

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

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## Abstract

*Cortinarius* is one of the most species-rich genera of mushroom-forming fungi. Based on phylogenetic and morphological evidence, a new section, *Cortinarius*, sect. *Riederi*, is introduced. The taxonomy, phylogeny, ecology and distribution of mainly European but also including some North American taxa of this section are treated, which includes 9 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), but 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.

## Key words

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 2–3 times increase in the number of species (see e.g., Niskanen et al. 2013 on sect. *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).

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Morphologically, *Cortinarius* has traditionally been subdivided into 5–8 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, 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), 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

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## Molecular data

A total of 112 specimens of clade Riederi from Europe and N 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, U.S.A.) 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, and LGC Genomics (Berlin, Germany) with the same primers as those applied in PCR. Chromatograms were assembled and edited with Sequencher 4.1 (Gene Codes, Ann Arbor, MI, U.S.A.) and CodonCodeAligner 4.1. (CodonCode Corporation, Centerville, MA, U.S.A.). 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 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 This is a post-peer-review, pre-copyedit version of an article published in Mycological Progress. The final authenticated version is available online at: <http://dx.doi.org/10.1007/s11557-018-1443-0>

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 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 Table 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 2-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).

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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 visualized 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<sub>2</sub>O, often with a drop of 40% KOH added subsequently, or from dried material mounted in H<sub>2</sub>O 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 lengths (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. Cléménçon). 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 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 describe this well-circumscribed group formally as a new section (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% (7

substitution 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% (3 substitutions and indel positions). This percentage is smaller than normally used 1% as a minimum cut-off value for recognizing 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 here 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. malachoides*). 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 to 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).

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Although seen in some other species, such as *C. dionysae*, *C. naps* 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 characterized 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. *dovreensis* (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 *Glaucopodes*

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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 characterized 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.

*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 characterized by the lack of distinct smells.

*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

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characterized 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, Dima, Niskanen & Liimat., sect. nov.

MycoBank MB 827874

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, gelatinized 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).

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MycoBank: MB 155615

Figs 8a and 8b

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: U.S.A., 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 fibers, 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 centre, the involute margin whitish brown. Universal veil remnants very sparse, hardly visible.

*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.

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

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

440 *Macrochemical reactions* negative, KOH somewhat brownish in context.

441 *Smell* faint, sometimes yeast-like with age.

442 *Exsiccata* pale brownish with vivid brown-redbrown pileus.

443 *Basidiospores* [10, 15, 249], 11.6–14.2 × 7.3–9 µm (MV = 12.9 × 8.2 µm); variation of MVs:  
444 12.3–13.6 × 7.9–8.7 µm; Q = 1.44–1.72 (MV = 1.58), ellipsoid-subamygdaloid, medium to  
445 strongly and densely verrucose, sometimes with an apical “lense” of confluent warts;  
446 suprahilar plague hardly visible.

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

448 *Pileipellis* duplex. Epicutis thin. At surface 2–5 µm wide, loosely erect-entangled, gelatinous  
449 hyphae, hyaline or with pale, refractive pigment when collapsed. Subcutis/hypodermium  
450 hyphae 5–20 µm wide, tightly cemented, with brown parietal-encrusting pigment, forming an  
451 amber-like embedment; in transition to epicutis with subparallel, interconnected bundles of 3–  
452 6(10) long and rather narrow 5–7(10) µm wide hyphae, with distinct to strong, brown, zebra-  
453 striped-crustulose encrusted pigment. These bundles are normally easy visible when the thin  
454 pellicle is peeled off.

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

456 *Habitat*: Associated with *Picea abies*, probably also *Pinus sylvestris* (cf. Favre 1960, Moser  
457 1961 as *C. lilacinopes*). In oligotrophic *Vaccinium myrtillus* type of forests, sometimes also in  
458 richer/mesotrophic low-herb spruce forests, sometimes in bog rims. Frequently in young,  
459 mossy *Picea* plantations.

460 *Distribution*: Mainly recorded from Fennoscandia where the species is widespread and rather  
461 frequent in boreal regions (Moser 1961 as *Phlegmacium fuscomaculatum* var. *smolandicum*;  
462 Soop 2011 as *C. fulvochrascens* p.p.; Jeppesen et al. 2012). Rarely occurring also in  
463 subalpine *Picea-Pinus* forests in the Alp-Prealp regions, so far recorded from S Tyrol, Italy

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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. fulvoohrascens* 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. fulvoohrascens* and *C. anomalohrascens*. Recorded also in western North America (Smith 1944, as *C. pseudoarquatus*; type conspecific with *C. riederi*).

*Comments:* *Cortinarius riederi* is characterized by its (i) distinctly innately fibrillose and vividly ochre brown-reddish 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 characterizing. *Cortinarius riederi* (= *C. fulvoohrascens* 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. fulvoohrascens* and *C. pallidoriederi* as well as *C. anomalohrascens* 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. anomalohrascens*. In C Europe about fifty-fifty of the collections belong to *C. fulvoohrascens* versus *C. anomalohrascens*, 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. fulvoohrascens*, and there is no consistent name-use for these in the literature. *Cortinarius fulvoohrascens* 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

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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  $\mu\text{m}$ , whereas MV's  $>13.0 \mu\text{m}$  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 J. 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  $13.0 \times 8.2 \mu\text{m}$  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).

530

531 *Collections examined:*

532 **Finland.** Savonia Borealis, Vehmersalmi, Pitkälähti, J. Vauras, JV 1475F (herb. TUR).

