

Description (according to the protologue):

Pileus: 8–12 cm diam., convex then plane with persistently decurved margin; colour initially purplish umber, then more olivaceous brown to cinnamon brown, margin with patches of whitish fibrils.

Lamellae: crowded, purplish (blue) when young, finally cinnamon brown.

Stipe: 10–12 × 2–3.5 cm, bulbose, bulb roundish, 3–4.5 cm wide, purplish (blue), fading rapidly to whitish lilac, silky shiny. Cortina whitish and not copious.

Context lilac grey in pileus, bright purple in the stipe apex, fading to white and pale lilac, resp.

Basidiospores: [1, 1, 50], 9.8–11.6 × 6.3–7.1 μm (MV = 10.7 × 6.7 μm); Q = 1.45–1.77 (MV = 1.61), ellipsoid, verrucose ('roughened').

Habitat: The type was collected under redwood (*Sequoia sempervirens*), within the N Californian belt of coastal redwood forests. Redwood does not form ectomycorrhiza, however, the ectomycorrhizal *Pseudotsuga mensiezii*, *Tsuga heterophylla* and *Abies grandis* might occur in the coastal redwood forests, and our species was probably associated with one of these trees at the site.

Distribution: only known from the type locality.

Comments: The above description is based on the original description in the protologue of Smith (1939). According to this, the species is a robust one, with (olive) brown tinges (no vividly ochraceous yellow or redbrown tinges), and with a bluish ('purplish') tinge when young. Furthermore, the spores are described as comparatively small, resembling those of *C. anomaloochrascens* or *C. malachioides*. Also, the western N American species *C. burlinghamiae* has been collected in a similar habitat (mixed *Pseudotsuga-Sequoia* forest of California), but the latter seems to have much more vivid pileus colours, and larger spores.

Collections examined: **USA.** California, Humboldt County, Trinidad, H.E. Parks estate, under *Sequoia sempervirens*, 12 Nov 1937, A.H. Smith, AHS 8695 (MICH 10393, holotype).

Cortinarius burlinghamiae Bojantchev, sp. nov.
MycoBank: MB 827877, Fig. 10a, b

Etymology: in honour of the American mycologist Gertrude Simmons Burlingham, one of the earliest researchers to work in the Pacific region of the USA.

Holotype: **USA.** Montana, Lincoln County, Cabinet Mountains, off NF-278 Rd. (N48° 12′ 23″ W115° 34′ 31″), elev. 3660 ft., under *Picea sitchensis*, *P. engelmannii*, *Pseudotsuga menziesii* and *Tsuga mertensiana*, 2 Oct 2010, D. Bojantchev, DBB37303 (UC2023490). GenBank: KX768115.

Pileus: 7–16 cm diam., hemispherical to convex then broadly plano-convex; margin involute, irregular, yellow to ochraceous or ochraceous brown near the disk, paler yellow to sulphur yellow towards the margin, whitish velar remnants often present.

Lamellae: crowded, 1.2–2.3 cm broad, pale bluish at first then yellow, bluish tints often remaining in maturity, edges even, attachment sinuate, lamellulae abundant.

Stipe: 5–12 cm long, 1.5–3 cm wide, cylindrical to subclavate, often attenuated at age, with a moderately emarginated bulb, white to pale bluish lilac, more so towards the apex, silky shiny, bruising ochraceous. Cortina whitish at first, leaving an annular zone of dense fibrils on the stipe.

Context: white to bluish, more so towards the margin of the apex. Taste mild, earthy.

Macrochemical reactions: 5% KOH on fresh material reaction variable on context, greyish to ochraceous orange towards the bulb, with a halo, ochraceous on pileus, on dry material consistently ochraceous on all parts.

Smell: indistinct or somewhat earthy.

Basidiospores: [1, 1, 21], 11.2–13.2 × 6.9–8.2 μm (MV = 12.2 × 7.5 μm), $Q = 1.51–1.75$ (MV = 1.63), subobovoid to amygdaliform, coarsely verrucose. Basidia 33–46 × 8–12 μm, 4-spored, cylindro-clavate, clamped. *Cystidia* not observed.