533 Uusimaa, Luukki, I. Kytövuori, IK93-664 (H). Kittilän Lappi, Kolari, I. Kytövuori, IK98-

534 1171 (H). **Italy.** S Tyrol, Anterselva, 19 Aug 2005, C. Rossi, Rossi 19-08-2005 (herb. Rossi);

535 S Tyrol, 25 Aug 2013, G. Turrini, TG25-08-2013 (herb. Turrini); 12 Aug 2012, F. Bellù, Bellu

536 12-08-2012 (herb. BOZ), 14 Aug 2012, C. Rossi (herb. Rossi). **Norway.** Oppland, Søndre

537 Land, Hov NW, T.E. Brandrud, B. Dima, TEB407-13/DB5109 (O); Vestre Slidre, Einang

538 Bridge S, T.E. Brandrud, TEB443-11 (O). Etnedal, Solbjør N, T.E. Brandrud & B. Dima,

539 TEB258-17 (O). Sør-Trøndelag, Trondheim, Ranheimsskogen, T.S. Jeppesen TSJ2001-004

540 (C), Nord-Trøndelag, Lierne, K. & E. Bendiksen, TE. Brandrud; KB-EB-TEB 2-10 (O).

541 **Sweden.** Jämtland, Bräcke, Ammersön, T.E. Brandrud, TEB141-10/SS10-066 (O). Småland,

542 Femsjö, M. Moser, MM 57/60 (M, holotype of *Phlegmacium fuscomaculatum* var.

543 *smolandicum*). **Switzerland.** Graubünden, Engadin, J. Favre, 26 Aug 1944, GK13347 (G,

544 neotype). **U.S.A.** Washington, Olympic National Park, Olympic Hot Springs, A.H. Smith,

545 AHS17141 (MICH10397, holotype of *C. pseudoarquatus*).

546

547 *Cortinarius pallidoriederi* Brandrud, Dima & Bellù, sp. nov.

548 MycoBank MB 827875

549 Fig. 8h

550

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

552

553 Holotype: Italy, S Tyrol, Val d'Ega (Eggental), Novale (Rauth), Wald Lagarn, between

554 Underkor and Oberkor, E. Castellini, F. Bellù, 30 Sept 2011, Bellu 30-09-2011 (BOZ).

555 GenBank: MH923049.

556

557

558 *Pileus* 4–8 cm, (hemi-)spherical, then plano-convex, viscid-glutinous, finely innately

559 fibrillose-rivulose from darker, innate fibers; uniform pale ochraceous yellow to ochraceous

560 brown, with an olivaceous ochre tinge. Universal veil remnants sparse, rendering surface

561 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 2–4 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 characterized 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 substitution 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.*

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*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

Figs 8c and 8d

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).

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*Cortinarius fulvochrascens* var. *cyanophyllus* Rob. Henry, Doc. Mycol. 19(73): 67 (1988).  
MycoBank: MB 134961. Type: France, Doubs, R. Henry 3258-a-29 (PC, as heterotype).  
*Cortinarius fulvochrascens* 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 fulvochrascens* 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],  $11.1\text{--}13.8 \times 7.2\text{--}8.6 \mu\text{m}$  (MV =  $12.5 \times 7.9 \mu\text{m}$ ); variation of MVs:  $12.1\text{--}12.7 \times 7.6\text{--}8.2 \mu\text{m}$ ; 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  $\mu\text{m}$  wide, loosely erect-entangled, gelatinous hyphae, hyaline or with pale, refractive pigment when collapsed, terminal hyphae sometimes clavate. Subcutis/hypodermium, hyphae 5–20  $\mu\text{m}$  wide, tightly cemented, with brown parietal-encrusting pigment, often forming an amber-like embedment; in transition to epicutis with narrow (5–8  $\mu\text{m}$  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 2–3 layers, hyphae rather thick (4–8(12)  $\mu\text{m}$  wide), some interconnected (H-shaped connections), some terminal elements slightly inflated; many with yellow parietal pigment, some with zebra-striped encrustations, 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)  $\mu\text{m}$ ) 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.

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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 characterized 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 characterized 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

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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, hétérotype 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

Figs 8e, 8f and 8g

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, Frasné, 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 fibers, sometimes with hygrophanous 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 ( $L = 70\text{--}100$ ), 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  $\times$  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],  $10.2\text{--}12.8 \times 6.3\text{--}8.1 \mu\text{m}$  ( $MV = 11.5 \times 7.2 \mu\text{m}$ ); variation of MVs:  $10.9\text{--}11.9 \times 6.9\text{--}7.6 \mu\text{m}$ ;  $Q = 1.43\text{--}1.78$  ( $MV = 1.60$ ), ellipsoid to subamygdaloid, distinctly and densely verrucose, suprahilar plaque hardly visible.

*Pileipellis* duplex. Epicutis thin. At surface of 3–5  $\mu\text{m}$  wide, loosely erect-entangled, gelatinous hyphae, hyaline or with pale pigment, some pale verrucose to zebra-striped.

Subcutis/hypodermium hyphae 5–20  $\mu\text{m}$  wide, tightly cemented, with brown parietal-

790 encrusting pigment, often forming an amber-like embedment; in transition to epicutis with  
791 subparallel, interconnected bundles, with some, encrusted pigment.

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

797 *Distribution*: Widely distributed in boreal-montane districts in Europe, but apparently  
798 everywhere rather rare. Reported from C and S Fennoscandia (Soop 2011 as *C.*

799 *fulvoochrascens* p.p.; Jeppesen et al. 2012), from The Black Forest region of Germany  
800 (Krieglsteiner and Gminder 2010) and from the Jura region of France (Henry 1989a; 1989b;  
801 Bidaud et al. 1999). In The Black Forest, the species occurs in the montane zone (450)600–  
802 1000 m asl., and in the lower montane mixed *Picea-Abies* forests it seems to be more frequent  
803 than *C. riederi* (Krieglsteiner and Gminder 2010; pers. obs.). The species is further collected  
804 by us in N Italy and the Czech Republic (see list of collections examined). Moser (1961) may  
805 have included *C. anomaloochrascens* in his wide concept of *Phlegmacium fuscomaculatum*  
806 which is reported not to be rare in the Alp-Prealp region.

807 *Comments*: *Cortinarius anomaloochrascens*, although widespread, is very little known and  
808 described, apparently mainly included in a broad concept of *C. riederi*. The species seems  
809 well illustrated in Bidaud et al. (1999; Pl. 213) and Soop (2017), although these specimens are  
810 not verified by sequencing. *Cortinarius anomaloochrascens* is characterized by its rather  
811 small and slender basidiocarps, pale ochraceous greybrown pileus, and smaller spores  
812 compared to *C. riederi* and *C. fulvoochrascens*. The spores are usually also somewhat more  
813 amygdaloid than those of *C. riederi* and *C. fulvoochrascens*. The contrast between the initially  
814 bright violaceous stipe and the pale greyish ochre pileus margin is often striking. The stipe  
815 furthermore normally has a more marginate bulb than that of *C. riederi*. Misidentifications  
816 under the name *C. riederi* or *C. fulvoochrascens* can easily be sorted out by the smaller spores  
817 of *C. anomaloochrascens*, which show no overlap with the spores of *C. riederi*/*C.*

818 *fulvoochrascens*, when mean values for measurement series are compared (spore MVs for *C.*  
819 *anomaloochrascens* always <12 µm long). *Cortinarius glaucocyanopus* and *C. malachoides*  
820 also have comparatively small spores, but these are associated with deciduous trees, mainly  
821 *Fagus* and *Betula*, respectively. These also have a paler coloured pileus, and *C. malachoides*  
822 usually lacks deep violet tinges on young lamellae and stipe.

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823

824 *Collections examined:*

825 **Czech Republic.** C Bohemia, Prague region, Borovsko, Hadce u Želivky Nature Reserve,  
826 mixed forest with *Picea*, *Pinus*, *Betula* on serpentinite soil, J. Borovicka 140519-29 (PRM  
827 924382). **Denmark.** Northern Jutland, Faurholt hede, A. Eriksen, AE2009-65377 (C77672).  
828 **Finland.** Kainuu, Paltamo, I. Kytövuori, IK92-2028 (H). **France.** Doubs, R. Henry 2805 (PC,  
829 holotype), R. Henry 2807 (PC, isotype); R. Henry 395 (PC, holotype for *C. imbricatoides*); R.  
830 Henry 85.13 (PC, holotype for *C. stilazureus*). Doubs, Levier, T.G. Frøslev, T.S. Jeppesen,  
831 TSJ2006-095 (C). Auvergne-Rhone-Alpes, Oyonnax, I. Kytövuori, IK94-1743 (H).  
832 **Germany.** Baden-Württemberg, Rottweil, Dunninger Wald, T.E. Brandrud, B. Dima, G. Saar,  
833 TEB762-12/DB4814 (O). Bayern, Sachsenkamm, Kirchsee Nord, 7 Oct 2013, M. Dondl,  
834 MD28/2013; Bayern, Mittenwald, Kranzbergregion, 21 Sept 2013, M. Dondl, MD 27/2013.  
835 **Italy.** Trentino-Alto-Adige, St. Valentin Atzwang, 30 July 2012, F. Bellù, Cester, Bellu 30-07-  
836 2012 (BOZ); Riscone, 14 Aug 2012, C. Rossi, Rossi 14-08-2012 (herb. Rossi); Redensberg,  
837 Nähe Olang, 13 Aug 2012, F. Bellù & Fuman, Bellu 13-08-2012 (BOZ). S Tyrol, Jenesien,  
838 Remphof, 4 Sept 2017, T. Errico, Bellu 04-09-2017 (O); Bolzano, Villnösstal, Malga Zannes,  
839 Val di Funes, C. Rossi, Rossi 31-08-2017 (O); Mölten, Kirchebene, pr. Mettina, C. Rossi,  
840 Rossi 07-09-2017 (O). **Norway.** Oppland, Lunner, S. Oppdalen, E. Bendiksen, TEB316-10  
841 (O). Østfold, Halden, Idd, T.E. Brandrud, TEB252-07 (O). Hordaland, Ulvik, Åsen peninsula,  
842 T.E. Brandrud, TEB175-07 (O). Nord-Trøndelag, Nærøy, Saglivatn, E. Bendiksen & T.E.  
843 Brandrud, EB-TEB 6-05 (O). Oslo, Oslo, Enebakkveien 866, 12 Sept 2014, T. Blakar, F-  
844 75650 (O). **Sweden.** Ångermanland, Säbrå, H. Marklund, CFP 1539 (S).

845

846 *Additional ITS sequence data from the public sequence repositories:*

847 **Germany.** KJ420997/TUB019758 (as *C. riederi*); KJ421008/TUB019769 (as *C. riederi*);  
848 KJ421012/TUB019770 (as *C. riederi*). **Italy.** JF907910/MCVE16165 (as *C. riederi*).

849

850

851 *Cortinarius glaucocyanopus* Rob. Henry, in Bidaud et al., Atlas des Cortinaires IX: 371  
852 (1999)

853 MycoBank: MB 461065

854 Figs 9h and 9i

855

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

858 Synonym: *Cortinarius glaucocyanopus* Rob. Henry, Bull. trimest. Soc. myc. Fr: 73: 32  
859 (1957), nom. inval.

860

861

862

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

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

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

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

874 *Macrochemical reactions* negative.

875 *Smell* indistinct.

876 *Exsiccata* pale brownish.

877 *Basidiospores* [2, 2, 68], 10.3–13.1 × 6.6–7.8 µm (MV = 11.7 × 7.2 µm), variation of MVs:  
878 11.2–12.0 × 7.2–7.3 µm; Q = 1.41–1.85 (MV = 1.63), ellipsoid to subamygdaloid, distinctly  
879 and densely verrucose, suprahilar plague hardly visible.