Pileipellis: an ixocutis, duplex, epicutis composed of parallel to interwoven hyphae in a dense gelatinous matrix 220–260 μm thick, made up of 3–10 μm wide, irregular hyphae, hypodermium composed of cylindrical to ventricose cells 12–28 μm wide.

Habitat and distribution: Under conifers (*Picea*, *Pseudotsuga*, *Tsuga* spp.) in montane to submontane areas of N America.

Comments: This species is a close relative of the European *C. fulvoochrascens* and differs by the distribution, slightly paler colours, somewhat smaller spores and several nucleotides in the ITS region. A common host between the two collections from Montana and California is the Douglas fir (*Pseudotsuga mensiezii*), but more research is needed to determine whether that was the primary host of the species.

A clade without acceptable statistical support including ectomycorrhiza sequences isolated from *Picea* roots from Alaska, Bonanza Creek (GenBank: KF617829, Taylor et al. 2014) and from Canada, British Columbia, Bulkley-Nechako (UNITE: UDB031686) as well as a sequence originated from

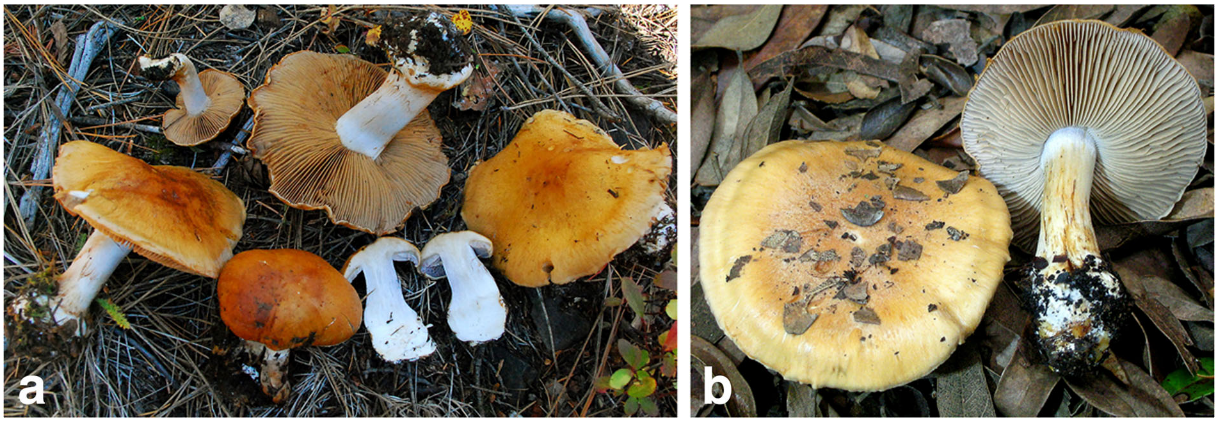


Fig. 10 Basidiocarps of *Cortinarius burlinghamiae* (**a** DBB37303 USA—holotype, **b** DBB57001 USA). Photos: Bojantchev

a basidiocarp sample (from the USA) may represent another complex of species in sect. *Riederi* that falls close to *C. burlinghamiae* (Fig. 2, treated as *Cortinarius* sp.).

Collections examined: **USA.** Montana, Lincoln County, Cabinet Mountains, D. Bojantchev, DBB37303 (UC2023490, holotype). California, Marin County, off Bolinas Ridge Road, elev. 1130 ft., under *Pseudotsuga menziesii*, *Sequoia sempervirens*, *Notholithocarpus densiflorus*, 30 Nov 2011, D. Bojantchev, DBB57001.

Additional ITS sequence data from the public sequence repositories: **USA.** AF389139/IB19970218 (as *C. fulvoochrascens*) (Wyoming, Teton National Forest, *Picea engelmannii*, 20 Aug 1997, V. McKnight).

Conclusion

Section *Riederi* is a striking example of a morphologically complex group that has not been well understood and where the taxonomy is very difficult to sort out without the aid of molecular methods. This is due to the overlapping morphological variation of many of the taxa, combined with their rarity, which makes it difficult to study the entire morphological variation and their characteristic, taxonomically relevant features.