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

885 *Habitat*: Apparently associated with *Fagus*, possibly also other deciduous trees; collected in  
886 *Fagus* dominated forest with small *Picea* trees and *Betula* in Hungary, and reported from  
887 *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 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. anomalochrascens* by 10 substitution and indel positions in the ITS regions. They also have different habitats; *C. glaucocyanopus* growing in *Fagus* forests, *C. anomalochrascens* 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. anomalochrascens*/*C. glaucocyanopus* (“spores..... de 15/8.8  $\mu$ .”). In fact, the sketched 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 (Bidaud, 27 Sept 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)  $\times$  7.5–8.5(9)  $\mu$ m, of the same size as those of *C. fulvochrascens*, 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

Figs 9a, 9b and 9c

Holotype: Austria, Holztal, 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 et al. (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 fibers 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.

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954 *Macrochemical reactions* negative, sometimes yellow-brownish with KOH in bulb context.  
955 *Smell* faint, indistinct.  
956 *Exsiccata* brownish to almost whitish.  
957 *Basidiospores* [8, 16, 319],  $10.7\text{--}13.7 \times 6.7\text{--}8.3 \mu\text{m}$  (MV =  $12.2 \times 7.5 \mu\text{m}$ ), variation of MVs:  
958  $11.6\text{--}12.9 \times 7.1\text{--}7.9 \mu\text{m}$ ; Q = 1.42–1.84 (MV = 1.63), ellipsoid to subamygdaloid, rather  
959 strongly to very strongly and rather densely verrucose, perisporium sometimes visible,  
960 ornaments often lense-like coalescent at apex, sometimes prominent, giving the spore a  
961 slightly citriform outline, often also with prominent, tooth-like warts subapically; suprahilar  
962 plague rarely visible.  
963 *Lamellar edge* more or less fertile, sterile cells small, clavate or cylindrical.  
964 *Pileipellis* duplex. Epicutis thin. At surface 3–5  $\mu\text{m}$  wide, loosely erect-entangled, gelatinous  
965 hyphae, hyaline or with pale, refractive pigment (especially when collapsed).  
966 Subcutis/hypodermium weakly developed, hyphae 5–15  $\mu\text{m}$  wide, tightly cemented, with pale  
967 yellow brown parietal-encrusting pigment, often forming an amber-like embedment; in  
968 transition to epicutis with subparallel, interconnected bundles of long and rather narrow  
969 hyphae (5–10  $\mu\text{m}$  wide), with distinct to strong zebra-striped/crustulose brown encrusting  
970 pigment, encrustation especially prominent on some slightly wider hyphae (8–10  $\mu\text{m}$  wide).  
971 *Veil hyphae at pileus surface* scattered, mainly narrow (3–6  $\mu\text{m}$ ), hyaline; some hyphae  
972 interconnected.  
973 *Habitat*: Associated mainly with *Fagus sylvatica*, in boreonemoral region also sometimes  
974 found under *Tilia cordata* and *Corylus avellana*, in richer to somewhat calcareous forests.  
975 *Distribution*: Distributed mainly in nemoral-(sub)montane areas of C Europe and S  
976 Scandinavia, more rare in boreonemoral areas of S Scandinavia. Apparently rare everywhere,  
977 very rare in S Europe. Little known, recorded only from SE Norway, S Sweden and Denmark  
978 (cf. Læssøe et al. 2011; pers. obs.), Tyrol, Austria (Moser 1961), Germany (Krieglsteiner  
979 1991; pers. obs.) and the French Jura (see collections examined). According to Mahiques  
980 (1999) it is found also in NE Spain (Catalonia).  
981 *Comments*: *Cortinarius argenteolilacinus* s. lato is characterized by its pale greyish, almost  
982 fibrillose pileus with bluish tinges when (very) young, and the initially deep violet lamellae  
983 and stipe. The basidiocarps are often robust. The spores often possess an apical, irregular,  
984 lense-like structure due to coalescent warts. *Cortinarius argenteolilacinus* var.  
985 *argenteolilacinus* and var. *dovreensis* deviate genetically by only two to three nucleotide and  
986 indel differences in the ITS region.

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*Cortinarius argenteolilacinus* var. *dovreensis* 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. malachoides*, 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. varicolor-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:*



1019 **Austria.** Holttal, M. Moser, MM 48/752 (M, holotype). **Denmark.** Sjælland, Vejlø skov, T.S.  
1020 Jeppesen, TSJ2010-004 (C), TSJ2012-044 (C). **France.** Jura, Prénovel, 10 Oct 2008, B.  
1021 Dima, DB3312 (BP). **Germany.** Baden-Württemberg, Schwaben, Ehingen a.d. Donau, T.E.  
1022 Brandrud, G. Schmidt-Stohn et al., TEB 418-10/SSSt10-174 (O). Bayern, Tegernsee,  
1023 Riederstein, M. Dondl, MD18/2013. **Hungary.** Heves, Mátra Mts, L. Nagy, NL-5262 (herb.  
1024 L. Nagy). **Norway.** Telemark, Drangedal, Sannes-Langen, T.E. Brandrud, TEB52-01 (O).  
1025 Aust-Agder, Risør, Dalsvann SW, Grønnefjell, I.L. Fonneland, ILF2013-98 (O); Vestfold,  
1026 Larvik, Kjøse, T.E. Brandrud, TEB370-08 (O); T.E. Brandrud, TEB381-08 (O). Buskerud,  
1027 Hole, Bråtåfjellet SV, T.E. Brandrud & B. Dima, TEB281-17/DB6361 (O). **Sweden.**  
1028 Bohuslän, Tanum, T.E. Brandrud et al., CFP1608 (S). Öland, Borg, I. Kytövuori, IK98-2617  
1029 (H). Skåne, Ivön, C. Ingvert, T.G. Frøslev, T.S. Jeppesen TSJ2011-025 (C)

1030

1031 *Cortinarius argenteolilacinus* var. *dovreensis* Brandrud, var. nov.

1032 MycoBank MB 827876

1033 Fig. 9d

1034

1035 Etymology: the epithet refers to the Dovre Mountains of S Norway, from where the type was  
1036 collected.

1037

1038 Holotype: Norway, Sør-Trøndelag, Oppdal, Kongsvoll, Dovre Mountains, 10 Aug 1980, T.E.  
1039 Brandrud, TEB112-80 (O). GenBank: MH923071.

1040

1041 Selected icones: Soop 2017, Pl. 5:20 as *C. "dovreensis"*.

1042

1043 *Pileus* 4–10 cm, (hemi-)spherical, then plano-convex (to broadly umbonate), viscid-glutinous,  
1044 towards margin weakly, finely (sometimes distinctly) innately fibrillose-rivulose, somewhat  
1045 silvery-micaceous, often faintly fibrillose-tomentose; pale grey, greyish ochre to greyish  
1046 white, often slightly more ochraceous brown at centre, sometimes almost whitish, initially  
1047 often with a bluish tinge towards margin, the involute margin (bluish) whitish. Universal veil  
1048 remnants very sparse, sometimes with whitish veil fibers towards margin when young.  
1049 *Lamellae* crowded (L = 80–110), 0.5–1 cm broad, initially deep violet to greyish violet, but  
1050 (very) soon fading to paler bluish grey and then greyish brown; edge even to crenulate.

1051 *Stipe* 6–10(11) × 1–2.5 cm, often robust, with a bulbous to often faintly marginate-bulbous  
1052 base (up to 4.5 cm), glossy to slightly fibrillose, initially greyish violet to deep violet in upper  
1053 part, whitish downwards (sometimes violet down to bulb), bluish tinges soon fading,  
1054 sometimes turning (spot wise) somewhat brass-brown with age. Universal veil near the bulb  
1055 sparse and hardly visible; white to sometimes bluish when very young.  
1056 *Context* initially deep violet to greyish violet in upper part of stipe (especially towards  
1057 cortex), bluish white in pileus and bulb, violet colour soon fading, becoming whitish with  
1058 brass brown spots where damaged.  
1059 *Macrochemical reactions* negative, sometimes yellow-brownish with KOH in bulb context.  
1060 *Smell* faint, indistinct.  
1061 *Exsiccata* whitish to (pale) brownish.  
1062 *Basidiospores* [9, 16, 264], 11.2–13.8 × 6.8–8.6 µm (MV = 12.5 × 7.7 µm); variation of MVs:  
1063 11.8–13.5 × 7.3–8.2 µm; Q = 1.45–1.79 (MV = 1.62), ellipsoid to subamygdaloid, medium to  
1064 rather strongly and densely verrucose, ornaments often lense-like coalescent at apex,  
1065 sometimes prominent; suprahilar plague rarely visible.  
1066 *Lamellar edge* more or less fertile, sterile cells small, clavate or cylindrical.  
1067 *Pileipellis* duplex. Epicutis thin, at surface of 3–5 µm wide, loosely erect-entangled,  
1068 gelatinous hyphae, hyaline or with pale, refractive pigment (when collapsed).  
1069 Subcutis/hypodermium weakly to distinctly developed, hyphae 5–15 µm wide, basally  
1070 sometimes with inflated elements up to 20 µm wide, tightly cemented, with pale yellow  
1071 brown parietal-encrusting pigment, often forming an amber-like embedment; in transition to  
1072 epicutis with subparallel, interconnected bundles of 5–8 µm wide hyphae, sometimes with  
1073 weak zebra-striped encrusting pigment (never distinct encrustations like in the main variety).  
1074 *Veil hyphae at pileus surface* scattered to almost lacking, mainly narrow (3–6 µm) and  
1075 hyaline.  
1076 *Habitat*: Associated mainly with *Betula pubescens* subsp. *tortuosa*, but also with *Betula*  
1077 *pendula* and *Tilia cordata*, more rarely with *Corylus avellana*.  
1078 *Distribution*: So far mainly known from NW Europe. Most records from subalpine/northern  
1079 boreal areas of Fennoscandia (known north to Nordland in Norway, Umeå in Sweden, and N  
1080 Finland (Lapland)), but also found in some boreonemoral fjord districts of W Norway.  
1081 Apparently no finds from nemoral-montane regions of C Europe. Once collected in Alberta,  
1082 Canada, indicating a probably wide, circumpolar distribution.

*Comments:* *Cortinarius argenteolilacinus* var. *dovreensis* is characterized 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. *dovreensis* mainly a northern, subalpine *Betula* taxon, var. *argenteolilacinus* a mainly nemoral-montane *Fagus*(-*Tilia*) taxon) and (ii) slightly differentiated also morphologically (*C. argenteolilacinus* var. *dovreensis* 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. *dovreensis* 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. *dovreensis* 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 3 indels from the European sequences. More material is needed to see if there is a phylogeographical differentiation within *C. argenteolilacinus* var. *dovreensis*. For the time being we keep this Canadian collection under var. *dovreensis* based on our phylogenetic analysis (Fig. 2).

*Cortinarius argenteolilacinus* var. *dovreensis* may sometimes be difficult to separate macromorphologically from the often co-occurring *C. malachoides*. However, the var. *dovreensis* 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, Skøyen, 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);