The present morphological circumscription of sect. *Riederi* is quite new, including species with an innately fibrillose, ochraceous red brown to grey brown or whitish pileus, most with initially bright violaceous blue lamellae, and a more or less bulbous to slightly marginate bulbous stipe. The spores are large and ellipsoid-subamygdaloid, not of the more acutely amygdaloid-citriform kind most frequently encountered in phlegmacioid taxa.

Many of the species are only known from a few collections, and optimal material including young specimens showing well-developed characters is very scarce for some of them (e.g. *C. pallidoriederi* (N Italy), *C. glaucocyanopus* (France, Hungary) and the N American *C. burlinghamiae* and *C. parksianus*). The phylogenetic analyses also clearly confirmed that the *C. argenteolilacinus* and *C. riederi*-*C. fulvoochrascens* groups (formerly treated in widely separated sections) are intimately related. Only after the phylogenetic structure was revealed, we were able to re-examine morphologically our material.

Key to the European taxa of sect. *Riederi*

- 1 Pileus when young pale ochre yellow to greyish, sometimes with a bluish tinge, sometimes almost white (resembling *C. talus* or *C. largus*); associated with deciduous trees (mainly *Fagus*, *Corylus*, *Tilia* and *Betula*). Pileus distinctly to only weakly innately fibrillose, somewhat micaceous, but rarely glossy, sometimes becoming faintly fibrillose-tomentose; lamellae pale to deep violet when young, soon fading; stem clavate to more distinctly marginate bulbous, fugacious violet 2
- 1* Pileus when young (pale) ochraceous brown, to warmer ochre-red brown; associated with conifers (mainly *Picea*). Pileus usually distinctly innately fibrillose, smooth-glossy to fibrillose; lamellae deep violet when young, soon fading; stem clavate to more distinctly marginate bulbous, fugacious violet 5
- 2 Spores normally < 11.5 μm long (10–11.5(12) × 6–7(7.5) μm); pileus when young pale ochraceous yellow to olivaceous ochre (like a *C. talus* or *C. anserinus*); basidiocarps rather small and slender 3
- 2* Spores normally > 11.5 μm long (11.5–13 × 7–8(8.5) μm); pileus when young pale (bluish) greybrown (like a *C. largus*); basidiocarps often large and robust. 4
- 3 Mainly under *Betula*. Known from Scotland, W Norway fjords and mountains of Norway and Sweden, recorded also from E Canada and SW France, probably circumpolar; pileus initially usually pale ochre yellow (like a *C. talus*); lamellae and stipe initially pale bluish, almost greyish white; stipe ± marginate bulbous . . . . ***C. malachioides***
- 3* Under *Fagus*. Known from France and Hungary; pileus initially usually pale ochre yellow with an olive tinge (like a pale *C. anserinus*), lamellae and stipe initially rather deep violet; stipe ± marginate bulbous . . . . . ***C. glaucocyanopus***
- 4 Mainly in C Europe under *Fagus*, but also in boreonemoral areas of S Fennoscandia under *Tilia* and *Corylus*. Basidiocarps large and robust; spores strongly verrucose, pileipellis with strongly encrusted hyphae. . .***C. argenteolilacinus* var. *argenteolilacinus***
- 4* Mainly in N Europe in subalpine *Betula pubescens subsp. tortuosa* forests, as well as in few cases with *Corylus* (once collected in Canada; probably circumpolar) Basidiocarps large to small; spores moderately to fairly strongly verrucose, encrusted pigment in pileipellis hyphae weak or absent . . . . . ***C. argenteolilacinus* var. *dovrensis***
- 5 Spore MVs < 12 μm long (MVs 10.9–11.9 × 6.9–7.6 μm); basidiocarps medium and slender. Pileus pale greyish ochraceous brown or tinged olive, stipe often slightly marginate bulbous, sometimes with watery bluish tomentum towards base; pileipellis without or with weak zebra-striped encrusted pigment; so far only known from Europe . . . .***C. anomaloochrascens***
- 5* Spore MVs > 12 μm long (MV's 12.1–13.6 × 6.9–8.7 μm); basidiocarps fairly large; pileipellis with distinctly zebra-striped encrusted pigment **8**
- 6 Veil remnants distinct, initially rendering base of stipe ± girdled and pileus ± fibrillose. Pileus vivid ochre brown, fulvous to red brown, stipe more or less marginate bulbous; stipe without white to bluish white tomentum towards base. So far only in Europe . . . . ***C. fulvoochrascens***