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- 1116 Nordland, Hattfjelldal, Storveltia nature reserve, Ø. Weholt, KB-EB-TEB 78-10 (O), Ø.  
 1117 Weholt, KB-EB-TEB 79-10 (O). Hordaland, Granvin, T.S. Jeppesen, TSJ2005-042 (C).  
 1118 **Sweden.** Härjedalen, Hamrafjället, 13 Aug 2008, K. Soop, KS-CO1703 (S-F251128); 20 Aug.  
 1119 2008, K. Soop, KS-CO1821 (S). Dalarna, Sollerön, Klikten, 11 Sept 2013, K. Soop, KS-  
 1120 CO2130 (S). Öland, Gråborg, T.G. Frøslev, T.S. Jeppesen TSJ2006-010 (C).  
 1121  
 1122  
 1123 *Additional ITS sequence data from the public sequence repositories:*  
 1124 **Italy.** JF907933/MCVE6043 (as *C. elotus*). **Sweden.** KJ421064/KS-CO770 (as *C.*  
 1125 *argenteolilacinus*), Öland, Gråborg, 28 Sept 1996, K. Soop, herb. S-F44342.  
 1126  
 1127  
 1128 *Cortinarius malachoides* P.D. Orton, Naturalist (Suppl.): 148 (1958)  
 1129 MycoBank MB 295890  
 1130 Figs 9e, 9f and 9g  
 1131  
 1132 Holotype: United Kingdom, Inverness-shire, Rothiemurchus, Loch-an-Eilean, P.D. Orton  
 1133 29/9/55 (K(M)94426). GenBank: MH846280.  
 1134 Icones: Soop (2011, Pl. 6, fig. 23, as *C. coniferarum* (M.M.Moser) Moënné-L & Reum); Soop  
 1135 2017, Pl. 5:18 as *C. jotunae*.  
 1136  
 1137  
 1138 *Pileus* 3–7(8) cm, (hemi-)spherical, then plano-convex to broadly umbonate, viscid-glutinous,  
 1139 towards margin finely and rather weakly innately fibrillose-rivulose, with a more net-like  
 1140 pattern at centre, somewhat silvery-micaceous when young, smooth to sometimes faintly  
 1141 fibrillose; initially rather uniformly and pale ochraceous yellow to almost ochraceous white,  
 1142 resembling *C. talus*, sometimes pale grey to greyish ochre, with a faint, fugacious, blush tinge  
 1143 towards margin, with age discolouring patchwise to ochraceous brown (almost redbrown).  
 1144 Universal veil remnants very sparse, hardly visible, sometimes with silky, white remnants at  
 1145 margin.  
 1146 *Lamellae* crowded (L = 60–90), 0.4–0.8 cm broad, initially pale greyish blue, especially  
 1147 towards pileus margin, very soon fading to pale greyish brown; edge even to crenulate.

1148 *Stipe* 5–10 × (0.8)1–1.5(2) cm, rather slender, with a faintly to rather distinctly marginate-  
1149 bulbous base (up to 3 cm), glossy to slightly fibrillose, initially pale greybluish white in upper  
1150 part, but soon almost white, sometimes more distinctly, fugacious violet at apex, turning brass  
1151 brown spotted with age (especially when bruised). Universal veil at or near the bulb very  
1152 sparse and hardly visible; whitish. Basal mycelium sparse, white.  
1153 *Context* initially pale greybluish in upper part of stipe (especially towards cortex), rarely more  
1154 pronounced violaceous; bluish colours soon fading, otherwise whitish, often with a brownish  
1155 line under pileipellis and with brass brown spots where damaged.  
1156 *Macrochemical reactions* negative (NaOH somewhat brownish).  
1157 *Smell* faint, indistinct to somewhat like bread dough.  
1158 *Exsiccata* more or less brownish; pileus margin and stipe sometimes remain whitish.  
1159 *Basidiospores* [9, 15, 276], 9.6–11.8 × 5.9–7.4 µm (MV = 10.7 × 6.7 µm); variation of MVs:  
1160 10.1–11.3 × 6.3–7.1 µm; Q = 1.42–1.79 (MV = 1.61), ellipsoid to subamygdaloid, rather  
1161 strongly and densely verrucose, warts diffuse or sometimes lense-like coalescent at apex,  
1162 suprahilar plague rarely visible. *Lamella edge* more or less fertile, sterile cells small, clavate  
1163 or cylindrical.  
1164 *Pileipellis* duplex. Epicutis thin, at surface of 3–5 µm wide, loosely erect-entangled,  
1165 gelatinous hyphae, hyaline, collapsed hyphae with pale, refractive pigment.  
1166 Subcutis/hypodermium weakly to distinctly developed, hyphae 5–15 µm wide, basally usually  
1167 with inflated elements up to 20 µm wide, tightly cemented, with pale yellow brown parietal-  
1168 encrusting pigment, often forming an amber-like embedment; in transition to epicutis with  
1169 subparallel, interconnected bundles of 5–8 µm wide hyphae with pale yellow brown parietal  
1170 pigment, sometimes a few hyphae with weak zebra-striped encrusting pigment.  
1171 *Veil hyphae at pileus surface* scattered or absent, hyaline and narrow (3–6 µm).  
1172 *Habitat*: Associated mainly with *Betula pubescens* subsp. *tortuosa* (subalpine), also with other  
1173 *Betula* taxa (boreal) and probably also *Tilia cordata* and *Corylus avellana* (boreonemoral),  
1174 possibly also with *Fagus* (subalpine). In somewhat richer low-herb birch forests, also found in  
1175 more open transition to alpine heaths (with *Betula nana* and *Betula pubescens* subsp. *tortuosa*  
1176 thickets), in fjord sides in rich *Tilia-Betula* scree forests, sometimes also in mixed boreal  
1177 coniferous forests with some *Betula pubescens* (Trøndelag, C Norway). In SW France  
1178 recorded in a subalpine *Fagus-Picea* forest (Henry 1981 as *C. fallaceicolor* “forma  
1179 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 characterized 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* undoubtedly 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 *Telamonina* 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 *Telamonina* 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 *Telamonina*/*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* (*Telamonina* 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.