- 6 Almost devoid of veil, pileus and stipe smooth-glossy. Stipe often irregularly clavate-bulbose **9**
- 7 Mean width of spores 7.9–8.7 μm, pileus vivid ochraceous brown, fulvous to redbrown, stipe often with watery bluish tomentum towards base; pileipellis hyphae with strong encrustations. In Europe and western N America . . . . ***C. riederi***
- 7 Mean width of spores 6.9–7.7 μm, pileus paler ochraceous brown, bluish tomentum at stipe base not seen; pileipellis hyphae with only weak encrustations. So far, only known from Europe . . . . ***C. pallidoriederi***

Acknowledgements We thank the curators of PC, G, M, MICH, O, S, K(M) and H for the loans of important specimens including types. We also thank many colleagues for their contribution with materials, sequences, discussions and photos: László Albert, Mika Bendiksby, Egil Bendiksen, Katriina Bendiksen, Jan Borovička, Matthias Dondl, Ingeborg Bjorvand Engh, Sigisfredo Garnica, Gábor M. Kovács, Doris Laber, P. Larsen, Håkan Lindström†, László G. Nagy, Karin Pätzold, Claudio Rossi, Svengunnar Ryman, Gianni Turrini, Martin Unterseher and Jukka Vauras.

Funding information We are very grateful for the Journées européennes du Cortinaire (J.E.C.), especially its president Oswald Rohner for the financial help of the sequencing work. The visit of Bálint Dima in PC was financially supported by SYNTHESYS, the European Union-funded Integrated Activities grant (application FR-TAF-4253).

References

Ammirati JF, Hughes KW, Liimatainen K, Niskanen T, Matheny PB (2013) *Cortinarius hesleri* from eastern North America and related species from Europe and western North America. Botany 91:91–98. https://doi.org/10.1139/cjb-2012-0154

Ariyawansa HA, Hyde KD, Jayasiri SC et al (2015) Fungal diversity notes 111–252—taxonomic and phylogenetic contributions to fungal taxa. Fungal Divers 75:27–274. https://doi.org/10.1007/s13225-015-0346-5

Ballarà J (1999) Alguns *Cortinarius* interessants dels Pirineus catalans, II. Rev Catal Micol 22:47–70

Bidaud A, Moënne-Loccoz P, Reumaux P, Henry R (1999) Atlas des Cortinaires. Pars IX. Ed Fédérat Mycol Dauphiné-Savoie, Seynod

Borchsenius F (2009) FastGap 1.2. Department of Bio-sciences, Aarhus University, Denmark. Published online at: http://www.aubot.dk/FastGap_home.htm

Brandrud TE (1996a) *Cortinarius* subgenus *Phlegmacium* section *Phlegmacium* in Europe: descriptive part. Edinb J Bot 53:331–400. https://doi.org/10.1017/S0960428600003772

Brandrud TE (1996b) *Cortinarius*, subgenus *Phlegmacium*, section *Phlegmacium* in Europe. A study of character variation and ecology including a numerical analysis of the *C. argutus* complex. Mycol Res 100(4):471–485

Brandrud TE (1998) *Cortinarius* subgenus *Phlegmacium* section *Phlegmacioides* (= *Variecolores*) in Europe. Edinb J Bot 55:65–156

Brandrud TE, Melot J (1990) Validations and new combinations in *Cortinarius*, with special emphasis on infrageneric taxa of subgenus *Phlegmacium* (Agaricales). Nord J Bot 10(5):535–538

Brandrud TE, Lindström H, Marklund H, Melot J, Muskos S (1989–2012) *Cortinarius*, Flora Photographica. Vol. 1–5. (Swedish version). Cortinarius HB, Matfors

Brandrud TE, Lindström H, Marklund H, Melot J, Muskos S (1990) *Cortinarius*, Flora Photographica. Vol. 1 (English version). Cortinarius HB, Matfors

Brandrud TE, Bellù F, Frøslev TG, Schmidt-Stohn G (2013) *Cortinarius* subgenus *Phlegmacium* section *Claricolores* and the story about *Cortinarius blattoi* Mazza. Journ JEC 15:14–30