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1246

1247 *Collections examined:*

1248 **Canada.** Newfoundland, Avalon Peninsula, Cape St. Mary, 28 Sept 2007, Andrus Voitk  
1249 TN07-313, H7000977 (H). **France.** Languedoc, Gard, Mont Aigoual, M. Chevassut 10 Oct  
1250 1980, R. Henry 80.811 (PC, type of *C. fallaceicolor* “forme méridionale”). **Norway.**  
1251 Hordaland, Granvin, Åsen, T.E. Brandrud, TEB176-07 (O); Granvin, Håstabbaneset V, T.S.  
1252 Jeppesen, B. Dima, TSJ2005-043/TEB371-05/DB2002 (C/O/BP); Ulvik, Eddagilet T.E.  
1253 Brandrud, TEB155-07 (O). Aust-Agder, Froland, Myklandvatna nature reserve, T.E.  
1254 Brandrud, TEB562-08 (O). Nord-Trøndelag, Høilandet, Folldalen, E. Bendiksen, T.E.  
1255 Brandrud, EB-TEB 58-05 (O); Levanger, Ytterøya, Sandstadkammen E, TEB245-13 (O).  
1256 Oppland, Vågå, Jotunheimen, Gjende, TEB469-11 & TEB473-11. **Sweden.** Ångermanland,  
1257 H. Marklund et al., CFP980 (S). Härjedalen, Tännäs, S Malmagen, S. Jacobsson, SJ 80075  
1258 (GB). Medelpad, Dysjöberget, D. Laber, K. Pätzold, TEB340-16/DB6138b (O). **United**  
1259 **Kingdom.** Inverness-shire, Rothiemurchus, Loch-an-Eilean, P.D. Orton 29/9/55 (holotype,  
1260 K(M)94426).

1261

1262 *Additional ITS sequence data from the public sequence repositories:*

1263 **Sweden.** KJ421177/KS-CO1708 (as *Cortinarius* sp.) (Holmvallen, 17 Aug 2006, J.  
1264 Vesterholt, herb. S, F251129).

1265

1266

1267 *Cortinarius parksianus* A.H. Smith, Contr. Univ. Mich. Herb. 2: 16 (1939)

1268 MycoBank: MB 253834

1269

1270 Holotype: U.S.A., California, near Trinidad, 12 Nov 1937, A.H. Smith 8695 (MICH 10393).

1271 GenBank: MH846283.

1272

1273 Description (according to the protologue):

1274 *Pileus* 8–12 cm diam., convex then plane with persistently decurved margin; colour initially  
1275 purplish umber, then more olivaceous brown to cinnamon brown, margin with patches of  
1276 whitish fibrils.

1277 *Lamellae* crowded, purplish (blue) when young, finally cinnamon brown.

1278 *Stipe* 10–12 × 2–3.5 cm, bulbous, bulb roundish, 3–4.5 cm wide, purplish (blue), fading

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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],  $9.8\text{--}11.6 \times 6.3\text{--}7.1 \mu\text{m}$  (MV =  $10.7 \times 6.7 \mu\text{m}$ ); 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. anomalochrascens* 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*: U.S.A. 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

Figs 10a and 10b

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

*Holotype*: U.S.A. 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*, *Tsuga mertensiana*, 2 Oct 2010, D. Bojantchev, DBB37303 (UC2023490). GenBank: KX768115.

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1312

1313 *Pileus* 7–16 cm diam., hemispherical to convex then broadly plano-convex; margin involute,  
1314 irregular, yellow to ochraceous or ochraceous brown near the disk, paler yellow to Sulphur  
1315 yellow towards the margin, whitish velar remnants often present.

1316 *Lamellae* crowded, 1.2–2.3 cm broad, pale bluish at first then yellow, bluish tints often  
1317 remaining in maturity, edges even, attachment sinuate, lamellulae abundant.

1318 *Stipe* 5–12 cm long, 1.5–3 cm wide, cylindrical to subclavate, often attenuated at age, with a  
1319 moderately emarginated bulb, white to pale bluish lilac, more so towards the apex, silky  
1320 shiny, bruising ochraceous. Cortina whitish at first, leaving an annular zone of dense fibrils on  
1321 the stipe.

1322 *Context* white to bluish, more so towards the margin of the apex. Taste mild, earthy.

1323 *Macrochemical reactions* 5% KOH on fresh material reaction variable on context, greyish to  
1324 ochraceous orange towards the bulb, with a halo, ochraceous on pileus, on dry material  
1325 consistently ochraceous on all parts.

1326 *Smell* indistinct or somewhat earthy.

1327 *Basidiospores* [1, 1, 21],  $11.2\text{--}13.2 \times 6.9\text{--}8.2 \mu\text{m}$  (MV =  $12.2 \times 7.5 \mu\text{m}$ ), Q = 1.51–1.75 (MV  
1328 = 1.63), subobovoid to amygdaliform, coarsely verrucose. Basidia  $33\text{--}46 \times 8\text{--}12 \mu\text{m}$ , 4-  
1329 spored, cylindro-clavate, clamped. *Cystidia* not observed.

1330 *Pileipellis* an ixocutis, duplex, epicutis composed of parallel to interwoven hyphae in a dense  
1331 gelatinous matrix 220–260  $\mu\text{m}$  thick, made up of 3–10  $\mu\text{m}$  wide, irregular hyphae,  
1332 hypodermium composed of cylindrical to ventricose cells 12–28  $\mu\text{m}$  wide.

1333 *Habitat and distribution*: Under conifers (*Picea*, *Pseudotsuga*, *Tsuga* spp.) in montane to  
1334 submontane areas of N America.

1335 *Comments*: This species is a close relative of the European *C. fulvoochrascens* and differs by  
1336 the distribution, slightly paler colours, somewhat smaller spores and several nucleotides in the  
1337 ITS region. A common host between the two collections from Montana and California is the  
1338 Douglas fir (*Pseudotsuga mensiezii*), but more research is needed to determine whether that  
1339 was the primary host of the species.

1340 A clade without acceptable statistical support including ectomycorrhiza sequences isolated  
1341 from *Picea* roots from Alaska, Bonanza Creek (GenBank: KF617829, Taylor et al. 2014) and  
1342 from Canada, British Columbia, Bulkley-Nechako (UNITE: UDB031686) as well as a  
1343 sequence originated from a basidiocarp sample (from the U.S.A.) may represent another

complex of species in sect. *Riederi* that falls close to *C. burlinghamiae* (Fig. 2, treated as *Cortinarius* sp.).

*Collections examined:* U.S.A. 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:*

U.S.A. Wyoming, AF389139/IB19970218 (as *C. fulvoochrascens*).