Brandrud TE, Dima B, Schmidt-Stohn G, Bellù F, Frøslev TG, Oertel B, Saar G, Soop K (2014) *Cortinarius* subgenus *Phlegmacium* section *Multiformes* in Europe. Journ JEC 16:162–199

Brandrud TE, Bendiksen E, Dima B (2015) Some new and little known telamonioid *Cortinarius* species from Norway. Agarica 36:11–42

Consiglio G, Antonini D, Antonini M (2006) II Genere *Cortinarius* in Italia. Parte quarta. A.M.B. Fond. Centro Studio Micologici, Trento

Cripps CL, Liimatainen K, Niskanen T, Dima B, Bishop RF, Ammirati JF (2015) Intercontinental distributions of species of *Cortinarius*, subgenus *Phlegmacium*, associated with *Populus* in western North America. Botany 93:711–721. https://doi.org/10.1139/cjb-2015-0089

Dima B (2015) Nomenclatural novelties. Index Fungorum 252:1

Dima B, Liimatainen K, Niskanen T, Kytövuori I, Bojantchev D (2014) Two new species of *Cortinarius*, subgenus *Telamonia*, sections *Colymbadini* and *Uracei*, from Europe. Mycol Prog 13:867–879. https://doi.org/10.1007/s11557-014-0970-6

Eberhardt U, Beker HJ, Vesterholt J, Dukik K, Walther G, Vila J, Fernandez-Brime S (2013) European species of *Hebeloma* section *Theobromina*. Fungal Divers 58:103–126. https://doi.org/10.1007/s13225-012-0188-3

Eberhardt U, Ronikier A, Schütz N, Beker HJ (2015) The genus *Hebeloma* in the alpine belt of the Carpathians including two new species. Mycologia 107(6):1285–1303. https://doi.org/10.3852/15-097

Favre J (1960) Catalogue descriptif des champignons supérieurs de la zone subalpine du Parc National Suisse. Ergebn Wiss Untersuch Schweiz 6:323–610

Fries EM (1836) Epicrisis systematis mycologici seu synopsis Hymenomycetum. Uppsala, Sweden

Frøslev TG, Matheny PB, Hibbett D (2005) Lower level relationships in the mushroom genus *Cortinarius* (Basidiomycota, Agaricales): a comparison of RBP1, RPB2 and ITS phylogenies. Mol Phylogenet Evol 37:602–618

Frøslev TG, Jeppesen TS, Læssøe T (2006) Seven new calochroid and fulvoid species of *Cortinarius*. Mycol Res 110:1148–1160

Frøslev TG, Jeppesen TS, Læssøe T, Kjøller R (2007) Molecular phylogenetics and delimitation of species in *Cortinarius* section *Calochroi* (Basidiomycota, Agaricales) in Europe. Mol Phylogenet Evol 44:217–227

Gardes M, Bruns TD (1993) ITS primers with enhanced specificity for basidiomycetes—application to the identification of mycorrhizae and rusts. Mol Ecol 2:113–118. https://doi.org/10.1111/j.1365-294X.1993.tb00005.x

Garnica S, Weiß M, Oertel B, Oberwinkler F (2003) Phylogenetic relationships of European *Phlegmacium* species (*Cortinarius*, Agaricales). Mycologia 95(6):1155–1170

Garnica S, Weiß M, Oertel B, Oberwinkler F (2005) A framework for a phylogenetic classification in the genus *Cortinarius* (Basidiomycota, Agaricales) derived from morphological and molecular data. Can J Bot 83:1457–1477

Garnica S, Münzmay T, Saar G (2006) *Cortinarius* Subsektion *Elegantiores* in Europa. Journ JEC 8:79–101

Garnica S, Weiß M, Oertel B, Ammirati J, Oberwinkler F (2009) Phylogenetic relationships in *Cortinarius*, section *Calochroi*, inferred from nuclear DNA sequences. BMC Evol Biol 9(1)

Garnica S, Schön ME, Abarenkov K, Riess K, Liimatainen K, Niskanen T, Dima B, Soop K, Frøslev TG, Jeppesen TS, Peintner U, Kuhnert-Finkernagel R, Brandrud TE, Saar G, Oertel B, Ammirati JF (2016) Determining threshold values for barcoding fungi: lessons from *Cortinarius* (Basidiomycota), a highly diverse and widespread ectomycorrhizal genus. FEMS Microbiol Ecol 92(4). https://doi.org/10.1093/femsec/fiw045

Gouy M, Guindon S, Gascuel O (2010) SeaView version 4: a multiplatform graphical user interface for sequence alignment and phylogenetic tree building. Mol Biol Evol 27:221–224

Harrower E, Ammirati JF, Cappuccino AA, Ceska O, Kranabetter JM, Kroeger P, Lim SR, Taylor T, Berbee ML (2011) *Cortinarius* species diversity in British Columbia and molecular phylogenetic comparison with European specimen sequences. Botany 89:799–810. https://doi.org/10.1139/b11-065

Harrower E, Bougher NL, Henkel TW, Horak E, Matheny PB (2015) Long-distance dispersal and speciation of Australasian and American species of *Cortinarius* sect. *Cortinarius*. Mycologia 107(4):697–709. https://doi.org/10.3852/14-182

Henry R (1943) Cortinaires nouveaux ou rares de la flore Française. Bull Soc Mycol Fr 59(1):52–60

Henry R (1957) Nouvelle contribution à l'étude de cortinaires rares ou nouveaux, principalement rencontrés en Franche-Comté. Bull Soc Mycol Fr 73(1):18–76

Henry R (1966) Étude ou révision de quelques cortinaires appartenant aux Myxacia et aux Scauri. Bull Soc Mycol Fr 82:135–178

Henry R (1981) Les Cortinaires. Bull Soc Mycol Fr 97(3):157–279

Henry R (1988) Novitates. Nouvelles validations et typifications. Doc Mycol 19(73):63–68

Henry R (1989a) Suite à l'étude des Cortinaires (Deuxième partie: clés). Bull Soc Mycol Fr 105(1):35–99

Henry R (1989b) Suite à l'étude des Cortinaires. Bull Soc Mycol Fr 105(2):113–138

Jeppesen TS, Frøslev TG, Brandrud TE (2012) Subgen. *Phlegmacium* (Fr.) Trog. In: Knudsen H, Vesterholt J (eds) Funga Nordica: agaricoid, boletoid, clavarioid, cyphelloid and gastroid genera, 2nd revised edition. Nordsvamp, Copenhagen, pp 782–826

Katoh K, Toh H (2008) Recent developments in the MAFFT multiple sequence alignment program. Brief Bioinform 9:286–298

Knudsen H, Vesterholt J (eds) (2012) Funga Nordica: agaricoid, boletoid, clavarioid, cyphelloid and gastroid genera. Nordsvamp, Copenhagen

Krieglsteiner GJ (1991) Verbreitungsatlas der Großpilze Deutschlands, vol 1. Ulmer, Stuttgart

Krieglsteiner GJ, Gminder A (eds) (2010) Die Großpilze Baden-Württembergs. Band 5, Ständerpilze: Blätterpilze III. Ulmer, Stuttgart

Kytövuori I, Niskanen T, Liimatainen K, Lindström H (2005) *Cortinarius sordidemaculatus* and two new related species, *C. anisatus* and *C. neofurvolaesus*, in Fennoscandia (Basidiomycota, Agaricales). Karstenia 45(1):33–49

Læssøe T (2011) Usædvanlige danske svampefund (Notes on rare fungi collected in Denmark). Svampe 64:56–59

Liimatainen K, Niskanen T (2013) *Cortinarius bovarius* (Agaricales), a new species from western North America. MycoKeys 7:23–30. https://doi.org/10.3897/mycokeys.7.5182

Liimatainen K, Niskanen T, Dima B, Kytövuori I, Ammirati J, Frøslev TG (2014) The largest type study of Agaricales to date: bringing identification and nomenclature of *Phlegmacium* (*Cortinarius*, Agaricales) into the DNA era. Persoonia 33:98–140

Löytynoja A, Goldman N (2005) An algorithm for progressive multiple alignment of sequences with insertions. Proc Natl Acad Sci U S A 102:10557–10562

Löytynoja A, Goldman N (2008) Phylogeny-aware gap placement prevents errors in sequence alignment and evolutionary analysis. Science 320:1632–1635