## 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*

- 1408 4 Mainly in C Europe under *Fagus*, but also in boreonemoral areas of S Fennoscandia under  
 1409 *Tilia* and *Corylus*. Basidiocarps large and robust; spores strongly verrucose, pileipellis with  
 1410 strongly encrusted hyphae ..... *C. argenteolilacinus* var. *argenteolilacinus*  
 1411
- 1412 4\* Mainly in N Europe in subalpine *Betula pubescens* subsp. *tortuosa* forests, as well as in  
 1413 few cases with *Corylus* (once collected in Canada; probably circumpolar) Basidiocarps large  
 1414 to small; spores moderately to fairly strongly verrucose, encrusted pigment in pileipellis  
 1415 hyphae weak or absent ..... *C. argenteolilacinus* var. *dovreensis*  
 1416
- 1417 5 Spore MV's <12 µm long (MV's 10.9–11.9 × 6.9–7.6 µm); basidiocarps medium and  
 1418 slender. Pileus pale greyish ochraceous brown or tinged olive, stipe often slightly marginate  
 1419 bulbous, sometimes with watery bluish tomentum towards base; pileipellis without or with  
 1420 weak zebra-striped encrusted pigment; so far only known from Europe .....  
 1421 ..... *C. anomaloochrascens*  
 1422
- 1423 5\* Spore MV's >12 µm long (MV's 12.1–13.6 × 6.9–8.7 µm); basidiocarps fairly large;  
 1424 pileipellis with distinctly zebra-striped encrusted pigment ..... 8  
 1425
- 1426 6 Veil remnants distinct, initially rendering base of stipe ±girdled and pileus ±fibrillose. Pileus  
 1427 vivid ochre brown, fulvous to red brown, stipe more or less marginate bulbous; stipe without  
 1428 white to bluish white tomentum towards base. So far only in Europe .....  
 1429 ..... *C. fulvoochrascens*  
 1430
- 1431 6 Almost devoid of veil, pileus and stipe smooth-glossy. Stipe often irregularly clavate-  
 1432 bulbous ..... 9  
 1433
- 1434 7 Mean width of spores 7.9–8.7 µm, pileus vivid ochraceous brown, fulvous to redbrown,  
 1435 stipe often with watery bluish tomentum towards base; pileipellis hyphae with strong  
 1436 encrustations. In Europe and western N America ..... *C. riederi*  
 1437 7 Mean width of spores 6.9–7.7 µm, pileus paler ochraceous brown, bluish tomentum at stipe  
 1438 base not seen; pileipellis hyphae with only weak encrustations. So far only known from  
 1439 Europe ..... *C. pallidoriederi*  
 1440

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1772 Legends

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1774 Fig. 1. Compressed phylogenetic tree based on RAxML analysis of the ITS region showing  
1775 the main infrageneric clades within *Cortinarius* in Europe. The clade Riederi is highlighted in  
1776 black. The genus Hebeloma was chosen as outgroup. Bootstrap supports values (>70%) are  
1777 shown at the branches. The bar indicates 0.1 expected change per site per branch.

1778

1779 Fig. 2. Mid-point rooted phylogenetic tree of sect. *Riederi* inferred from ITS dataset and  
1780 RAxML analysis. Bayesian posterior probabilities (>0.90) and RAxML bootstrap supports  
1781 values (>70%) are indicated on the branches at nodes (PP/ML). The bar indicates 0.01  
1782 expected change per site per branch.

1783

1784 Fig. 3 Spore photos of selected specimens of each species in sect. *Riederi*.

1785

1786 Fig. 4 Mean values of spore lengths of species in sect. *Riederi*. Bars indicate 95% confidence  
1787 interval. The missing bars are due to the limited number of available collections of those  
1788 species.

1789

1790 Fig. 5 Scatter diagram of mean values of spores of each measured collection in sect *Riederi*.

1791

1792 Fig. 6 95% confidence ellipses of spore variations of the conifer associated species in sect.  
1793 *Riederi*

1794

- 1795 Fig. 7 95% confidence ellipses of spore variations of the species associated with deciduous  
1796 trees in sect. *Riederi*  
1797
- 1798 Fig. 8 Basidiocarps of *Cortinarius* species in sect. *Riederi* associated with coniferous trees: a–  
1799 b *C. riederi* (a TEB258-17 Norway, b SSt10-066 Sweden); c–d *C. fulvoochrascens* (c  
1800 TEB530-13 Norway, d TEB-292-13 Norway); e–g *C. anomaloochrascens* (e TEB762-  
1801 12/DB4814 Germany, f SSt17-202 Germany, g PRM924382 Czech Republic); h *C.*  
1802 *pallidoriederi* (FB30-09-2011 Italy). Photos: a, c, e B. Dima; b, f G. Schmidt-Stohn; d T.E.  
1803 Brandrud; g J. Borovička; h E. Castellini.  
1804
- 1805 Fig. 9 Basidiocarps of species in sect. *Riederi* associated with deciduous trees: a–c *C.*  
1806 *argenteolilacinus* var. *argenteolilacinus* (a ILF2013-98 Norway, b TSJ2011-025 Sweden, c  
1807 TEB281-17 Norway); d *C. argenteolilacinus* var. *dovrensis* (KS-CO1703 Sweden); e–g *C.*  
1808 *malachioides* (e–f TEB245-13 Norway, g TEB340-16/DB6138 Sweden); h–i *C.*  
1809 *glaucocyanopus* (h DB2072 Hungary, i AL99/51 Hungary). Photos: a I.-L. Fonneland; b T.S.  
1810 Jeppesen; c, e, f T.E. Brandrud; d K. Soop; g, h B. Dima, i L. Albert.  
1811
- 1812 Fig. 10 Basidiocarps of *Cortinarius burlinghamiae* (a DBB37303 USA – holotype, b  
1813 DBB57001 USA). Photos: D. Bojantchev.