Mahiques R (1999) Flora corològica i bibliogràfica dels cortinaris iberoinsulars I. Bull Soc Micol Valenciana 4–5(B):147–364

Melot J (1986) Contribution à l'étude du genre *Cortinarius*. Doc Mycol 16(63–64):109–142

Moser M (1961) Die Gattung *Phlegmacium* (Schleimköpfe). Die Pilze Mitteleuropas, Band IV. Klinkhardt, Germany

Moser M (1967) Die Röhrlinge und Blätterpilze. In: Gams H (ed) Kleine Kryptogamenflora 3 Aufl. 2 (b/2). Stuttgart, New York

Moser M, McKnight KH, Ammirati JF (1995) Studies on North American cortinarii I. New and interesting taxa from the Greater Yellowstone area. Mycotaxon 55:301–346

Nagy LG, Kocsubé S, Csanádi Z, Kovács GM, Petkovits T et al (2012) Re-mind the gap! Insertion–deletion data reveal neglected phylogenetic potential of the nuclear ribosomal internal transcribed spacer (ITS) of Fungi. PLoS One 7(11):e49794

Niskanen T (2014) Nomenclatural novelties. Index Fungorum 201:1–5

Niskanen T (2015) Nomenclatural novelties. Index Fungorum 221:1

Niskanen T, Liimatainen K, Kytövuori I (2006) Taxonomy, ecology and distribution of *Cortinarius rubrovioleipes* and *C. hinnuleoarmillatus* (Basidiomycota, Agaricales) in Fennoscandia. Karstenia 46(1):1–12

Niskanen T, Kytövuori I, Liimatainen K (2009) *Cortinarius* sect. *Brunnei* (Basidiomycota, Agaricales) in North Europe. Mycol Res 113:182–206. https://doi.org/10.1016/j.mycres.2008.10.006

Niskanen T, Kytövuori I, Liimatainen K (2011) *Cortinarius* sect. *Armillati* in northern Europe. Mycologia 103:1080–1101. https://doi.org/10.3852/10-350

Niskanen T, Liimatainen K, Kytövuori I, Lindström H (2012a) Subgen. *Telamonia* (Fr.) Trog. In: Knudsen H, Vesterholt J (eds) Funga Nordica: agaricoid, boletoid, clavarioid, cyphelloid and gastroid genera, 2nd revised edition. Nordsvamp, Denmark, pp 826–885

Niskanen T, Liimatainen K, Kytövuori I, Ammirati JF (2012b) New *Cortinarius* species from conifer-dominated forests of North America and Europe. Botany 90(8):743–754. https://doi.org/10.1139/b2012-038

Niskanen T, Laine S, Liimatainen K, Kytövuori I (2012c) *Cortinarius sanguineus* and equally red species in Europe with an emphasis on northern European material. Mycologia 104(1):242–253. https://doi.org/10.3852/11-137

Niskanen T, Kytövuori I, Liimatainen K, Lindström H (2013) The species of *Cortinarius*, section *Bovini*, associated with conifers in northern Europe. Mycologia 105(4):977–993

Niskanen T, Liimatainen K, Kytövuori I, Ammirati JF (2015) Nomenclatural novelties. Index Fungorum 256:1–2

Nylander JAA, Wilgenbusch JC, Warren DL, Swofford DL (2007) AWTY (are we there yet?): a system for graphical exploration of MCMC convergence in Bayesian phylogenetics. Bioinformatics 24:581–583. https://doi.org/10.1093/bioinformatics/btm388

Orton PD (1958) The genus *Cortinarius* II. *Inoloma* and *Dermocybe*. The Naturalist London 1958:81–149

Osmundson TW, Robert VA, Schoch CL, Baker LJ, Smith A, Robich G, Mizzan L, Garbelotto MM (2013) Filling gaps in biodiversity knowledge for macrofungi: contributions and assessment of an herbarium collection DNA barcode sequencing project. PLoS One 8(4):E62419

Papp V, Dima B (2017) New systematic position of *Aurantiporus alborubescens* (Meruliaceae, Basidiomycota), a threatened old-growth forest polypore. Mycol Prog 17:319–332. https://doi.org/10.1007/s11557-017-1356-3

Peintner U, Bougher NL, Castellano MA, Moncalvo JM, Moser MM, Trappe JM, Vilgalys R (2001) Multiple origins of sequestrate fungi related to *Cortinarius* (Cortinariaceae). Am J Bot 88:2168–2179

Peintner U, Moser MM, Thomas KA, Manimohan P (2003) First records of ectomycorrhizal *Cortinarius* species (Agaricales, Basidiomycetes) from tropical India and their phylogenetic position based on rDNA ITS sequences. Mycol Res 107:485–494

Peintner U, Moncalvo JM, Vilgalys R (2004) Toward a better understanding of the infrageneric relationships in *Cortinarius* (Agaricales, Basidiomycota). Mycologia 96:1042–1058

Peintner U, Dresch P, Bellú F, Borghi E (2014) *Cortinarius microglobisporus* (Basidiomycota), a new species with roundish spores related to *C. illuminus*. Mycol Prog 13(3):899–904. https://doi.org/10.1007/s11557-014-0975-1

Ronquist F, Huelsenbeck JP (2003) MRBAYES 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19:1572–1574

Saar G, Brandrud TE, Dima B, Schmidt-Stohn G, Bellù F, Frøslev T, Oertel B, Soop K (2014) *Cortinarius* Untergattung *Phlegmacium* Sektion *Purpurascentes* in Europa. Journ JEC 16:140–161

Schäffer J (1947) Beobachtungen an oberbayerischen Blätterpilzen. Ein Beitrag zur Kenntnis der oberbayerischen Pilzflora. Ber bayer bot Ges 27:201–225

Schmidt-Stohn G (2011) Fotografie ornamentierter Sporen mit der Methode des "Focus-Stacking". Journ JEC 13:79–87

Seress D, Dima B, Kovács GM (2016) Characterization of seven *Inocybe* ectomycorrhizal morphotypes from a semiarid sandy area. Mycorrhiza 26:215–225. https://doi.org/10.1007/s00572-015-0662-3

Silvestro D, Michalak I (2012) RaxmlGUI: a graphical front-end for RAxML. Org Divers Evol 12:335–337. https://doi.org/10.1007/s13127-011-0056-0

Simmons MP, Ochoterena H, Carr TG (2001) Incorporation, relative homoplasy, and effect of gap characters in sequence-based phylogenetic analysis. Syst Biol 50:454–462. https://doi.org/10.1080/106351501300318049

Smith AH (1939) Studies in the genus *Cortinarius* I. Contrib Univ Mich Herb 2:4–42

Smith AH (1944) New and interesting Cortinarii from North America. Lloydia 7:163–235

Smith JE, Molina R, Huso MMP, Luoma DL, McKay D, Castellano MA, Lebel T, Valachovic Y (2002) Species richness, abundance, and composition of hypogeous and epigeous ectomycorrhizal fungal sporocarps in young, rotation-age, and old-growth stands of Douglas-fir (*Pseudotsuga menziesii*) in the Cascade Range of Oregon, USA. Can J Bot 80:186–204

Soop K (2011) *Cortinarius* in Sweden (thirteenth edition). In: Éditions Scientrix. Mora, Sweden

Soop K (2017) *Cortinarius* in Sweden (fifteenth edition). In: Éditions Scientrix. Mora, Sweden

Stamatakis A (2014) RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30:1312–1313

Stensrud Ø, Orr RJS, Reier-Røberg K, Schumacher T, Høiland K (2014) Phylogenetic relationships in *Cortinarius* with focus on North European species. Karstenia 54:57–71

Tamura K, Stecher G, Peterson D, Filipski A, Kumar S (2013) MEGA6: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. Mol Biol Evol 30:2725–2729. https://doi.org/10.1093/molbev/mst197

Taylor DL, Hollingsworth TN, McFarland JW, Lennon NJ, Nusbaum C, Ruess RW (2014) A first comprehensive census of fungi in soil reveals both hyperdiversity and fine-scale niche partitioning. Ecol Monogr 84:3–20

Weinmann JA (1836) Hymeno- et gasteromycetes hucusque in Imperio rossico observatos. Inpensis Academiae Imperialis Scientiarum, Petropoli

White TJ, Bruns T, Lee S, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (eds) PCR protocols: a guide to methods and applications. Academic, New York, pp 315–322